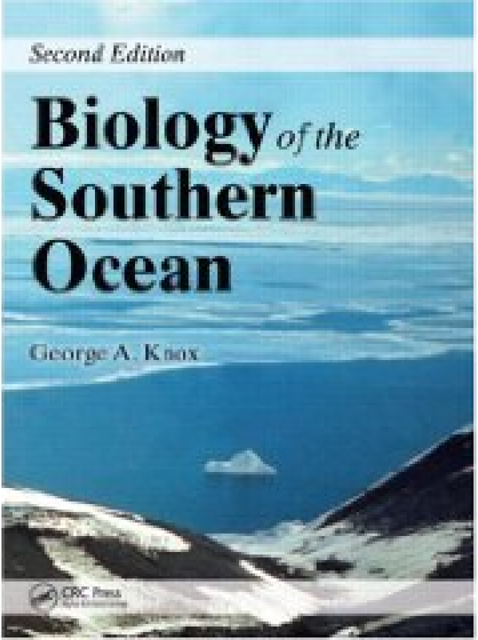
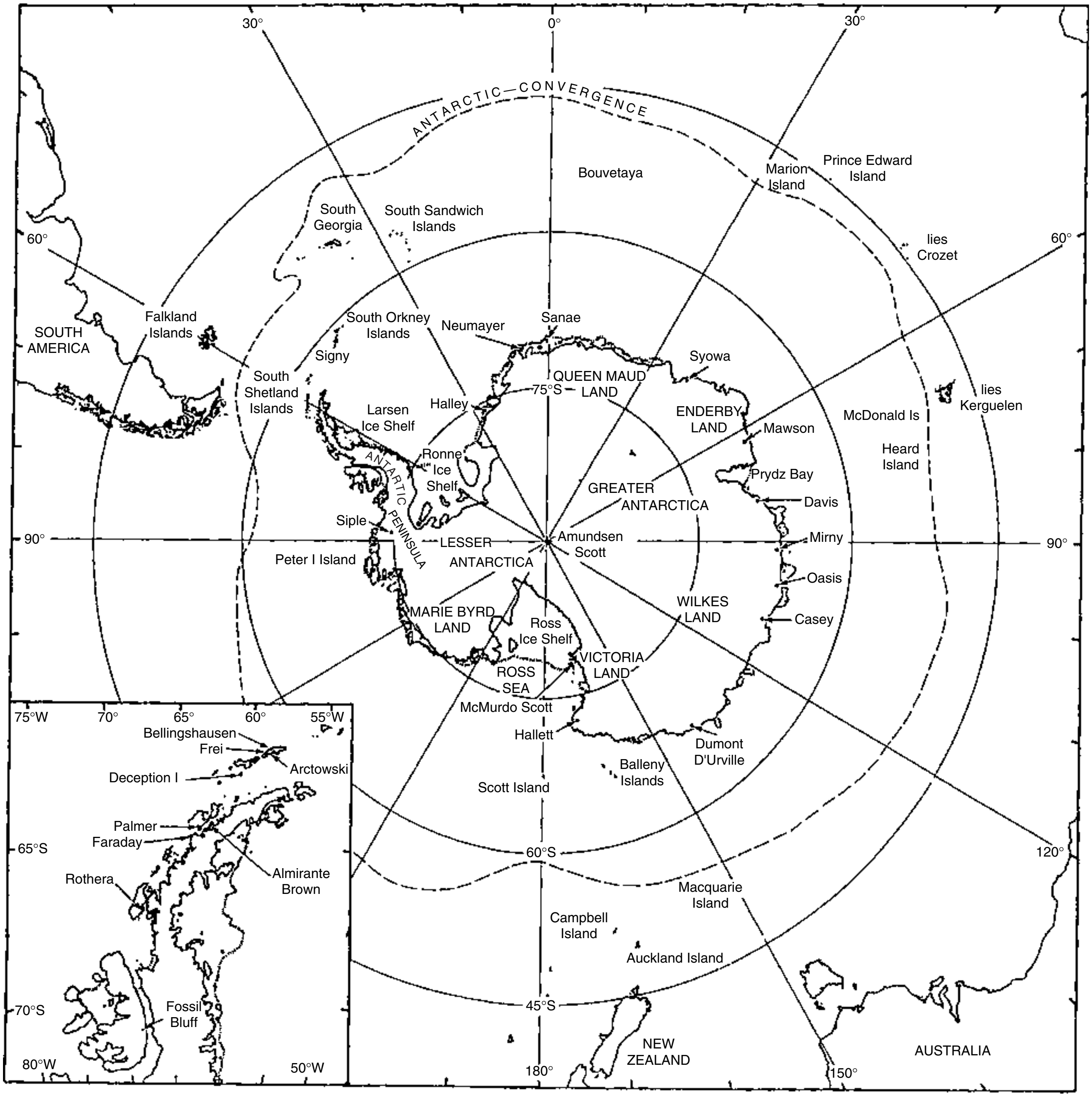


Second Edition

Biology *of the* Southern Ocean

George A. Knox

CRC Press



Antarctica is both a continent and an ocean. The continent is inextricably linked to the vast extent of the Southern Ocean surrounding it, an ocean that supports a teaming array of life, ranging from microscopic plants that form part of the phytoplankton responsible for primary production to the mighty whales, our largest marine mammals. Whilst our knowledge of the biology of these waters has been accumulating since the first voyages of discovery in the 18th century, there is yet to be a comprehensive, single-author synthesis of the current state of that knowledge. This book sets out to correct that deficiency.

MARINE BIOLOGY

SERIES

Peter L. Lutz, Editor

PUBLISHED TITLES

Biology of Marine Birds
E. A. Schreiber and Joanna Burger

Biology of the Spotted Seatrout
Stephen A. Bortone

The Biology of Sea Turtles, Volume II
Peter L. Lutz, John A. Musick, and Jeanette Wyneken

Biology of Sharks and Their Relatives
Jeffrey C. Carrier, John A. Musick, and Michael R. Heithaus

Early Stages of Atlantic Fishes: An Identification Guide for the Western Central North Atlantic
William Richards

The Physiology of Fishes, Third Edition
David H. Evans

Biology *of the* Southern Ocean

Second Edition

George A. Knox

University of Canterbury
New Zealand

CRC Press
Taylor & Francis Group
Boca Raton London New York

CRC Press is an imprint of the
Taylor & Francis Group, an informa business

CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

© 2007 by Taylor & Francis Group, LLC
CRC Press is an imprint of Taylor & Francis Group, an Informa business

No claim to original U.S. Government works
Printed in the United States of America on acid-free paper
10 9 8 7 6 5 4 3 2 1

International Standard Book Number-10: 0-8493-3394-6 (Hardcover)
International Standard Book Number-13: 978-0-8493-3394-1 (Hardcover)

This book contains information obtained from authentic and highly regarded sources. Reprinted material is quoted with permission, and sources are indicated. A wide variety of references are listed. Reasonable efforts have been made to publish reliable data and information, but the author and the publisher cannot assume responsibility for the validity of all materials or for the consequences of their use.

No part of this book may be reprinted, reproduced, transmitted, or utilized in any form by any electronic, mechanical, or other means, now known or hereafter invented, including photocopying, microfilming, and recording, or in any information storage or retrieval system, without written permission from the publishers.

For permission to photocopy or use material electronically from this work, please access www.copyright.com (http://www.copyright.com/) or contact the Copyright Clearance Center, Inc. (CCC) 222 Rosewood Drive, Danvers, MA 01923, 978-750-8400. CCC is a not-for-profit organization that provides licenses and registration for a variety of users. For organizations that have been granted a photocopy license by the CCC, a separate system of payment has been arranged.

Trademark Notice: Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation without intent to infringe.

Library of Congress Cataloging-in-Publication Data

Knox, G. A.
Biology of the Southern Ocean / George A. Knox. -- 2nd ed.
p. cm. -- (Marine biology series)
ISBN 0-8493-3394-6
1. Marine ecology--Antarctic Ocean. 2. Biotic communities--Antarctic Ocean. 3. Ecosystem management--Antarctic Ocean. I. Title. II. Series: CRC marine biology series.

QH95.58.K58 2006
577.709167--dc22 2006045562

Visit the Taylor & Francis Web site at
http://www.taylorandfrancis.com

and the CRC Press Web site at
http://www.crcpress.com

Preface

Our knowledge of the biology of the seas surrounding the Antarctic continent began with descriptions and specimens brought back by early naturalists on voyages of discovery in the Southern Ocean. Prominent among these were the early French navigators such as Bouvet de Lozier, who discovered Bouvet Island in 1739, and Yves Joseph de Kerguelen-Tremarez, who discovered the island that bears his name some 30 years later. These were followed by the voyages of Captain Cook, who, in 1772, reached 71° 10′ S in the Bellingshausen Sea. In 1819, the Russian explorer Admiral Bellingshausen was first to tow a net at the stern of his ship and he found that it collected more organisms during the night than during the day. He was probably the first to collect the Antarctica krill, *Euphausia superba*.

The first serious scientific marine research was carried out by James Eights who sailed in 1929 with the American sealing Captains Palmer and Pendleton. Eights described the natural history of the South Shetland Islands. His best known discovery was of a ten-legged pycnogonid. Soon after, there followed a series of national expeditions led by Dumont D'Urville of France (1837–1840), Charles Wilkie of the United States (1838–1842), and Sir James Clark Ross of Britain (1939–1943). Among the naturalists who accompanied these expeditions, the most notable were J.D. Dana, on the Wilkie expedition, and J.D. Hooker, on the Ross expedition. These expeditions all made extensive collections of marine organisms.

There was a renewal of Antarctic exploration at the end of the nineteenth century. Major expeditions included the British (1899–1900), the Belgian (1898), the Swedish National Expedition (1902–1904), the Scottish National Antarctic Expedition (1902–1904), the German expedition (1901–1903) in the *Gauss*, and the French Expedition in the *Pourquoi Pas* (1908–1910). All of these expeditions resulted in taxonomic studies that laid the foundation for later studies of the marine flora and fauna.

Ecological studies in the Southern Ocean began with the work of naturalists attached to land-based, over-wintering parties such as those of Sir Ernest Shackleton's 1907–1909 expedition and Captain Scott's two polar expeditions. Antarctic marine studies received a tremendous impetus from the investigations that began in 1925 with the study of whale carcasses at the whaling stations at Grytviken in South Georgia. The work of the scientists expanded to include, not only studies on whale demography and ecology, but also of the physical, chemical and biological oceanography of the Southern Ocean in order to gain an understanding of the factors influencing the distribution, reproduction, and growth of whale stocks. These investigations contributed to the first long-term studies of the Antarctic pelagic ecosystem, and they were the first that extended right around the Antarctic continent. The voluminous reports of these *Discovery* expeditions laid the indispensable foundation for subsequent studies.

Southern Ocean marine research entered a new phase following the establishment, in 1957, of the Special (later the Scientific) Committee on Antarctic Research (SCAR). This initiated the modern era of Southern Ocean research in which many countries played roles, notably the Soviet Antarctic Expeditions in the *Vitez* and *Ob* and the United States *Eltanin* cruises. Other countries such as Great Britain, France, South Africa, Chile, Argentina, Australia and Japan were also very active during this period. In 1972, a coordinated international research program was initiated with the establishment of the BIOMASS (Biological Investigations of Antarctic Systems and Stocks) Program (El-Sayed 1996).

My own involvement in Antarctic research began with a visit to McMurdo Sound in 1960 where one of my staff in the Department of Zoology at the University of Canterbury, Dr. Bernard Stonehouse, was initiating a research program on Adelie penguins and McCormick skuas. This led to the establishment of the University of Canterbury Antarctic Research Unit (Knox 1986, 1988) that carried out continuous summer research in the McMurdo Sound region over the period 1960–1983, the last twelve years of which I was director of the unit. During the summers of 1969 and 1970, I initiated an inshore marine research program that continued until the 1982–1983 season. Throughout the operation of the unit, some sixty research students participated in its activities. Interaction with these enthusiastic young minds had a significant influence on many of the concepts developed in *The Biology of the Southern Ocean.* I also have had the good fortune to become involved in international Antarctic science activities, first as a member and secretary of the SCAR Biology Working Group on Biology and as a member of SCAR since 1969. I was a member of the Group of Specialists on the Living Resources of the Southern Ocean from its inception and I attended the first two meetings of CCAMLR (Convention on the Conservation of Antarctic Marine Living Resources). These activities brought me into contact with a wide range of Antarctic scientists from all the SCAR countries.

The suggestion for *The Biology of the Southern Ocean* was made by Dr. Bernard Stonehouse and, without his encouragement, it would not have been written. Discussions with Antarctic colleagues throughout the SCAR community have had a profound influence on its development. Amongst these I particularly wish to thank Professor Sayed El-Sayed, the late Sir George Deacon, Professor A.L. DeVries, Professor M. Fukuchi, Sir Martin Holdgate, Professor T. Hoshiai. Dr. J.C. Hureau, Dr. K.B. Kerry, Dr. Y. Naito, the late Dr. T. Nemoto, Dr. J. Oliver, Dr. J. Warham, and Professor E.C. Young. Access to literature was greatly facilitated by periods spent in the libraries of the British Antarctic Survey and the National Institute of Polar Research, Tokyo. Dr. D.W.H. Walton reviewed all chapters of the original edition in various drafts and I am grateful for his assistance and encouragement. I would also like to thank Dr. Maria Murphy and the staff of Cambridge University Press for their patience and support during the preparation of the first edition and for seeing the project through to completion.

The first edition of *The Biology of the Southern Ocean* was published in 1993 and was well received. The print run was sold out a number of years ago. Some 13 years have passed since then and a considerable amount of research has been carried out during this period. The original SCAR countries engaged in marine research in the Southern Ocean have been joined by other countries including China, Ukraine, Uruguay, Korea, Ecuador, India, Peru and Spain, resulting in a much increased research effort.

The last decade in particular had seen the initiation of several scientific programs to study phenomena and processes of global significance in which the Southern Ocean plays a key role. Some of the major programs are listed below and brief descriptions of the objectives of these are given in El-Sayed (1991).

- Antarctic Marine Living Resources (AMLR) program (1986-present)
- Antarctic Marine Ecosystem Research at the Ice-Edge Zone (AMERIEZ) (1983–1988)
- Research on Antarctic Coastal Ecosystem Rates Program (RACER) (1986–1993)
- Long-Term Ecological Research (Palme LTER) (1980-present)
- Southern Ocean Joint-Global Ocean Ecosystem Dynamics (SO-GLOBEC) (1991–2009)
- Coastal and Shelf Ecology of the Antarctic Sea-Ice Zone (CS-EASIZ) (1993–2004)
- Antarctic Pack-Ice Seals (APIS) (1995-present)
- European Polarstern Study (EPOS) (1988–89)
- Research on Ocean-Atmosphere Variability and Ecosystem Response in the Ross Sea (ROAVERRS) (1996–1998)

The multi-disciplinary, multi-national cruises of the R/V *Polarstern* have been of particular importance in recent years, especially the ANDEP cruises (2002–2005) that investigated the benthic fauna of the deep Weddell Sea. Over the period 2000–2002, a series of iron fertilization experiments (SOIRE, SOFex and EISENEX) investigated the potential role of iron in controlling algal production in the Southern Ocean. Recently, the New Zealand National Institute of Water and Atmospheric Research (NIWA) investigated the richness and diversity of the benthos in a latitudinal gradient in the western Ross Sea in relation to broader-scale environmental factors and local-scale variation in productivity sources.

As the result of the research activities listed above, there has been a considerable volume of published research on the biology of the Southern Ocean in the 13 years since the publication of the first edition of *The Biology of the Southern Ocean.* While some of the information in the first edition is retained, it is essentially a new account. The task of summarizing the large volume of research has proved a difficult task. Most of the figures in the text have been redrawn from the originals.

The book commences with a description of the physico-chemical environment of the Southern Ocean and then follows a logical sequence covering phytoplankton and primary production, the sea ice microbial communities, and the secondary consumers, the zooplankton. There is an extended chapter on the biology and ecology of Antarctic krill, in view of its central position in the Southern Ocean food web. Additionally, krill has been the subject of intensive research programs over the past decades, especially during the BIOMASS Programmes and subsequently by CCAMLR. A series of chapters consider the higher consumers, nekton (with an emphasis on cephalopods), fish, seals, whales and seabirds. A series of chapters then follow on selected ecosystem components: the benthic communities, life beneath the fast ice and ice shelves, recent advances in understanding decomposition processes, and the role of bacteria and protozoa. These are followed by an attempt at a synthesis of ecosystem dynamics, with an emphasis of the pelagic ecosystem and then three chapters dealing with resource exploitation, the impact of such exploitation on the marine ecosystem, and the problems involved in the management of the living resources. Three new chapters have been added to the second edition exploring the impact of increased UV radiation, human impact on the marine environment, and the impact of global warming on Southern Ocean marine ecosystems.

As can be seen by the reference list at the end of this volume, there is a considerable body of recent literature on the biology of the Southern Ocean. Because of the growth of published research, I have had to be selective in the material that is included. Examples have been carefully chosen from the pool of published research to illustrate the concepts discussed. There are, doubtless, others that could have been used and I apologize to authors whose work has not been included.

In the preparation of this volume I have been supplied with advanced copies of papers prepared or accepted for publication and I am grateful to all who supplied them. I am also appreciative of the support and encouragement of John Sulzycki and the staff of CRC Press, in particular Pat Roberson, during the preparation of this edition and for seeing the project through to the completion of a high quality product.

This book is an attempt to synthesize the available information into a coherent account of one of the most fascinating systems on the globe. I hope that it will prove useful to advanced undergraduates and to professionals engaged in Antarctic marine research, as well as to all interested or involved in Antarctic marine conservation and management. It will have been worthwhile if it stimulates others to work on the fascinating aspects of Antarctic marine research that have been discussed in this book.

Acknowledgments

I would firstly express my indebtedness to the many international Antarctic scientists, some of whom have been listed in the Preface, who I have interacted with over the years. Discussions with them have influenced the development of many of the concepts dicussed in this book. I acknowledge the outstanding contribution of Cambridge University Press, in the preparation of the first edition of this book. I owe a great debt to the staff members and students who participated in the research activities of the University of Canterbury Antarctic Research Unit.

I owe a great deal to John Sulzycki and the staff of CRC Press, in particular Pat Roberson for their patience and support during the preparation of this second edition. Together with the staff of Alden Press Services who typeset this book they have produced a high quality product.

Author

George A. Knox, C.N.Z.M., M.B.E., F.R.S.N.Z., was head of the Department of Zoology, University of Canterbury, Christchurch, New Zealand, from 1959 to 1976. He is now professor emeritus of zoology.

Professor Knox was born in New Zealand and received his education at the University of Canterbury, where he was appointed a staff member in 1948. He has been a visiting fellow at the East-West Center, Honolulu, and a visiting professor at the Department of Oceanography, Texas A&M University and the Department of Environmental Engineering, University of Florida, Gainesville. He has visited and worked in laboratories in the U.S., Canada, Chile, Japan, Australia, Western Europe, the USSR, and China.

Professor Knox's research has been wide ranging and includes: (1) the systematics and distribution of polychaeta with special reference to New Zealand and Antarctica; (2) rocky shore intertidal ecology and biogeography; (3) the ecology and conservation of islands; (4) studies on the pelagic and benthic ecosystems beneath the sea ice in McMurdo Sound, Antarctica; and (5) estuarine and coastal ecology and management. He established and directed the Estuarine Research Unit in the Department of Zoology and the University of Canterbury Antarctic Research Unit. He has participated in many field expeditions, including the Chatham Islands 1954 Expedition (leader); the Royal Society of London Darwin Centennial Expedition to southern Chile (marine biologist and deputy leader); thirteen summer expeditions to McMurdo Sound, Antarctica; the establishment of the Snares Islands Research Program (he participated in three field expeditions); and participation in field expeditions to Campbell and Auckland Islands. He has published over 100 scientific papers and 28 environmental reports, written five books, and edited and co-authored three other volumes.

Professor Knox has received a number of awards and fellowships for his contributions to science, including Fellow of the Royal Society of New Zealand (FRSNZ), 1963; Hutton Medal, Royal Society of New Zealand, 1978; Conservation Trophy, New Zealand Antarctic Society; Honorary Member of Scientific Committee on Antarctic Research, 1982; member of the Most Excellent Order of the British Empire (MBE), 1985; the New Zealand Association of Scientists' Sir Ernest Marsden Medal for Service to Science, 1985; and Companion of the New Zealand Order of Merit (CNZM), 2001.

Contents

Chapter 6 Nekton

Chapter 7 Fish

Chapter 8 Seals

Chapter 9 Whales

Chapter 10 Birds

Chapter 11 Benthic Communities

Chapter 12 The Fast Ice and Ice Shelves

Chapter 13 Ice-Edge Processes

Chapter 14 Decomposition and the Roles of Bacteria and Protozoa

Chapter 15 Ecosystem Dynamics

Chapter 16 Resource Exploitation

Chapter 17 Ecosystem Changes Resulting from Resource Exploitation

Chapter 18 Management of Living Resources

Chapter 19 Ultraviolet Radiation

Chapter 20 Global Warming and Antarctic Marine Ecosystems

Chapter 21 Human Impact

1 The Southern Ocean

CONTENTS

1.1 INTRODUCTION

Over the past two decades in particular there has been an increasing emphasis on integrated studies of the Southern Ocean (Figure 1.1) aimed at understanding what has been termed "the Antarctic or Southern Ocean ecosystem." While the Southern Ocean can be considered a single ecosystem, it is actually a series of interconnected ecosystems. These will be discussed in subsequent chapters. Descriptions of the Southern Ocean system have been given by several workers over the years (Hart 1942; Currie 1964; Holdgate 1967; Knox 1970, 1983; Everson 1977a, 1984c; Bengtson 1978, 1985a; Baker 1979; Tranter 1982; Hempel 1985a, 1985b, 1987)

The living resources of the Southern Ocean and their past and future exploitation have been reviewed by the SCAR/SCOR Group of Specialists on the Living Resources of the Southern Ocean (El-Sayed 1977, 1981, 1996; Sahrhage 1988a), and they have also been the subject of numerous reviews: Everson (1977b), Bengston (1978, 1985a), Knox (1983, 1984), and Anonymous (USSR) (1984a, 1984b). The physical structure of the system has been described by Deacon (1937, 1982, 1984b), Brodie (1965), Gordon (1967, 1983), Gordon and Goldberg (1970), Gordon et al. (1978), Forster (1981, 1984), Gordon and Molinelli (1982), Amos (1984), Gordon and Owens (1987), Squire (1987), Foldvik and Gammelsrad (1988), and Smith (1990b). Environmental data for the Southern Ocean is available from a variety of sources. Some of the most valuable are the *Discovery Reports*, the Soviet *Atlas of Antarctica* (Makismov 1966), the U.S. Navy Hydrographic Office *Oceanographic Atlas of the Polar Seas*, the U.S. National Center for Atmospheric Research *Climate of the*

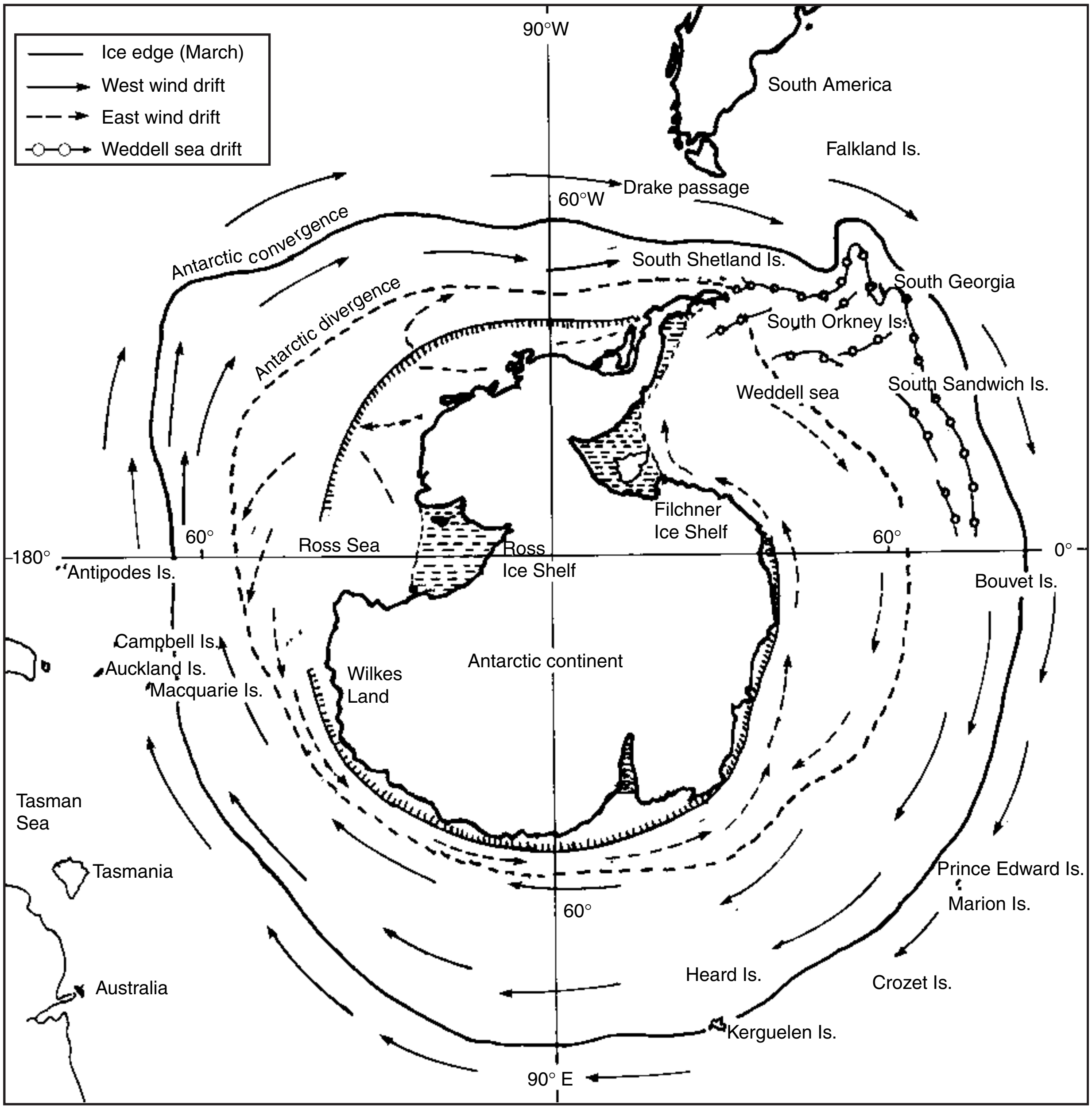


FIGURE 1.1 Antarctica and the Southern Ocean showing the positions of oceanic fronts and surface currents. (From Knox, G.A., *Antarctic Resources Policy: Scientific Legal and Political Issues*, Vicuna, F.O., Ed., Cambridge University Press, Cambridge, 21, 1983. With permission.)

Upper Air: Southern Hemisphere (Taljaard et al. 1971), and the American Geophysical Union *Antarctic Research Series* (1964a). The interlinking of the biological and physical components of the system have been discussed by Knox (1960, 1970, 1983, 1994), Holdgate (1967), Lubimova, Naumov, and Lagunov (1973), Lubimova et al. (1980), Deacon (1982), Lubimova (1982, 1983), Tranter (1982), and Hempel (1985a, 1985b).

Hedgpeth (1977b) Points out that the Southern Ocean is "a rich, apparently high productive plankton–pelagic system supporting (at least in the past) great populations of whales and millions of penguins, and seals, and abundant intermediate populations of fish and cephalopods, depending on the near surface productivity." Among the important characteristics of the Southern Ocean system are the following:

1. It is a large system, indeed probably the largest marine ecosystem on the globe.
2. It is semi-enclosed, especially in the overlying water masses, and the Polar Front forms a distinct northern boundary.

3. It is an old system with a long evolutionary history (Knox and Lowry 1977). The main circulation patterns and water mass distributions were established at least 20 million years ago (Knox 1980).
4. Most of the major taxonomic groups are circumpolar in distribution. The principal variation is that of productivity, which is greater in certain regions than in others.
5. The quantitative and qualitative features of the basic processes in the Southern Ocean system differ obviously from those of other oceanic systems, as demonstrated by the distribution of the dominant herbivore and key species of the system, *Euphausia superba*.

1.2 THE EVOLUTION OF THE SOUTHERN OCEAN

The unique characteristics of the Southern Ocean are the result of a long evolutionary history that can only be understood within a palaeo-geographic framework of continental drift, plate tectonics and polar wandering (Knox 1979, 1980; Norton and Slater 1979; Kennett 1983; Elliot 1985; Anderson 1999). Kennett (1977) has provided a detailed synthesis of the information concerning the evolution and palaeooceanography of the Southern Ocean, while Kemp (1972) has discussed the broad trends in climate since the Paleocene.

A summary of the major events in this evolution follows: during the Cretaceous period equatorial seas extended almost uninterrupted throughout the globe (Frakes and Kemp 1972). In the Southern Hemisphere, Antarctica (then part of Gondwanaland) was very close to its present position near the rotational pole, but with South America, New Zealand, and Australia attached (Figure 1.2). New Zealand separated from Australia and Antarctica in the Cretaceous, 60–80 million years before present (my BP). By the late Paleocene (50 my BP) the Tasman Sea had formed and Australia had begun to separate from Antarctica. However, the South Tasman Rise, which is of continental origin, was still part of

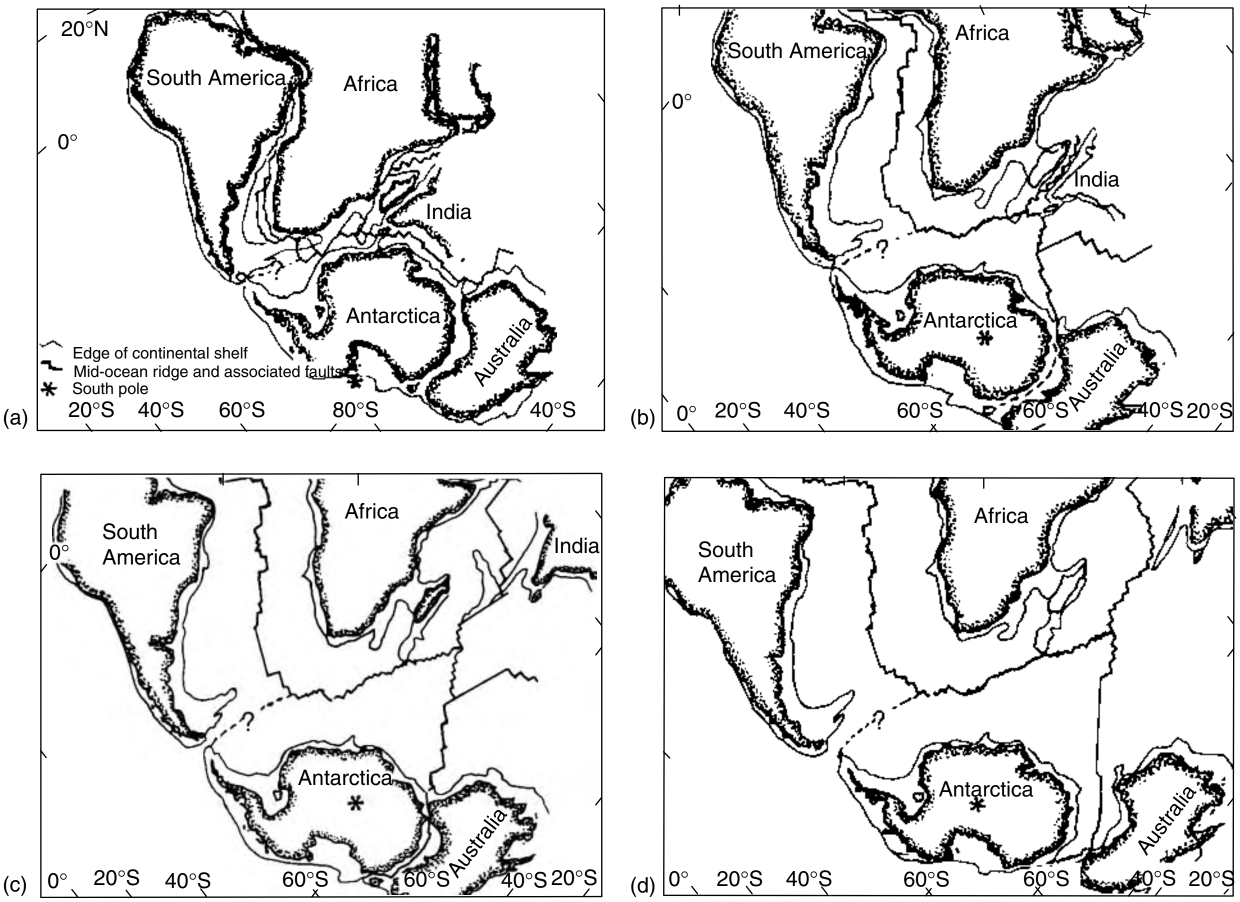


FIGURE 1.2 Stages in the dispersal of the Gondwana continents (after Norton and Sclater 1979). No account is taken of the possibility of rearrangement of West Antarctica. Note that only a very limited separation of Australia and Antarctica had occurred by 53 my BP, and also that South America and the Antarctic Peninsula were most likely still abutting each other at 39 my BP. The position of the South Pole is that inferred for the time given in each diagram. (From Elliot, D.H., *Antarctica*, Key Environment Series, Pergamon Press, Oxford, 39, 1985. With permission.)

Victoria Land, and because of this no major current system could develop between Australia and Antarctica. Frakes and Kemp (1972) postulated that during the Eocene large oceanic gyres extended from the equator to high latitudes and brought warm water to the Antarctic coastline. Their reconstructed palaeotemperatures at 60°S latitude are 24°S for Queen Maude Coast, 17°C for the shallow sea between Australia and Antarctica, and 7°C for the attached South American–Antarctic Peninsula coastline.

In the Late Eocene-Early Oligocene (39 my BP), major changes began to occur which transformed the global warm climate into the modern climatic regime of today. At that time there was a dramatic lowering of austral temperatures. This resulted in near-freezing surface coastal waters along the Antarctic coastline, which probably caused sea level glaciation around the continent, and the formation of cold Antarctic Bottom Water. Associated with the development of the thermoclinal circulation system was an increase in the calcium carbonate compensation depth (CCD) (Heath 1969; Van Andel and Moore 1974). Evidence from sediment macrofossils (foraminiferans, diatoms, and radiolarians) indicated a marked change to a cold water biota (Margolis and Kennent 1970; Jenkins 1974).

In the Late Oligocene (25–28 BP) the South Tasman Rise finally separated from Victoria Land sufficient enough to allow the formation of the Antarctic Circumpolar Current (West Wind Drift) (Figure 1.1). The Drake Passage had formed some time between the initial separation of Australia from Antarctica and the final separation of the Tasman Rise. In the Early Miocene (22 my BP) the Polar Front (Antarctic Convergence) formed, producing a major biological barrier which is still operating today. Large ice sheets developed rapidly in East Antarctica during the Middle Miocene. Dell and Fleming (1975), using fossil molluscan evidence, suggested that the sheltered rocky coastline of the Ross Sea was, at that time, probably ice-free and kelp-fringed, not unlike Tierra del Fuego today. By the Late Miocene-Early Pliocene, the West Antarctic ice sheet had formed and was much thicker than it is today (Shackleton and Kennett 1975). During this time the production of siliceous phytoplankton steadily increased. Hays (1969) observed two intervals of distinct cooling at 2.5 and 0.7 my BP, and climatic oscillations during the last 3.5 million years, with a steadily increasing coolness up to the present time.

1.3 BATHYMETRY

The bathymetry of the Southern Ocean is shown in Figure 1.3. Three deep-water basins (4,000–6,000 m deep) surround the Antarctic continent: the Atlantic–Indian Basin, the Indian–Antarctic Basin, and the Pacific–Antarctic Basin. These basins are partially bounded on the north by a series of ridges or rises; the Scotia Ridge and the Atlantic–Indian Ridge, the Southeast Indian Ridge, and the Pacific Atlantic Ridge respectively. These ridges and the Kerguelen Plateau tend to restrict the flow of bottom water and in some areas they even deflect surface currents. The Drake Passage between South America and the Antarctic Peninsula restricts the circulation of water masses and, as will be discussed later, has a profound effect on circulation in the Southern Ocean.

The continental shelf of the Southern Ocean differs from that surrounding other continents in that it is unusually deep, with the "shelf break" (the transition between the continental shelf and the continental slope) lying two to four times deeper than in other oceanic regions. This is partly due to the isotactic equilibrium adjustment of the continent to the large mass of the Antarctic ice sheets. Both the Weddell Sea and the Ross Sea are characterized by broad ice shelves: the Filchner and Ronne Ice Shelves and the Ross Ice Shelf respectively. These shelves, as we shall see, profoundly influence the near-shore circulation and water properties.

1.4 CLIMATE

1.4.1 WIND

A ring of low pressure surrounds the Antarctic continental plateau, while tropical anti-cyclones lie to the north. Winds in the Southern Ocean blow towards the trough of low pressure, but are directed to the left by the earth's rotation (Coriolis effect). As a result, at about 50°S of the Southern Ocean, westerly winds occurs. The westerlies within this circumpolar belt are quite strong, with maximum intensity in the region of the Antarctic Circumpolar Current (ACC) (see Figure 1.6). It is this wind that drives the Southern Ocean circulation. Superimposed upon this westerly circulation are northwest–southeast moving depressions.

Over the Antarctic continent itself, katabatic winds dominate the weather system. These winds, driven by very cold and dense air flowing down the glaciers and ice streams of the ice cap, can often reach very high velocities, and they are also responsible for the strong southeast–northwest winds extending many kilometers from the coast out to sea. Near the peri-Antarctic trough of low pressure there is a belt of easterly winds.

To summarize, the prevailing wind system of the Southern Ocean comprises three main elements: a southeasterly component near the coast, a zone of easterly flow encircling the continent and extending north to about 65°S, and a wide zone of westerlies reaching as far north as about 40°S (Squire 1987). This zonal circulation pattern is more intense and constant here than in any other region of the globe.

1.4.2 TEMPERATURE

The Southern Ocean is cold. Across the Polar Frontal Zone the temperature range in the summer is from 4 to 8°C, and in

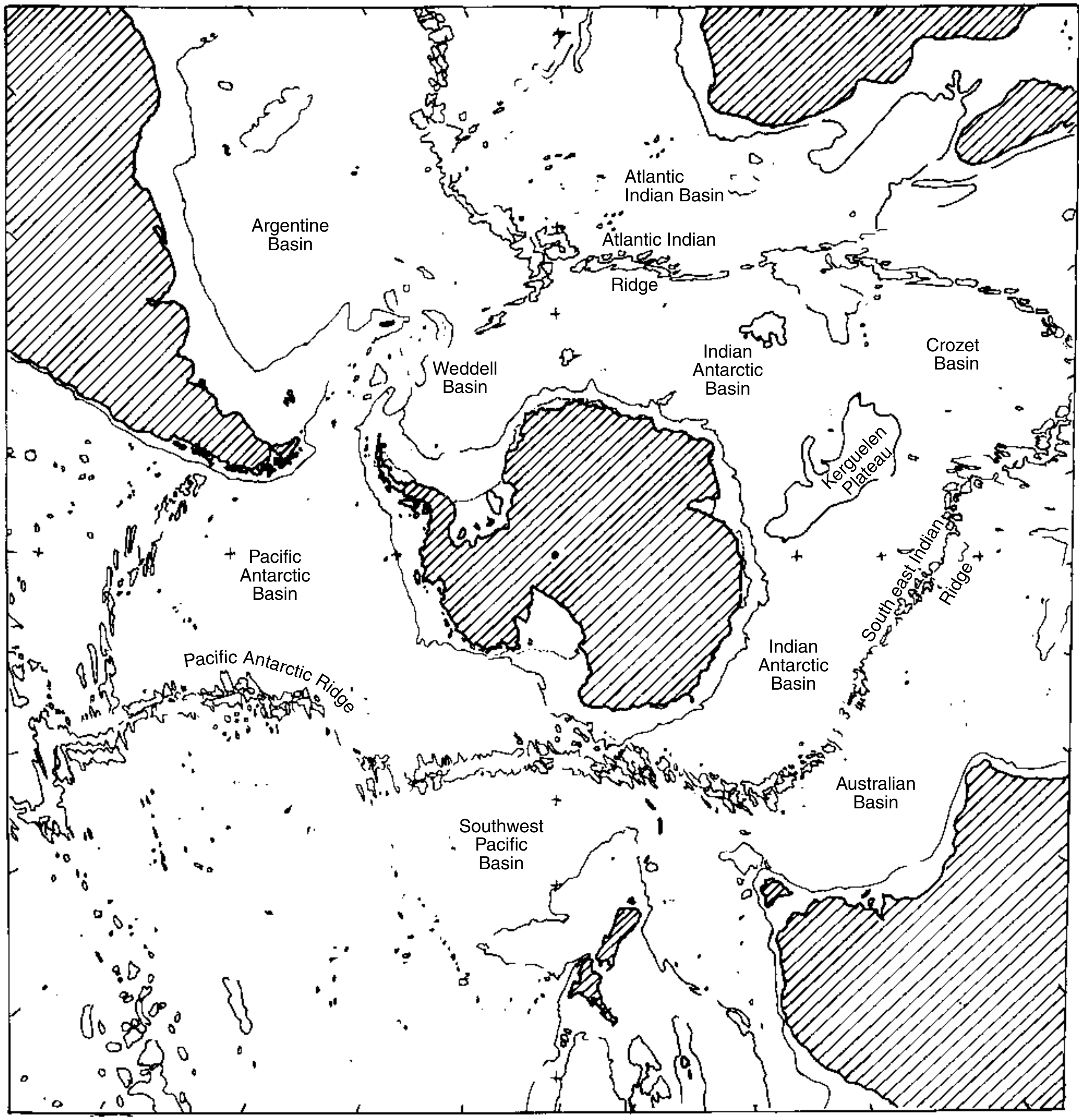


FIGURE 1.3 Map of the sea bed surrounding Antarctica showing the principal deep water basins and submarine ridges. (From Squire, V.A., *Primer Symposium Espanol de Estudiios Antarcticos Palma de Mallorca June–July*, 201, 1987. With permission.)

the winter from 1 to 3°C. Surface waters south of the Polar Front have an average temperature of about 1–2°C in the winter and 3–5°C in the summer, while further south near the continent temperatures range from only about −1.0 to −1.9°C. Temperature differences between cold surface and bottom layers and intermediate warmer layers is less than 5°C; thus the total annual range throughout does not exceed 4–5°C and is considerably less for the greater part of the area (e.g. in McMurdo Sound temperatures range seasonally only from −1.7 to −1.9°C).

1.4.3 SOLAR RADIATION

In the far south near the continent, the alternation between total darkness for half of the year and continuous daylight for the other half imposes a seasonal light regime in contrast to the diurnal cycles of lower latitudes. In addition, the amount of light penetrating the surface waters of the ocean is determined not only by its intensity, angle of incidence, surface reflection (up to 50% according to data given in 1967 by El-Sayed for Marguerite Bay in February 1965), and absorption by suspended particles, but also by the presence of sea ice and snow cover (see Section 2.8.7). Light penetration is also influenced by the transparency of the atmosphere. Anti-cyclonic conditions near the coast result in skies that are often lightly cloudy or clear. In the region of the ACC there is a continuous passage of low pressure systems and a predominance of cloudy weather resulting in lower insolation in this region relative to areas close to the continent (Holm-Hansen et al. 1977).

Oceanic waters surrounding Antarctica are typically blue and highly transparent with a maximum Secchi depth (the depth at which a standard Secchi disc becomes invisible) of about 40 m (Slawyk 1979). The 1% light level is relatively deep at about 100 m. Tilzer et al. (1986) attribute the low concentrations of dissolved organic compounds and the low abiotic turbidity to the very low terrestrial input of sediment and organic matter.

1.5 ICE COVER

1.5.1 SEASONAL VARIATION

One of the salient characteristics of the Southern Ocean is the dramatic changes that occur in sea ice cover, from about 20×10^6 km^2 in late winter to about 4×10^6 km^2 in late summer (Zwally et al. 1983a,1983b; Comiso and Zwally 1984). The ways in which sea ice forms and decays and the characteristics of the different types of sea ice are considered in Section 3.2. While the general distribution of sea ice has been known for many years from scattered ship observations, it is only recently that continuous year-round observations have been available as a result of satellite imagery, thus enabling the detailed changes over the year and year-to-year variations to be documented.

Figure 1.4 illustrates the growth and decay of the sea ice in the Southern Ocean. The months of minimum extent are February and March, while those of maximum extent are September and October. The northern limit of the sea ice changes by no more than a few degrees from year to year. The most rapid advance of the ice edge occurs in May and June, when it moves northward at a rate of 4.2 million km^2 per month; November and December are the months of the most rapid retreat when the ice edge recedes at 6.9 million km^2 per month (Squire 1987). The average rates of advance and retreat are respectively 2.4 and 3.3 million km^2 per month. Figure 1.5 depicts the average seasonal cycle of the monthly Southern Ocean sea ice over the period 1978–1987, which was calculated from Nimbus 7 satellite imagery.

Over time the sea ice records show considerable variability from year to year in: (1) sea ice extent, (2) the spatial range experienced in the monthly average Southern Ocean sea ice distribution, and (3) the length of the sea ice season. Using the Nimbus 7 data, Parkinson (1992) has examined this variability. Regarding the three variables listed above, (1) maximum sea ice extent varied by approximately 12%, decreasing during the mid-1970s, followed by increases over the next few years and leveling off for much of the 1980s, and (2) the area of intra-annual variability in monthly average sea ice distributions in summer far exceeded the summer-time area of consistent ice coverage, this in sharp contrast to the winter-time situation, when the area of consistent sea ice coverage is considerably larger. In winter, the sea ice distribution variability is largely confined to two regions: a relatively narrow band, generally 2–5° of latitude, surrounding the region of consistent ice coverage, and, for the mid-1970s, the region of an occasional large open water area within the pack ice in the Weddell Sea, termed the Weddell polyna. The length of the sea ice season, calculated for the years 1979–1986, with satellite passive-microwave data coverage through all months of the year, showed increases over the period in the Ross Sea but decreases in the Weddell and Bellinghausen Seas. In both cases it appears through comparisons with data from 1973–1976, that the 1979–1986 changes more likely reflect a fluctuating behavior of the ice cover than a long-term trend.

At the minimum extent scattered areas along the Antarctic coast retain some ice coverage. Most of this ice is found in the eastern Weddell Sea and the Bellinghausen–Amundsen Sea sector. No ice is found north of the Ross Ice Shelf at this time. Around the margins of the continent areas of unbroken fast ice (ice attached to the shore) may persist for two or more years, forming thick multi-year ice. This is in contrast to the pack ice (drifting ice floes) zone of annual sea ice, which is 1–2 m in thickness. The distribution of ice in the pack ice zone is highly variable as the ice cover is frequently broken up by storms, and the resulting floes, driven by surface currents and wind, drift considerable distances. Leads of open water (open channels in the ice within the pack) are highly variable.

1.5.2 ICE SHELVES AND ICEBERGS

The Antarctic continent is largely covered by ice, and around the margins the extensive ice sheets extrude from the continent into the sea. In the Ross and Weddell Seas these ice sheets float on the ocean forming the extensive Ross, Filchner, and Ronne Ice Shelves. The layer of water under the Ross Ice Shelf varies from a few meters to several hundred meters thick. The ice layer varies from 200 m thick at the seaward edge to over 800 m at the grounded edge. The ice shelves are continually moving seaward at about 1 m per day due to the accumulation of snow on the continent. As they extend into the open ocean, they are exposed to the action of long period waves and eventually they crack and calve icebergs. The large tabular icebergs so produced can range from a few hundred meters up to 100 km in horizontal extent and usually are about 200–300 m thick. It has been estimated (Radok, Streten, and Weller 1975) that the total mass of icebergs is about one-third of the mass of sea ice at

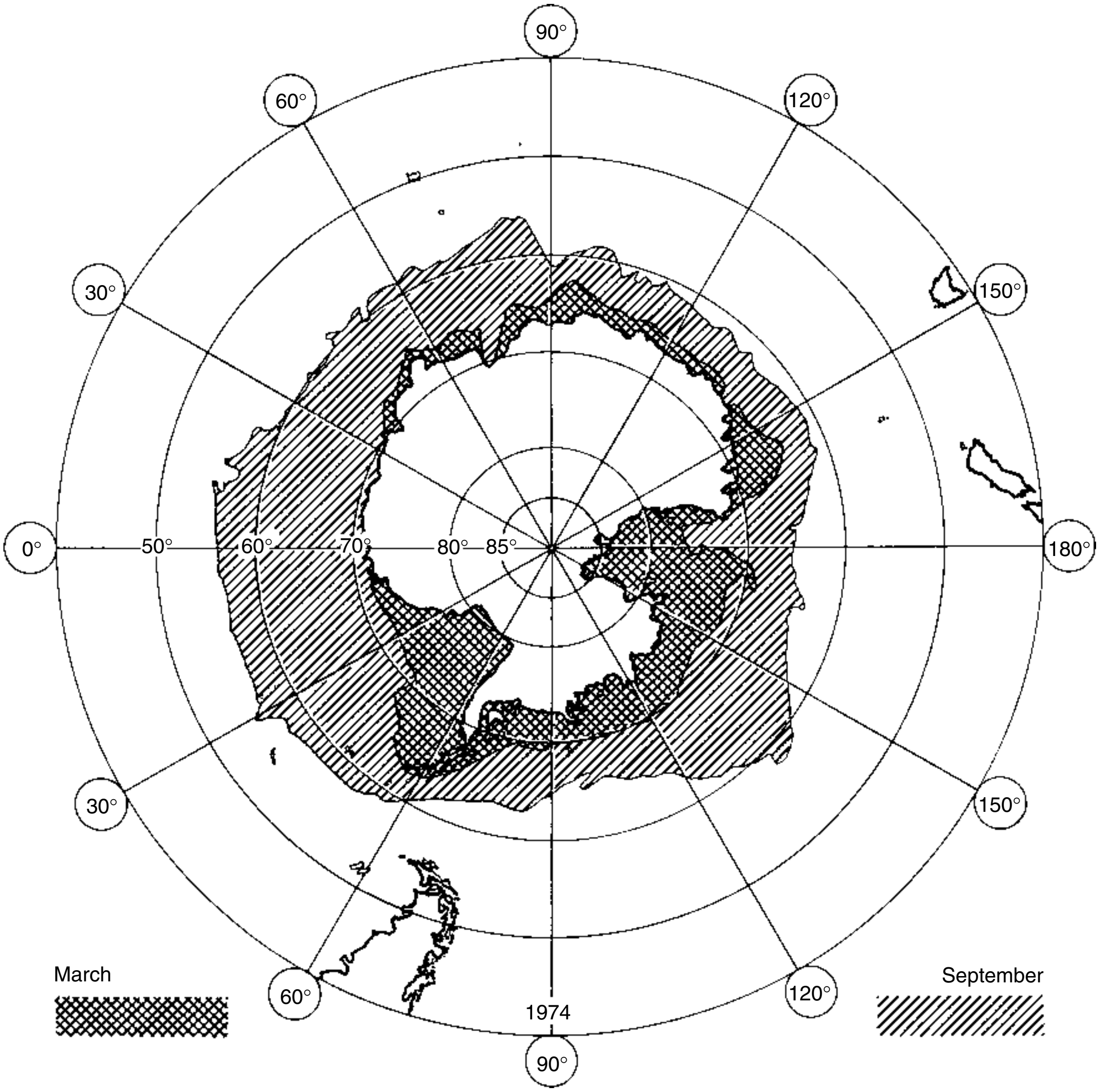


FIGURE 1.4 The distribution of the pack-ice in winter (September) and summer (March). (From Knox, G.A., *Ocean Management*, 9, 113, 1984. With permission.)

maximum extent. The average life of icebergs is about four years, but large ones have been tracked for much longer periods (Swithinbank, McClain, and Little 1977).

Figure 1.6. gives estimates of the variation of Antarctic ice sheet parameters with time. It can be seen that a rapid change in the mass budget of the Antarctic ice sheet occurred around 10 my BP when the total budget was two to three times its present level (Robin 1988). The curve "total discharge to the sea" is ice lost by basal melting beneath the ice shelf and ice tongues and by the calving of icebergs. Both of these have decreased markedly since that period. The extent of the pack ice (Figure 1.6c) shows the large increase in extent, especially during winter, since the opening of the Drake Passage resulted in Antarctic waters becoming thermally isolated as the circumpolar current developed (Robin 1988).

1.6 CIRCULATION PATTERNS AND WATER MASSES

1.6.1 Introduction

The basic feature of the circulation patterns and hydrographic processes in the Southern Ocean were first described by Deacon (1937, 1963, 1964a, 1964b, 1977, 1984b). Since then there have been a number of reviews including those of Gordon, George, and Taylor (1977a, 1977b), Forster (1981, 1984), Gordon and Molinelli

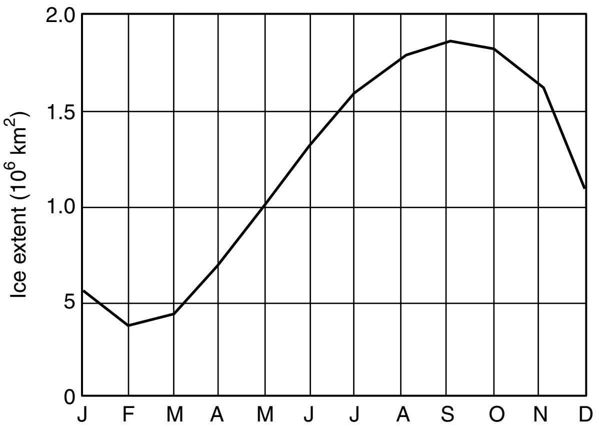


FIGURE 1.5 Average seasonal cycle of monthly average Southern Ocean sea ice extents over the period with full-month coverage of Nimbus 7 SMMR. November 1978 through July 1987. Ice extents are calculated from passive-microwave SMMR data as the aerial coverage of the Southern Ocean with ice concentrations exceeding 15%. (From Wadhams, P., *Ice in the Oceans*, Gordon & Breach Science Publishers, London, 45, 1967. With permission.)

(1982), Gordon (1983, 1988), Amos (1984), Gordon and Owens (1987), Squire (1987), and Carmack (1992). The Southern Ocean-atmosphere-ice coupled system is extremely complex. Processes within the Southern Ocean are responsible for the production of water characteristics below the main thermocline of the world's oceans. Associated with this is significant heat flux across the ACC.

While the summary of circulation patterns given below represents a generalized picture of the system dynamics, it should be emphasized that, superimposed upon this, is a great amount of temporal, seasonal, and year-to-year variability (see Chapter 15). The Southern Ocean is not radically symmetric, and many of the circulation and water mass features vary markedly with longitude. The cryosphere complicates water mass properties in two ways: (1) the highly spatially and temporarily variable sea ice cover strongly influences the coupling of ocean and atmosphere in regard to momentum, heat, water and gas exchange, and (2) ocean interaction with glacial ice has a marked influence on the characteristics of water masses (Gordon 1988).

1.6.2 DRIVING FORCES

1.6.2.1 Wind

In general, the principle driving force for the Southern Ocean circulation is the wind field. The westerlies within the circumpolar belt are quite strong with the maximum westerlies situated in close proximity to the ACC. The wind field produces Ekman divergence (upwelling) south of the ACC and convergence (sinking) to the north. The upwelling poleward of the ACC carries about 45 Sv ($1\text{Sv}=1\times10^6\ \text{m}^2\ \text{s}^1$) into the mixed layer, two-thirds of

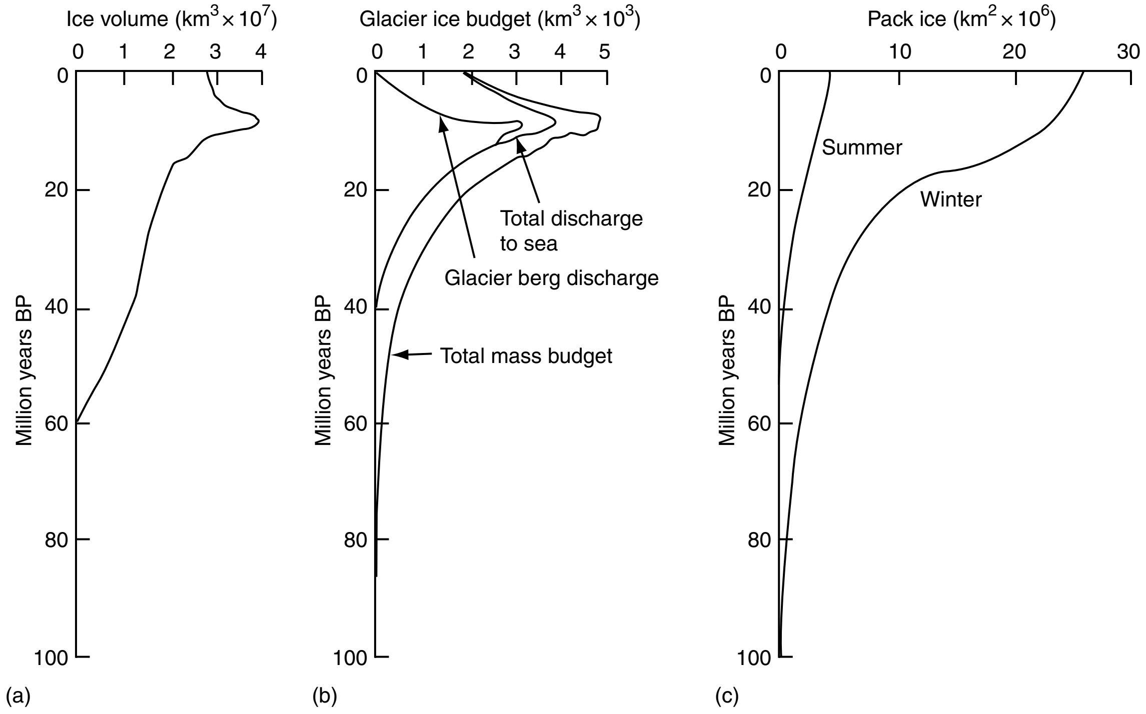


FIGURE 1.6 Estimated variation of the Antarctic ice sheet parameters with time. (a) Volume of ice sheet including the ice shelves; (b) Annual (total) mass budget of the Antarctic ice sheet, together with annual ice discharge to sea across the flotation line, and the annual volume discharged by glaciers directly to open water but not to ice shelves (glacier berg discharge); (c) Changes of the area extent of pack ice around Antarctica. (From Robin, G. DeQ., *Palaeogr. Palaeoclimat. Palaeoecol.*, 67, 45, 1988. With permission.)

which is directed the north, with the rest towards the continent, where coastal sinking occurs (Gordon 1988).

Along the margins of the continent, south of about 60°S, the wind field results in westerly flowing water—the Antarctic Coastal Current (East Wind Drift). Between the two well-defined current systems there is a series of eddies. Figure 1.7 shows the general pattern of surface currents in the Southern Ocean. Since the water column is weakly stratified south of the Polar Front, the ocean currents extending to the bottom result in the deep circulation being similar to that of the surface circulation, although the former is more strongly influenced by bottom topography.

1.6.2.2 Ocean-Atmosphere Heat and Fresh Water Flux

Within the region of the Southern Ocean there is a slight excess of precipitation over evaporation (Gordon 1981). The annual freezing and thawing of the sea ice is a significant factor in the redistribution of freshwater. In addition,

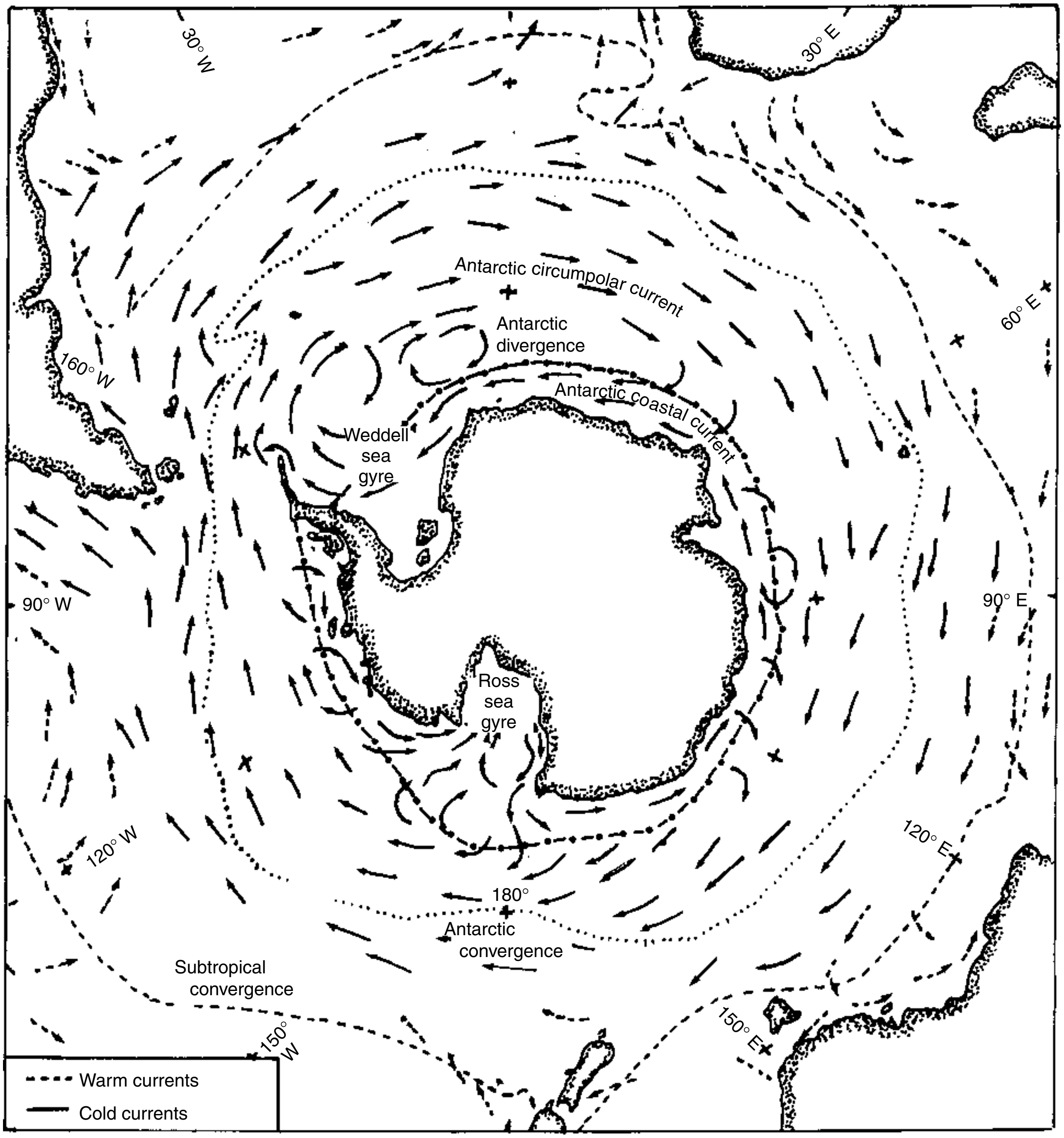


FIGURE 1.7 Surface currents in the Southern Ocean and the mean positions of the principal frontal zones. Warm currents are shown dotted and cold are shown solid. (From Knox, G.A., *Antarctic Resources Policy: Scientific, Legal and Political Issues*, Cambridge University Press, Cambridge, 21, 1983. After Brodie [1975], adapted from Sverdrup, Johnson, and Fleming [1942]. With permission.)

the waters of the Southern Ocean play a primary role in the wastage of glacial ice, mainly by direct melting of the ice along the underside of the shelf ice (Jacobs, Fairbanks, and Horibe 1985; Schlosser 1986).

As Gordon (1988) points out, estimates of ocean-atmosphere flux are subject to large errors due to the lack of meteorological and sea ice (concentration, thickness) data, and especially the paucity of data from the winter period. The strong seasonal variability of the sea ice cover, coupled with approximately 10–20% inter-annual variability in maximum winter sea ice cover (Zwally et al. 1983a, 1983b), further complicates estimates of the mean ocean-atmosphere energy exchange. South of 60°S, the northern limit of sea ice cover, heat loss is large an annual average of 30 W m^2 (Gordon 1981) but it is highly dependent on ice cover. Heat flux across the ACC and Polar Front (average 55°S) is 3.1×10^4 W, while that across 60°S is larger, amounting to 5.4×10^4 W (Gordon and Owens 1987). In order to maintain a steady state condition, the net poleward heat flux must involve the poleward transport of a large volume of water.

1.6.3 OCEANIC CIRCULATION (FIGURE 1.7)

1.6.3.1 Antarctic Circumpolar Current (West Wind Drift)

The Antarctic Circumpolar Current (ACC) is unique in that it is the only zonal current encircling the globe, and it is almost unobstructed by land masses, being constricted only in the region of the Drake Passage. It displays significant variations with longitude and is principally related to bottom topography, being deflected where it passes over submarine ridges with a strong northerly component after it passes through the Drake Passage. Its width varies from less than 200 km south of Australia to over 1,000 km in the Atlantic. Mean current speeds within the ACC are relatively low (0.04–0.25 m s^{-1}, some 2–3% of the wind velocity). Although the predominant movement is to the east, there is a strong northerly component. There is also some evidence that there are meanders and even loops within the current (Tchernia 1974, 1980; Joyce and Patterson 1977). The ACC joins the great current gyres of the South Atlantic, South Indian, and South Pacific Oceans.

1.6.3.2 Antarctic Coastal Current (East Wind Drift)

In the vicinity of the Antarctic continent south of about 65°S, where winds from the east and southeast blow off the ice sheet, there is a surface current which flows westward. This Antarctic Coastal Current generally follows the coastline with two important indentations in the Ross and Weddell Seas. Its flow is estimated at 10 million m^3 s^{-1}, while its speed is variable between 0.1 and 1 m s^{-1}, with the largest values near the Ross Sea Shelf (Squire 1987). The current may not be continuous but rather broken up by a series of gyres (Figure 1.7).

1.6.3.3 Circumpolar Frontal Zones

There are number of fronts within the Southern Ocean (Deacon 1982). While some are circumpolar, such as the Polar Front (Antarctic Convergence) they display much variability in characteristics with longitude. The most significant of these fronts is the Polar Front which divides the Southern Ocean into two distinct regions: SubAntarctic to the north and Antarctic to the south. It is a zone of variable width characterized by steep gradients in sea-surface temperature, abrupt changes in phytoplankton abundance, zooplankton distribution, pelagic bird species, weather conditions, and sometimes by a salinity maximum at the surface. A circumpolar subsurface salinity minimum closely follows the surface position of the front (Gordon, George, and Taylor 1977a, 1977b; Joyce, Zenk, and Toole 1978; Sciermammano 1989).

To the north of the Polar Front lies the SubAntarctic Front, while to the south lies the Antarctic Divergence. This divergence is caused partly by the northward component associated with the ACC and the southward component of the Antarctic Coastal Current, and partly by circulatory and thermohaline factors of the southern density gradient and the distribution of pressure and winds. In the region of the divergence deep water upwells to reach the surface. The classical schematic diagram of the horizontal and vertical movements of the Antarctic circumpolar water is presented in Figure 1.8.

1.6.3.4 Gyres, Eddies, and Rings

A characteristic of the zonation of circumpolar currents is the development of eddies of variable size and duration. This eddy variability is due to a combination of factors (Gordon 1988). The current cores migrate laterally (Nowlin, Whitworth, and Pillsbury 1977) by as much as 100 km in 10 days. Meanders or waves form and propagate along the ACC fronts (Legechis 1977; Sciermammano 1989). These meanders sometimes develop into closed rings (Joyce and Patterson 1977). Cold and warm water core rings have both been observed. The eddies are generally 30–100 km wide with surface velocities typically 30 cm s^{-1} or more, and they are vertically coherent from the surface to the bottom. Numerous current rings and meanders have been reported from the Drake Passage.

In addition to eddies there are large permanent cyclonic flowing gyres. The largest and best-defined of these is the Weddell Gyre, extending east of the Antarctic Peninsula to about 20°W and from Antarctica near 70–60°S (Deacon 1979; Gordon, Martinson, and Taylor 1981; Comiso and Gordon 1987). Others are the Ross Sea Gyre, north and east in the Ross Sea (Tchernia and Jeannin 1984; Gouretski 1999). A review of the Weddell Gyre system is found in Deacon (1977).

1.6.3.5 Polynas

As the sea ice cover expands in winter, areas of open water occur polewards of the ice limit which do not freeze but

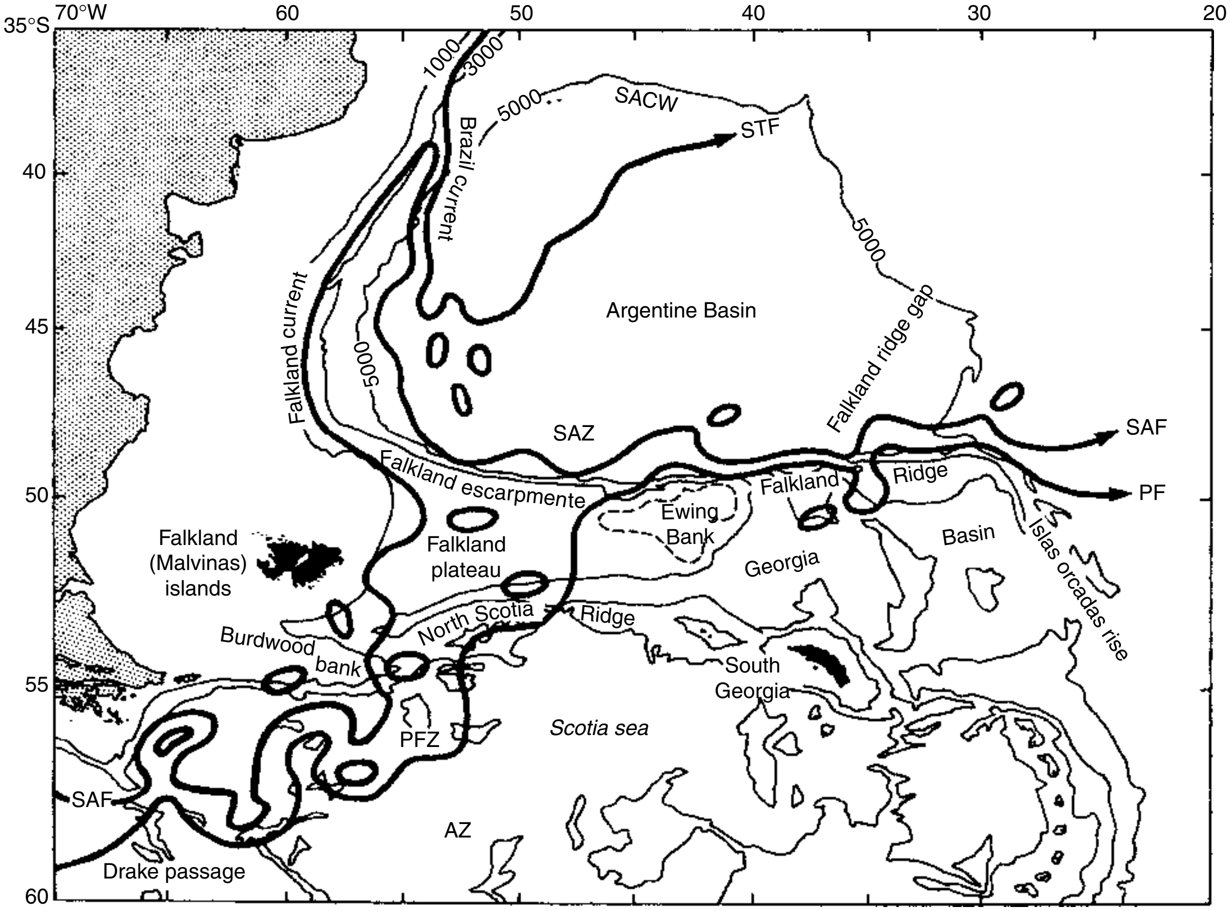


FIGURE 1.8 The upper ocean water masses and fronts in the western South Atlantic, SACW, South Atlantic Central Water; PF, Polar Front; SAZ, Subantarctic Zone; STF, Subtropical Front; PFZ, Polar Frontal Zone; SWAF, Subantarctic Front; AZ, Antarctic Zone; The broken line around the Ewing Bank is the 2,000 m isobath. (From Stein, M., Heywood, R.B., *Southern Ocean Ecology: The BIOMASS Perspective*, Cambridge University Press, Cambridge, 12, 1996. With permission.)

instead remain open to the atmosphere through all or part of the winter. These regions of long-lived open water are called *polynas*. Polynas tend to occur where high winds rapidly disperse freshly-formed ice at times when air temperatures are well below the freezing point of sea water (Van Woert 1999). Polynas play an important role in heat transfer from the oceans to the atmosphere, ice production, the formation of dense shelf water, spring disintegration of sea ice, phytoplankton and zooplankton production, and the distribution of higher trophic animals such as cephalopods, fish, birds, seals, and cetaceans. Within polynas, the oceanic heat loss may be 10–100 times above that of the ice-covered surface.

A review has categorized two distinct types of polynas (Smith et al. 1990b). A *latent heat polyna* is formed when sea ice is continually removed from the region in which it is formed by winds or ocean currents, the heat needed to balance the loss to the atmosphere being provided by the latent heat of fusion of the ice which continually forms. A *sensible heat polyna* is formed when a continued source of heat from the ocean prevents ice formation.

Coastal polynas are a common feature of the continental shelf round the Antarctic continent. They are primarily latent heat polynas where heat loss from the ocean surface is balanced by the latent heat of new ice formation and the polyna is maintained by wind or current removal of the new ice. The coastal polynas around Antarctic can be further subdivided into two categories: those off the front of major bay ice shelves (the Ross, Filchner–Ronne, Amery etc.) and those in the lee of ice tongues or other coastal projections such as the Terra Nova Bay polyna in the Ross Sea (Bromwich, Liu, and Rogers 1998) or along the Wilkes Land coast. Those off the front of the ice shelves involve processes of water circulation under the shelves and katabatic winds, whilst inhibition of ice drift into polyna areas is important for those in the lee of ice tongues (Smith et al. 1990).

Processes inside latent heat polynas are significant for the sea ice zone as a whole. Being regions of intense heat loss from the ocean to the atmosphere, these polynas can behave as "ice factories," contributing a significant fraction of the total annual sea ice production; it has been estimated, for instance that the small polyna in Terra Nova Bay contributes

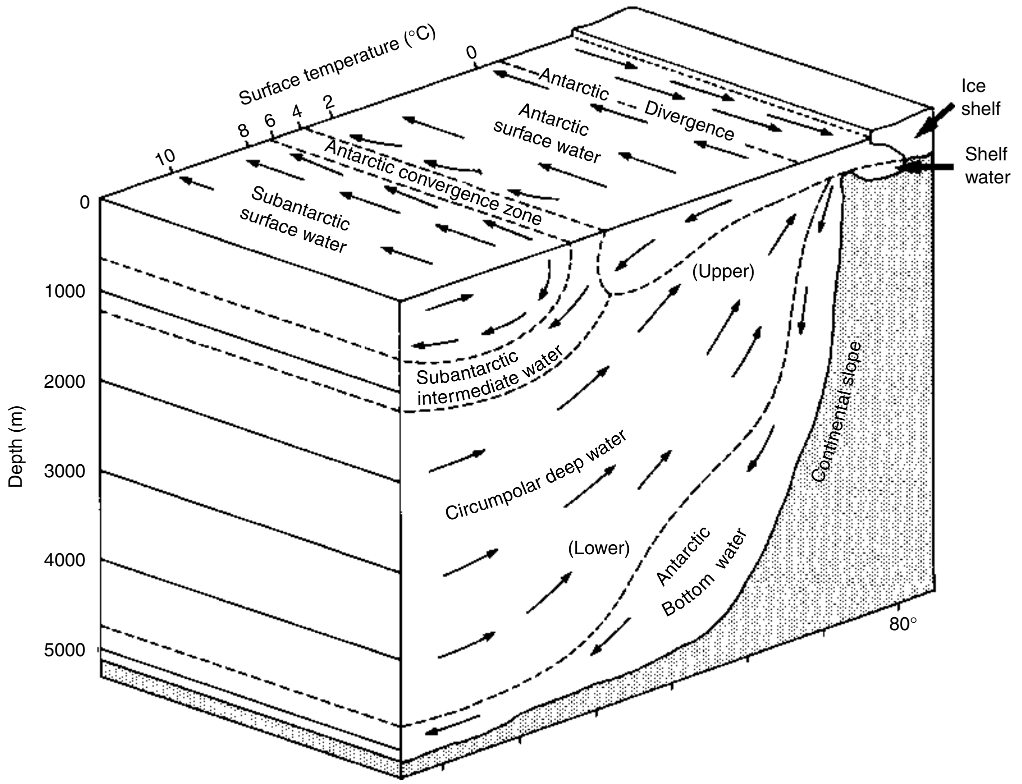


FIGURE 1.9 Schematic diagram of the meridional and zonal flow and water masses of the Southern Ocean. The diagram represents average summer conditions and applies particularly to the Atlantic sector. (From Knox, G.A., *Antarctic Resources Policy: Scientific, Legal, and Political Issues*, Vicuna, F.O., Ed., Cambridge University Press, Cambridge, 113, 1983. After Brodie [1965], adapted from Sverdrup, Johnson, and Fleming [1942]. With permission.)

10% of the ice production in the Ross Sea (Kurtz and Bromwich 1985). Brine rejected during the ice growth is concentrated in the polyna areas and can cause intense localized water mass modification as well as significantly increasing the salinity of the Antarctic shelf water. The ice-free polynas also play an important role for Antarctic marine ecosystems and in the control of biogeochemical fluxes.

A summary of recurrent polynas that have been detected and studied using passive microwave data has been given by Zwally, Comiso, and Gordon (1985). These include the coastal polyna in the Cosmonaut Sea (Comiso and Gordon 1987, 1996) and in Terra Nova Bay in the Ross Sea (Kurtz and Browich 1983; Bromwich, Liu, and Rogers 1998). Zwally, Comiso, and Gordon (1985) and Bromwich, Liu, and Rogers (1998) have reviewed the occurrence, extent, and variability of the Ross Sea polyna, which covers an area of about 27,000 km^2. This polyna owes its existence to a persistent cyclone near Roosevelt Island, which induces a sea level pressure distribution over the Ross Ice Shelf. This phenomenon results in an intensification and northward propagation of katabatic winds across the ice shelf and out to the sea. The immediate effect of such katabatic surge events is the development of the Ross Sea Polyna.

Other polynas which also occur in the Ross Sea include small polynas off Cape Royds, Ross Island, and a larger one in Terra Nova Bay (Kurtz and Bromwich 1985; Van Woert 1999). The Terra Nova Bay polyna is a stable feature, recurring annually and persisting throughout the winter, although it appears to vary in extent from less than a kilometer to 5,000 km^2. Van Woert (1999) suggests that the extent of the polyna is due to both local and katabatic winds at Terra Nova Bay and regional katabatic winds blowing off the Ross Ice Shelf.

1.6.4 WATER MASSES

Figure 1.9 presents an idealized schematic diagram of the meridional and zonal flow in the Southern Ocean. There are three principal hydrographic regimes: the area north of the Polar Front, the area south of the Polar Front, and the area on the continental shelf round Antarctica. Excluding the surface waters, three water masses dominate the deep ocean: the Subantarctic Intermediate Water north of the Polar Front near the 1,000 m level, the Antarctic Bottom Water near the bottom, and the Antarctic Circumpolar Deep Water in between at various depths.

Warm Deep Water upwells at the Antarctic Divergence. Here the oxygen minimum and the temperature maximum coincide and rise together with the underlying salinity maximum. The cold, low-salinity, high-oxygen Antarctic surface waters move north to the Polar Front where they sink and contribute to the formation of the low salinity Intermediate Water. North of the Polar Front is the warmer SubAntarctic Surface Water.

Near the bottom of the ocean, very cold Antarctic Bottom Water moves north from its primary site of generation around the continental margin, especially in the Weddell Sea. Sandwiched between the two Antarctic water masses is the broad compensatory flow of high-salinity Warm Deep Water. The south-flowing Deep Water mixes with the Antarctic waters above and contributes to the Circumpolar Deep Water which, in terms of volume, is the dominating water mass of the Southern Ocean. Mixing takes place across the boundaries between the water masses.

1.7 SOME REGIONAL HYDROGRAPHIC FEATURES

1.7.1 Southwest Atlantic and the Antarctic Peninsula Region

Stein and Haywood (1994) have reviewed the physical oceanography of the Southwest Atlantic region and the Antarctic Peninsula area (Figure 1.8). On leaving the confines of the Drake Passage and entering the Scotia Sea the Antarctic Circumpolar Current (ACC) is deflected north and west by the submerged ridge of the Scotia Arc, before it turns east again to flow round South Georgia and across the Atlantic Ocean sector of the Southern Ocean (Deacon 1937; Gordon and Goldberg 1970). It consists of Subantarctic and Antarctic Surface waters from the Pacific Ocean sector of the Southern Ocean and from the Bellinghausen Sea (Nowlin and Clifford 1977). Some mixing with Weddell Sea Surface Water occurs in the Scotia Sea. However, the southern arm of the Scotia Arc effectively restricts the flow of water out of the Weddell Sea (Carmack and Foster 1975) and most enters the Scotia Sea across the Weddell–Scotia Confluence east of the South Orkney Islands (Gordon 1967). Consequently there is a marked gradient of mixing across the Scotia Sea with the influence of the Weddell Sea Surface Water being greatest to the south and east of South Georgia (Anonymous 1983; Heywood, Everson, and Priddle 1985).

From north to south a number of fronts separate distinct water masses. The most northerly front, the Subtropical Front, marks the northern boundary of the sub-Antarctic Zone, while the Subantarctic Front marks its southern boundary. South of this front is the Polar Frontal Zone with its southern boundary marked by the Polar Front. To the south lies the Antarctic Zone. This complex of fronts and water masses (Zones) is the result of the passage of water through the Drake Passage being influenced by the various banks and ridges: the Burwood Bank, the North Scotia Ridge, the Ewing Bank, and the Falkland Ridge.

1.7.2 The Ross Sea (Figure 1.10)

Three main oceanic fronts occur within the Ross Sea region: the Polar Front (Antarctic Convergence), the Antarctic Divergence, and the Antarctic Slope Front. These fronts separate water masses of different temperature and salinity, and they exhibit marked biological and physical changes. The interchange of these water masses, especially at the Antarctic Divergence, provides the minerals and nutrients fundamental to marine biological production.

The Polar Frontal Zone lies between about 55°S and 60°S and separates Subantarctic Water to the north from Antarctic Water to the south. This is a zone of variable width, characterized by steep gradients in sea surface temperature and abrupt changes in phytoplankton composition, zooplankton distribution, pelagic bird species, and weather conditions. The Polar Front lies within the Antarctic Circumpolar Current (West Wind Drift). It is a complex system where wave-like disturbances frequently close on themselves to form rings and eddies with lifetimes that vary from days to years (Forster 1984).

South of about 65°S, where winds blow from the east and southeast off the ice sheet, the Antarctic Coastal Current (East Wind Drift) flows in the opposite direction—from east to west. The boundary between the East

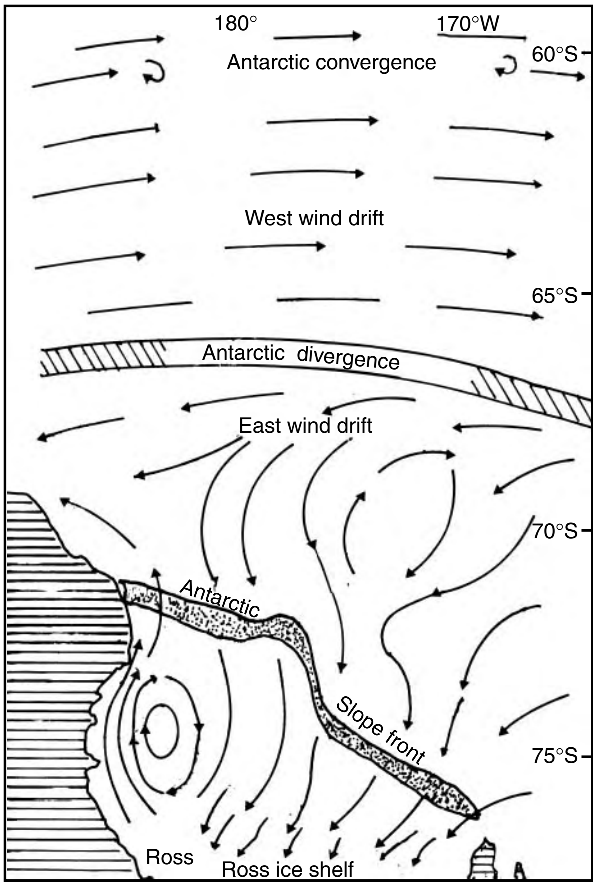


FIGURE 1.10 Oceanic fronts and surface water circulation in the Ross Sea region. Three main oceanic fronts occur: the Polar Front (Antarctic Convergence), the Antarctic Divergence, and the Antarctic Slope Front. (From Knox, G.A., *Ross Sea Region: State of the Environment Report for the Ross Sea Region of Antarctica*, Antarctic Institute, Christchurch, 54, 2001. With permission.)

and West Wind Drifts forms the second frontal zone, the Antarctic Divergence, where deeper water rich in nutrients upwells to the surface, resulting in enhanced phytoplankton production.

A third frontal zone, the Antarctic Slope Front, lies over the edge of the continental shelf in the southern Ross Sea (Ainley and Jacobs 1981; Jacobs 1991) and it is centered 10–45 km seaward of the shelf break, placing it just south of the 1,000 m depth contour. This topographically controlled front is marked by strong subsurface gradients in ocean currents and temperature, and by along-shore currents that are stronger than those occurring in most surface waters of the adjacent continental shelf. The slope front lies at the northern margin of the massive phytoplankton bloom that occurs over the Ross Sea continental shelf in summer.

Warm deep water approaches the continental slope of the Ross Sea from the northeast in the west and from the east-northeast in the east. These waters are seasonally cooled and warmed, Stalinized by the formation of sea ice, and freshened by water from melting ice. Ice and water is then moved west and north by surface circulation, which is mainly due to the extensive cyclonic gyre on the western side of the Ross Sea. Surface waters move to the southeast along the eastern periphery of this cyclonic system. As the southeast flowing water approaches the Ross Ice Shelf, the current is deflected to the west, with part joining the cyclonic circulation and part passing beneath the shelf. Along the Victoria Land coast, a northward flowing coastal current forms a well defined and comparatively narrow stream (Tressler and Ommundsen 1962). Some of this water returns to the cyclonic circulation, while the rest turns round Cape Adare and eventually joins the Antarctic Coastal Current.

Subsurface circulation is formed by two different anti-cyclonic gyres at each end of the Ross Sea, which are connected by a U-shaped cyclonic feature in the vicinity of the Ross Ice Shelf.

In the Ross Sea region, several distinct water masses can be distinguished and are generally defined by the particular relationships between temperature and salinity (Jacobs and Comiso 1989, 1992; Jacobs and Giulivi 1989; Carmack 1992). Three water masses can be distinguished in the deeper oceanic waters of the Ross Sea and five over the continental shelf and slope (Gouretski 1999).

Antarctic Surface Water, Circumpolar Deep Water, and Antarctic Bottom Water occupy the oceanic parts of the region. Of these, Circumpolar Deep Water constitutes the greatest volume of water in the Southern Ocean and is characterized by high nutrient levels, generated from phytoplankton as it sinks through the water column. Antarctic Bottom Water occupies the deepest region of the water column and plays a major role in the global oceanic system.

Antarctic Surface Water, High Salinity Shelf Water, Low Salinity Shelf Water, Ice Shelf Water, and modified Circumpolar Deep Water can be identified over the continental shelf and slope of the Ross Sea, although in contrast to other water masses, those of the continental shelf are highly variable. Antarctic Surface Water is found throughout the Ross Sea during the summer, with surface temperatures generally higher in the south where the pack ice opens up earlier in the summer and a wide range of salinities occur. Below this layer are dense shelf waters. High Salinity Shelf Water is the densest water found in the Southern Ocean and these high salinities are explained by the intensive processes of ice formation in polynas along the coast (Jacobs, Fairbanks, and Horibe 1985). Low Salinity Shelf Water is found in the eastern Ross Sea and it is marked by slightly warmer sea surface freezing temperatures, and low salinities. Ice Shelf Water exhibits temperatures below the sea surface freezing point, an indication of interaction with the Ross Ice Shelf at depth. This water is concentrated in the west of the Ross Sea where it emerges from under the ice shelf (Jacobs and Giuvili 1999). Modified Circumpolar Deep Water represents deep oceanic waters that have penetrated the continental shelf. This water is warmer and occupies depths between 100 and 300 m.

1.8 BOTTOM WATER FORMATION

Antarctic Bottom Water is an important component of the Southern Ocean system, responsible for about 34 Sv of the northward flow, and providing cold water at depth to all the oceans of the southern hemisphere. Its formation involves a mixing of water types, helped by surface interaction. Observations from the *Discovery* Expeditions (Deacon 1937) confirmed the Weddell Sea as the main source of Bottom water. It accounts for more than 50% of the total volume produced. Second to this is the Ross Sea Shelf (Jacobs, Amos, and Buckhausen 1970; Jacobs, Fairbanks, and Horibe 1985) with some other sites in the sector from 30°E to 170°E also being possible sources (Baines and Condie 1998).

According to Gordon (1988), postulated processes and sources contributing to Weddell Sea Bottom Water formation include haline convection by evaporation or freezing in open leads and polynas, cooling under the Filchner Ice Shelf, Ekman-layer effects, sinking along frontal zones, derivation form deeper oceanic areas, overflow of dense water from the Bransfield Strait, and soluble diffusive convection. Estimates of the circumpolar production rates of Bottom Water are in excess of 13 Sv (Jacobs, Fairbanks, and Horibe 1985). The principal mechanism was believed to involve frontal zone mixing between water masses at the continental shelf break, with the dense water sinking down the slope (Gill 1973; Foster and Carmack 1976). Recent observations by Norwegian scientists (Foldvik and Gammelsrad 1988) have shown that large volumes of Weddell Sea Bottom Water originate from Ice Shelf Water formed under floating ice shelves by flowing down the continental slope as organized plumes and mixing with the overlying Weddell Sea Deep Water.

1.9 NUTRIENTS

In the Southern Ocean the concentration of nutrients is lowest in the surface waters and greatest in the Warm Deep Water for nitrate and phosphate, and usually near the bottom for silicate. In general, the concentration of nutrients in surface waters south of the Polar Front is much higher than that found in other oceanic waters (Knox 1970; El-Sayed 1978). Nutrient rich water upwells at the Antarctic Divergence spreading out to ultimately downwell at the Polar Front. On the basis of data from other upwelling regions, with time one would expect to find almost complete stripping of plant nutrients in the upper 50–100 m due to the growth of phytoplankton (Barlow 1982). Holm-Hansen (1985) estimated that between 25 and 30 μM of nitrate per liter would have been consumed by the time the upwelled water reached the zone of the Polar Front (approximately 200 days in transit), and postulated that one would expect to find almost complete stripping of the nutrients in aged waters close to the Polar Front. However, data from studies by Kuramoto and Koyama (1982), and Watanabe and Nakajima (1982) from a transect along 45° longitude reveals a completely different picture. Nitrate was 27 μM at 62°S, 22 μM at the Polar Front (52°S) and 20 μM a few degrees south of the Subtropical Convergence (41°S). Silica, on the other hand, was high (57 μM) at 67°S and it decreased sharply to 15 μM at 60°S, and dropped to low values (approximately 1 μM) just north of the Polar Front, reflecting its assimilation and polymerization by diatoms and silicoflagellates. The significance of these data and the degree to which nutrient depletion can occur in the waters of the Southern Ocean will be considered in detail in Chapter 2 (Figure 1.10).

2 Phytoplankton and Primary Production

CONTENTS

2.1 INTRODUCTION

Organisms in the plankton are generally assigned to one of three compartmental groups: bacterioplankton, phytoplankton, and zooplankton. These groups are further subdivided into trophic groups on the basis of taxonomic categories well above the species level. Unfortunately, this causes organisms with differing modes of nutrition to be grouped together, e.g., non-photosynthetic flagellates are grouped with the algae and are considered to be phytoplankton, while other protozoan groups like ciliates and sarcodinians are assigned to the zooplankton as microplankton. To overcome these and other problems, Siebruth et al. (1978) proposed a scheme based on the level of organization, i.e., the ultrastructure, and the mode of nutrition (Figure 2.1).

The heterotrophic organisms fall into five major compartments: viroplankton (viruses), bacterioplankton (free-living bacteria); mycoplankton (fungi); protozooplankton (apochloritic flagellates, amoeboid forms, and ciliates); and the metazooplankton (the multicellular ingesting forms). The metazooplankton range in size from the mesozooplankton through the macrozooplankton to the megaplankton. The mesozooplankton consist mainly of copepods, while the macrozooplankton comprise mainly the larger crustaceans such as mysids and euphausiids. Juvenile stages of the latter, however, fall within the mesozooplankton size range. The megazooplankton comprise the larger drifting forms, including coelenterates and appendicularians.

The protozooplankton, mycoplankton, and phytoplankton are unicellular eucaryotes and fall into three size groups: picoplankton (<2.0 µm), nanoplankton (2.0–20 µm), and microplankton (20–300 µm). The bacterioplankton compartment consists of unattached unicellular bacteria, which can be selectively filtered with 0.1 and 1.0 µm porosity filters. In the scheme depicted in Figure 2.1, the heterotrophic components of the plankton have been reassigned to more discrete taxonomic

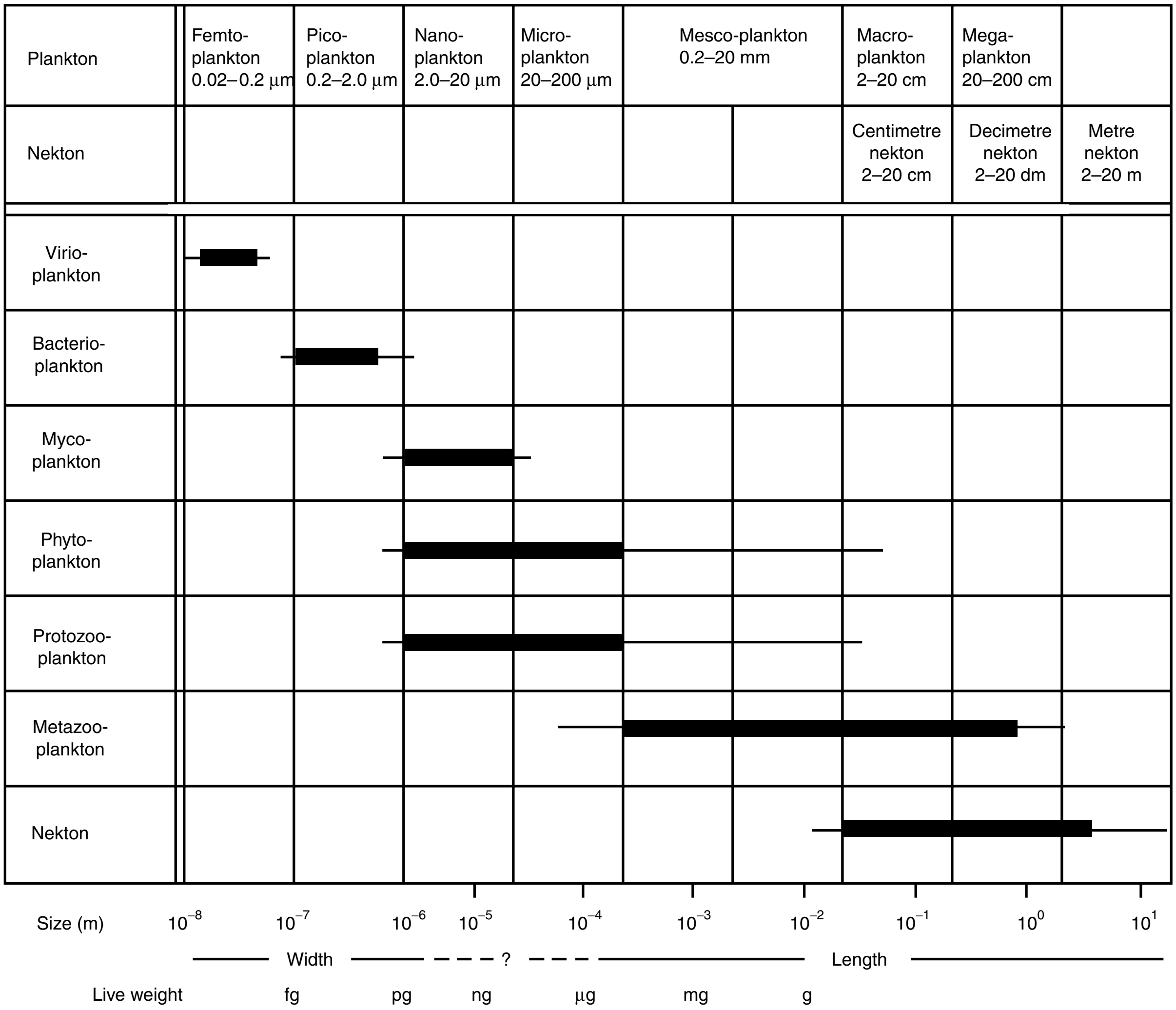


FIGURE 2.1 Distribution of different taxonomic-trophic compartments of plankton in a spectrum of size fractions, in comparison with a size range of nekton. (From Siebruth, J. McN, Smetacek, V., Lenza, J., *Limnol. Oceanogr.*, 23, 1256, 1978. With permission.)

groupings; the size groupings are redefined to include expanded ranges. These size groupings are indicative of the organisms' growth and metabolic rates, which are generally a function of size (Ikeda 1970; Sheldon et al. 1972). Figure 2.1 shows that there is little overlap between the size categories and compartmental groups of plankton organisms, with the exception of the phytoplankton and protozooplankton, which occupy the same size categories. These, however, are distinguished by the presence or absence of chlorophyll, although it has now been shown that many chlorophyll-containing flagellates and ciliates are mixotrophic, i.e., capable of ingesting phytoplankton (see Chapter 14).

2.2 DATA BASE

The study of marine phytoplankton in the Southern Ocean dates back over a century and a half, to when J. D. Hooker, the noted botanist and surgeon of the HMS *Erebus* and HMS *Terror* expedition under James Clark Ross (1839–1943), reported the ubiquitous presence of diatoms during the Antarctic summer: "They occurred is such countless myriads, as to stain the Berg and the Pack-Ice…. They imparted to the Brash and Pancake-Ice a pale ochreous color" (Hooker 1847). Hooker sent some of the samples collected between Cape Horn and the Ross Sea to the German botanist Ehrenberg, who published the first paper on Antarctic diatoms in 1844.

The distribution, productivity, and ecology of the phytoplankton in the Southern Ocean have been reviewed by many scholars, including El-Sayed (1968a, 1968b, 1968c, 1970a, 1970b, 1971c, 1978, 1984, 1985, 1987, 1988a, 1988b, 1996), El-Sayed et al. (1979, 1983), El-Sayed and Turner (1977), El-Sayed and Weber (1986), Heywood and Whitaker (1984), Sakshaug and Holm-Hansen (1984), Priddle et al. (1986a, 1986b), Jacques (1989), Medlin and Priddle (1990), Sakshaug and Slagstad (1991), Sullivan et al. (1993), Mathot et al.(1992), Dower et al. (1996), Smith et al. (1996), Park et al. (1999), and Di Tuillo et al. (2003). Despite the large amount of data collected over the past two decades, both the geographic and temporal coverage are rather sparse, due to the vastness of the Southern Ocean. Observations of the standing crop and productivity have largely been dictated by logistics and the workload of research vessels, rather than by sampling designed to answer questions concerning the ecology of the flora. The majority of expeditions have been limited to the austral spring and summer; autumn and winter observations have been somewhat limited, although in recent years there have been a number of expeditions undertaken to sample winter conditions. In addition, methods and techniques have been modified over the past three decades, making it difficult to compare more recent data with those of earlier decades. These limitations must be kept in mind when discussing the phytoplankton of the Southern Ocean.

2.3 SPECIES COMPOSITION AND DISTRIBUTION

2.3.1 Net Phytoplankton (Microplankton)

The net phytoplankton group is generally dominated by diatoms, and diatom blooms generally contain several species. Around South Georgia, for instance, the diatom community comprised dense growths of *Thalassiosira scotia* and *Chaetoceros socialis*, or *Euchampia antarctica* with *Odontella weisflogii, Rhizosolenia* and *Proboscia* spp., *Corethron* spp. (Figure 2.2) and *Thalassiosira* (see Priddle 1990). A very dense bloom of diatoms near King George Island, of the South Shetland Islands chain, contained *Odontella weisflogii, Proboscia alata, Chaaetoceros curvisetum*, and *Thalasssiosira tumida* (Heywood and Priddle 1987). This predominance of colonial and chain-forming taxa appears to be typical of many regions of the Southern Ocean, although other species may dominate under certain conditions.

Other important species are the dinoflagellates and silicoflagellates. Over 100 species of diatoms and some 60 species of dinoflagellates have been found in Antarctic waters. While most of the diatom species are cosmopolitan, Hasle (1969) lists three species that have distributions limited to the Antarctic zone and 20 diatom taxa that are restricted to the southernmost part of the Antarctic zone. Endemism in the net phytoplankton appears to be high, but

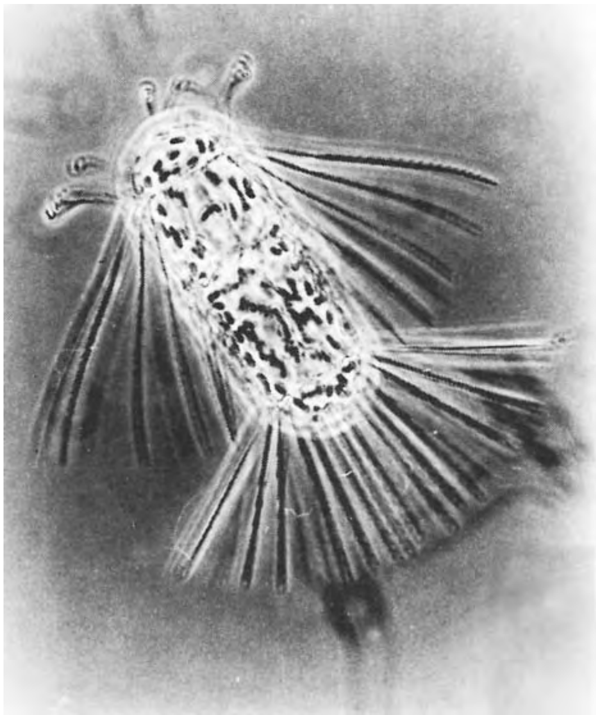


FIGURE 2.2 *Corethron criophilum*, a common Southern Ocean diatom. (Photograph courtesy of Dr. Greta Fryxell, Department of Oceanography, Texas A&M University, College Station, Texas. With permission.)

early work by Hart (1934, 1942) indicates that most of the species are circumpolar in their distribution (Baker 1954). Fryxell and Hasle (1979) came to similar conclusions about the *Thalassiosira* species.

Little is known about the distribution and abundance of dinoflagellates in the waters of the Southern Ocean, and their contribution to phytoplankton biomass has probably been underestimated (El-Sayed 1985). The most important species belong to a few thecate genera (those enclosed in cellulose plates), chiefly the genera *Protoperidium* and *Dinophysis*. The genus *Ceratium*, which is common in other oceans, is absent south of the Antarctic Convergence. Some 15 species of naked, or thin-walled, dinoflagellates have been recorded (Balech 1975), but it is probably false to assume that these species are rare, since they do not preserve well. Endemism here is higher (80–85%) than in any other oceanic region.

Of the other algal groups, the *Phaeocystis Antarctica*, the unicellular motile and colonial brown-yellow prymnesiophyte belonging to the order Prymnesiales, can be exceedingly abundant. It is one of the few marine phytoplankton species that exhibits a life-cycle alternation between free-living flagellated zoospores and a gelatinous colonial aggregation of non-motile cells. It occurs prominently in the plankton in this latter stage, containing hundreds of thousands of 3–8 μm cells in colonies that can exceed 10 mm in diameter. In the colonial form, this species can produce very dense gelatinous blooms which are characteristic of the marginal ice zone and shelf waters, especially in polynas. The dominance of *Phaeocystis* along the southeast coast of the Weddell Sea both before and when the ice melts has been noted by a number of investigators (Hayes et al. 1984; von Brockel 1985; Boltovoskoy et al. 1988).

Silicoflagellates are unicellular chrysophycean algae with an internal skeleton of conspicuous siliceous tubes. Only one species, *Dictyota (Distephanas) speculum*, is common in Antarctic waters, where it may sometimes outnumber any of the diatom species (Figure 2.3).

2.3.2 NANOPLANKTON

It is only relatively recently that attention has been paid to the role of nanophytoplankton (greater than 2.0 μm and less than 20 μm) in the waters of the Southern Ocean. This was because most of the early investigations of phytoplankton were based on samples obtained with phytoplankton nets (usually about 35 μm mesh), which had led to the view that the flora were dominated by relatively large-volume diatoms (Hart 1934, 1942; Hasle 1969; Nemoto and Harrison 1981). However, in water samples from the Weddell and Scotia Seas, Holm-Hansen and Forster (1981) found that the nanophytoplankton generally accounted for 25–75% of the total estimated phytoplankton carbon. These percentages are in agreement with those found by other investigators: Fay (1973), 69–85%; El-Sayed (1971b), 38–87%; El-Sayed and Taguchi (1981), 64–80%; Koike et al. (1981), 97%; Yamaguchi and Shibata (1982), 54%; Ronner et al. (1983), 45%; Sasaki (1984), 43%; Weber (1984), 64%; Kosaka et al. (1985), 64%; Lipski (1985), 65%; Weber and El-Sayed (1986a), 47%; Weber and El-Sayed (1986b), 64–78%. The average percentage for these widely distributed localities is 66%. In Arthur Harbour, Anvers Island, Heinbokel and Coats (1985) found that in December and January between 47 and 75% of the total chlorophyll *a* passed through a 10 μm mesh, and as much as 49% passed through a 5 μm nucleopore filter. At Elephant Island during the 1984–1985 austral summer, the contribution of the less than 20 μm size fraction was 76% (the picophytoplankton fraction was not measured) (El-Sayed and Weber (196). The proportion was somewhat higher (83%) in the surface waters than in the deeper samples (68%). The *Africana* samples showed a lower mean contribution to the total chlorophyll *a* from cells less than 20 μm of 47% (range 29–84%). In contrast to the Elephant Island samples, the contribution of the nanophytoplankton increased with depth, averaging 37% at the surface and 62% at 150 m deep. Gieskes and Elbrachter (1986), in samples taken during a cruise in the Antarctic Peninsula region, found that between 8 and 80% of the chlorophyll *a* containing particles were smaller than 8 μm. In a study of the seasonal variation of phytoplankton and sea ice microalgae off of Davis Station, Perrin et al. (1987) found that for most of the year the nanophytoplankton accounted for the major part of the chlorophyll in the water column; this was particularly the case during the winter, when it sometimes approached 100% of the total chlorophyll *a* (Figure 2.4). Only during blooms of *Phaeocystis Antarctica* and large diatoms did the relative contribution of the nanophytoplankton decrease.

The principal components of the nanophytoplankton are (a) small diatoms (5–10 μm), e.g., *Chaetoceros neglectus* and *Nitzschia curta*, which at times can contribute up to 50% of the total phytoplankton cells (Brandini and Kutner 1997) in oceanic areas; and (b) pyrmnesiophytes, cryptomonads, and other green flagellates (e.g., *Prochlorococcus, Synechoccus)*, and cyanobacteria, which may dominate under certain conditions (Gieskes and Elbrachter 1986; Jacques and Panouse 1991).

According to Nishida (1986), the majority of the nanophytoplankton are composed of unicellular flagella-bearing organisms that have calcareous or siliceous skeletal elements. Nishida identified four nanophytoplankton assemblages in the Southern Ocean between Australia and the Antarctica continent: subtropical, Sub-Antarctic, Antarctic, and circum Antarctica pack ice assemblages. The first three assemblages were composed mainly of calcareous nanophytoplankton dominated by species of Coccolithophyceae; the fourth assemblage was dominated by dense populations of a single siliceous species, *Eumiliana huxylei*. The maximum number of individuals recorded was ca 226×10^3 individuals 1^{-1} at 100 m depth in the circum-Antarctic pack ice zone.

Siliceous cysts in the size range of. 2.0–5.5 μm are important components of the nanophytoplankton of the Southern Ocean. Early research suggested that these may be cysts in the life cycle of choanoflagellates. However, Marchant and McEldowney (1986) have concluded from the study of living cells that these contain chlorophyll. This was

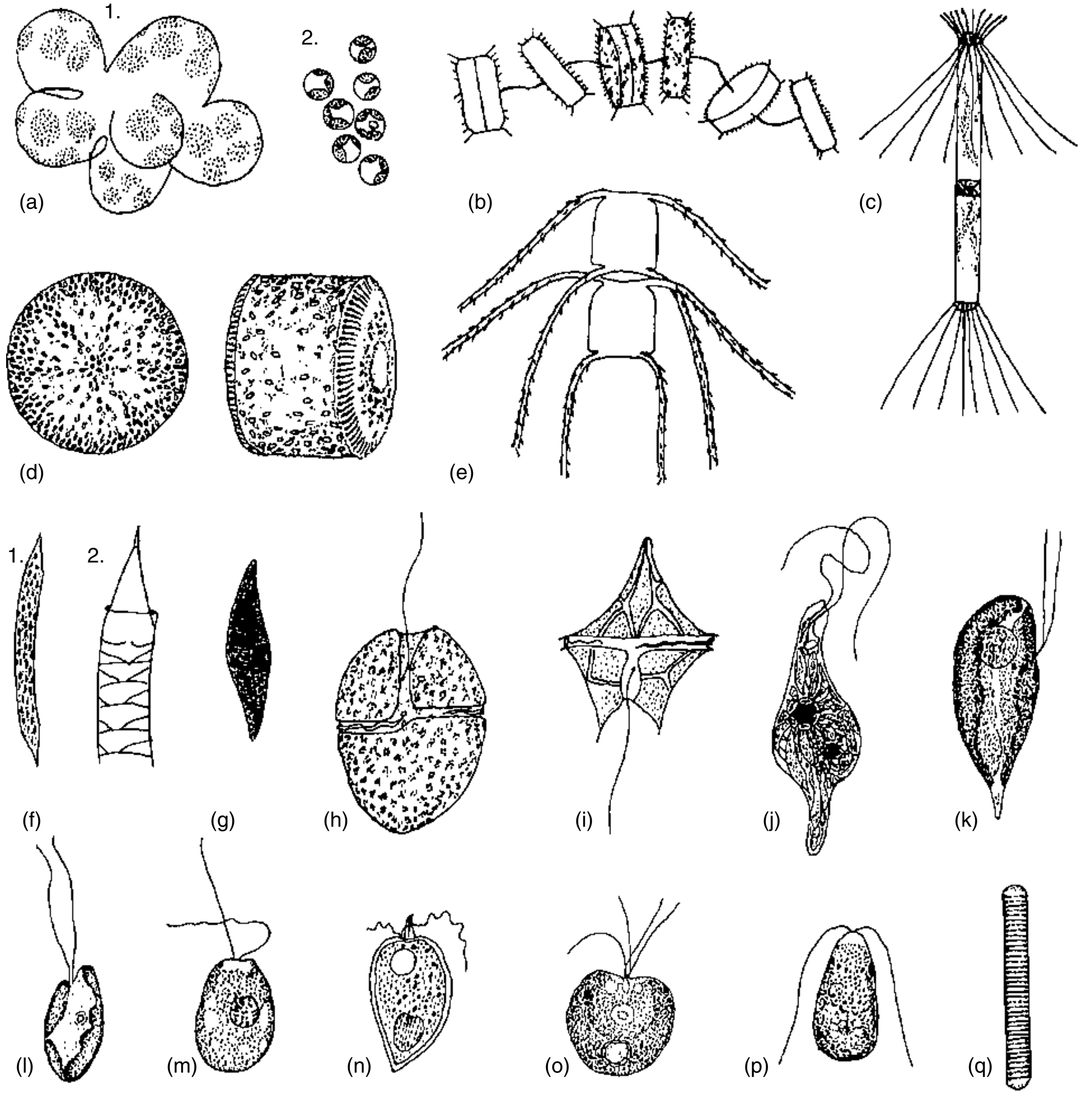


FIGURE 2.3 Some characteristic phytoplankton species: (a)–(g) microplankton species; (j)–(q) nanoplankton species. (a) *Phaeocystis Antarctica* (Pyremnesiophyte), (1) colony, (2) individual cells. (b)–(g): diatoms. (b) *Thalassiosira gravida*; (c) *Corethron criophyllum*; (d) *Coscinodiscus* sp.; (e) *Chaetoceros criophyllum*; (f) *Rhizosolenia curvata*, (1) whole cell, (2) cell apex; (g) *Pleurosigma* sp. (h)–(i) dinoflagellates: (h) *Gymnodinium* sp.; (i) *Peridinium* sp. (j)–(p) flagellates: (j) *Eutreptia* sp. (Euglenophyceae); (k) *Cryptomonas* sp. (Cryptophyceae); (l) *Rhodomonas* sp. (Cryptophyceae); (m) *Pleuromonas* sp. (Desmophyceae); (n) *Procentron* sp. (Desmophyceae); (o) *Pyramimonas* sp. (Prasinophyceae); (p) *Chlorella*-like flagellate (Chlorophyceae); (q) *Nitzschia cylindrica* (diatom).

confirmed by transmission electron microscope studies that showed the presence of chlorophyll.

Dubreuil et al. (2003) investigated the distribution of the nanophytoplankton in three different subsystems belonging to the Antarctic Circumpolar Current in the vicinity of the Kerguelen Islands: the Subtropical Zone (STZ), the Convergence Zone, and the Polar Frontal Zone (PFZ). A strong contrast was observed in the nanophytoplankton composition and vertical distribution between the three zones. The oligotrophic waters of the STZ were characterized by the dominance of cyanobacteria, with *Prochlorococcus* exhibiting the highest concentration (up to 150×10^3 cell cm^{-3}), while *Synechococcus* had a maximum integrated abundance of $218\text{–}287 \times 10^{10}$ cells m^{-3}. The absence of *Prochlorococcus* south of the PF is in agreement with previous studies, e.g., Fiala et al. (2003). Temperature is

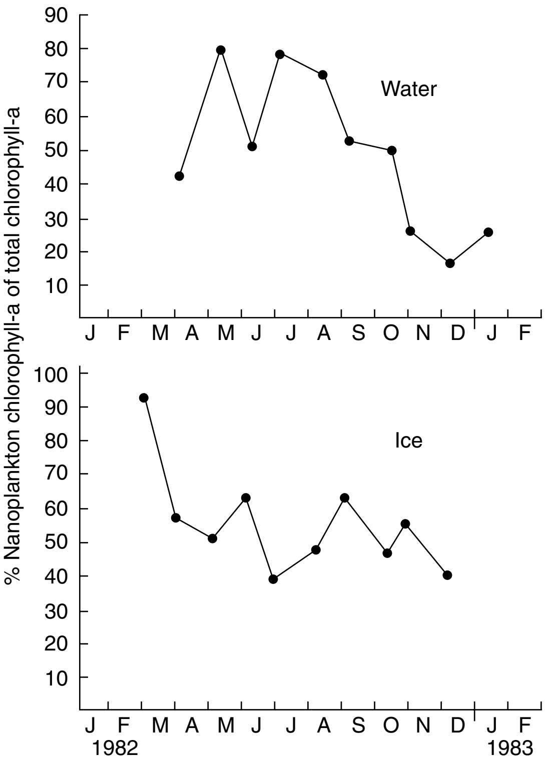


FIGURE 2.4 Contribution of nanoplankton to total chlorophyll *a* in (a) the seawater and (b) the sea ice 1 km offshore of Davis Station (68°35′S 77°50′E). (From Perrin, R.A., Lu, R., Marchant, J., *Hydrobiolobia*, 146, 17, 1987. With permission.)

considered to be the main factor determining its absence (Cavender-Bares et al. 2001).

The Polar Frontal Zone was characterized by the dominance of picoeucharyotes (<3 μm). *Synechococcus* integrated abundance was 30 times lower in the PFZ cold water (<10°C) than in the STZ, where the temperature was >15°C. Between the Agulhas Front and the Subtropical Front, all integrated values were lower than in the subtropical waters. In the STZ, the absence of wind stabilized the water column, favoring the development of cyanobacteria within the entire surface layer. In contrast, in the PFZ, there was a strong wind generating much turbulence within the upper surface layer, resulting in the concentration of picoeukaryptes and *Synechococcus* at the thermocline.

Burma et al. (1992) investigated the abundance of Chryptophyceae and chlorophyll *b*-containing nanophytoplankton in the Weddell-Scotia Confluence area in the spring. The highest cryptophyte biomass was found along the retreating ice edge; the contribution of cryptophytes increased over time, reaching monospecific bloom conditions at the end of the investigation. Chlorophyll *b*-continuing organisms and Prymnesiophyceae were present everywhere, and they dominated the ice-covered part of the survey area. They were mainly represented by *Phaeocystis* (colonies and flagellates), and species of *Chrysochromulina*, Coccolithophorids, mainly in the size fraction <5 μm, were found to be a characteristic component of the phytoplankton in most areas, with the most dominant species being *Trigonaspis melvillea* and *Wigwamma Antarctica*. North of the Scotia Front where pyremnesiophytes and diatoms dominated, the coccolithophorid *Emilainia huxlyi* and *Phaeocystis* flagellates were the most abundant pyremnesiophytes. Green algae were very common, with *Pyramimonas* cf. *garlestonae* (Prasinophyceae) abundant.

2.3.3 PICOPHYTOPLANKTON

Attention has also only recently been focused on the significance in the world's oceans of the photosynthetic picoplankton, those chlorophyll-containing organisms that are less than 2.0 μm in size (see Li et al. 1983; Takahashi and Beinfang 1983; Platt et al. 1993). There are, however, a limited number of studies on the role of picophytoplankton in the Southern Ocean (see Hewes et al. 1983,1985; Sasaki 1984; Probyn and Painting 1985; El-Sayed and Weber 1986; Heinbokel and Coats 1986; Brandini and Kutner 1987a; Weber and El-Sayed 1987; Jacques and Panouse 1991). In their study of the size fractionation of phytoplankton in the southwestern Drake Passage and Bransfield Strait, El-Sayed and Weber (1986) found that the picophytoplankton contribution to the photoautotrophic biomass varied considerably from station to station, ranging from 3 to 70%, with a mean of 40%. Hosaka and Nemoto (1986) reported that the chlorophyll *a* in the <1 μm size fraction accounted for 18% of the total in the sub-Antarctic Pacific. In contrast, in the western Indian Ocean sector south of 60° S, the picophytoplankton biomass was much lower, ranging from 7 to 43%, with a mean of 14%. According to Kosaka et al. (1985), the relative abundance of phytoplankton in the size range of 0.2–1.0 μm in the Southern Ocean is low in comparison to tropical and subtropical seas.

In an investigation of picoplankton biomass in the Ross Sea, Acosta Pomar et al. (1993) found that picoplankton (both autotrophic and heterotrophic) having a cellular diameter of between 1.0 and 2.0 μm (PP1) generally predominate, accounting for 73% of the whole picoplankton biomass. However, smaller cells (PP2) could represent 28% of the picoplankton biomass.

Prominent among the picophytoplankton are phycoerythrin-rich chrococcoid cycanobacteria 90.8 to 1.4 μm in diameter, either in coastal (Marchant et al. 1987) or oceanic areas; the most commonly reported eucaryote is a *Chorella*-like green flagellate. Although representatives of other algal groups have been reported as members of the picophytoplankton community, their taxonomy has been little studied in Antarctic waters.

2.3.4 *PHAEOCYSTIS*

Blooms of the colonial haplophyte *Phaeocystis Antarctica* (previously known as *P. pouchetii*) are a common feature of the phytoplankton dynamics of Antarctic coastal waters. The Ross Sea polyna is the site of the most spatially extensive phytoplankton bloom in the entire Southern Ocean (Sullivan et al. 1993; Arrigo and McClain 1994; Smith and Gordon 1997; Smith et al. 1996, 1990; Di Tuillo et al. 2003), and pigments of ca 25 μg l^{-1} have been measured at the time of the bloom maximum. The bloom forms early in the season, and peak biomass and production are reached by mid- to late December, soon after the ice completely melts or is advected to the north. The bloom decreases in extent and magnitude throughout January, and in February chlorophyll levels are approximately 1 μg l^{-1} or less (Arrigo and McClain 1994; Smith et al. 1996). The processes responsible for the bloom's decline are unknown, although active grazing and sinking of colonies and aggregates derived from *Phaeocystis* have been suggested to be quantitatively important loss processes from surface waters.

While particulate carbon concentrations increase by more than an order of magnitude within the *Phaeocystis* bloom, integrated stocks of dissolved organic carbon (DOC) levels change only slightly (Carlson et al. 1998). The limited DOC accumulation is surprising when compared to other systems. For example, *Phaeocystis* blooms in the North Sea generate large amounts of dissolved organic material, which ultimately result in the large accumulations of emulsions that appear on European beaches after the bloom (Lancelot et al. 1998). *Phaeocystis* also generates a substantial amount of extracellular polysaccharide mucus in its colonial matrix, and it has been suggested that large amounts of this material ultimately enter the DOC pool. *Phaeocystis* blooms are also a feature of ice-edge blooms (see Chapter 15, Section 3.6).

Phaeocystis blooms are also of importance as producers of dimethylsulphide (DMS). DMS emission from the ocean is the largest source of reduced sulfur to the atmosphere (Bates et al. 1987) and is estimated to be approximately $0.6–1.6\times10^{12}$ mol yr^{-1} (Andreae 1990). DMS is theorized to play a role in global thermoregulation through the creation of clouds over oceanic areas. DMS molecules produced in the ocean are oxidized in the atmosphere to sulfate and act as condensation nuclei for water vapor, causing cloud formation. Cloud reflectivity is a factor in the earth's albedo, regulating the amount of sunlight that is reflected into space from the earth.

Crocker et al. (1995) investigated DMS fluxes into the atmosphere in a *Phaeocystis* spp. spring bloom (Bigidare et al. 1995) to determine the relationships between pigment concentrations, ultraviolet light, and DMS production. The mean flux of DMS from this bloom into the atmosphere was calculated to be 67 ± 55 μmol m^{-2} day^{-1}, which yields a flux of 1.3×10^{6} μmol DMS day^{-1}. It is thus clear that *Phaeocystis* blooms in Antarctic seas are a major source of DMS to the atmosphere.

2.3.5 PHYTOPLANKTON COMMUNITY COMPOSITION AND SIZE STRUCTURE

As will be discussed in detail in the next section, different water masses in the Southern Ocean have differing degrees of dominance of the various groups of phytoplankton. Suskin (1985) in a review of the phytoplankton communities of the Atlantic sector of the Southern Ocean noted that while the Antarctic Circumpolar Current was dominated by diatoms, in the Weddell Sea the predominant species were *peridinidae, coccolithophorids*, and *silicoflagellates*. In the southwest Indian Ocean, between Africa and the Antarctic continent, Kopczynska et al. (1986) found that diatoms dominated in the net phytoplankton, with numbers generally increasing southward with peaks of abundance in the northern Antarctic zone and south of the Polar Front. Dinoflagellates, flagellates, and "monads" occurred in the highest concentration north of the Polar Front, with their numbers somewhat reduced toward the south.

The proportions of the various size classes of the phytoplankton not only vary geographically but also seasonally and with depth. For the Southern Ocean south of Australia, Yamaguchi and Shibata (1982) found that the mean percentage contribution of the nano- (<10 μm micro- (10–60 μm) and net-phytoplankton (>60 μm) to the total standing stock of chlorophyll *a* in the upper 200 m were 52.6, 25.2, and 22.3%, respectively. Sasaki (1984) in the Indian Ocean sector found that the mean contribution of the microphytoplankton (>10 μm) in the Subtropical, sub-Antarctic, and Antarctic zones in December were 24.1, 64.8 and 68.9%, respectively.

In their study on the composition, abundance, and distribution of the phytoplankton in the northwest Weddell Sea, Kang and Fryxell (1993) found over 70 species. The highest number of total cells (integrated through the top 150 m) were found in open water, well separated from and to the east of the ice edge with 6.10×10^{10} cells m^{-2}. The relative abundance of the diatoms was low at ice-covered stations ($<35\%$ of the total phytoplankton) and high at open-water stations ($>80\%$); however, the relative abundance of the pyremnesophyte *Phaeocystis Antarctica* was high at ice-covered stations ($>60\%$) and low at open-water stations ($<16\%$). In the open ocean, the dominants were the pennate diatoms *Fragilariopsis cylindricua, Pseudonitzschia prolongatoides, F. curta*, and a small form of the centric diatom *Chaetoceros dichaeta* in chains.

Bracher (1999) has recently reviewed the composition and distribution of phytoplankton communities in the Southern Ocean. Blooms that are typically observed in the vicinity of fronts and in the Marginal Sea Ice Zone (MIZ) tend to be dominated by microphytoplankton (>20 μm), as opposed to areas between fronts, where mainly nanophytoplankton (<20 μm) form the community (Holm-Hansen and Mitchell 1991; Laubscher et al. 1993; Bracher 1999) (Figure 2.5). Only in early summer are the microphytoplankton consistently the major component of the frontal blooms. In late summer (March), the phytoplankton community at the Polar Front is mainly formed by nanophytoplankton, with major microphytoplankton blooms only encountered south of the Polar Front, where silicate levels exceed 20 μm.

The microphytoplankton that form the Southern Ocean blooms consist of large-celled and colonial diatoms (e.g., El-Sayed and Taguchi 1981; Jacques 1983;

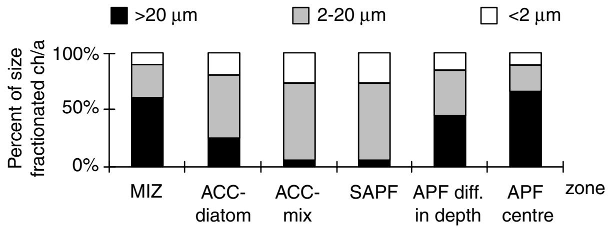


FIGURE 2.5 Size fractionated (>20 µm, 2–20 µm and <2 µm) Chl *a* concentration within the euphotic zone, where SAPF = stations within the ACC, but south of the APF, APF diff (different in depth) = APF stations, where P_m^* 1% light depth $>P_m^*$ surface, ACC diatom stations close to the ice edge with a high proportion of diatoms in the phytoplankton community, and ACC mix = ACC stations with equal contributions of phytoplankton groups in the community. MIZ, Marginal Ice Zone; ACC, Antarctic Circumpolar Current; SAPF, South of the Antarctic Polar Front; APF, Antarctic Polar Front. (From Bracher, A.W., *Ber. Polarforsch*, 341, 38, 1999. With permission.)

von Brockel 1985; El-Sayed and Weber 1982; Heywood and Priddle 1987; Bianchi et al. 1992; Crawford 1995; Savidge et al. 1995; Bracher et al. 1999). Blooms formed by *Phaeocystis* colonies are often observed in the coastal and continental shelf zone (CCSZ), especially in the Ross Sea (Palmisano et al. 1985c; SooHoo et al. 1987; Carrada et al. 1999; Vanucci and Bruni 1998; Saggiomo et al. 2000), and in the Weddell Sea (Hayes et al. 1984; Nothig 1985). They also often form the second period of MIZ blooms (Hart 1942; El-Sayed 1984; Garrison et al. 1984; Fryxell 1989; Smetacek et al. 1990; Jacques and Panouse 1991; Stoeckner et al. 1995; Bracher et al. 1999) (Figure 2.5 and Figure 2.6). The second period of blooms at fronts north of the Polar Front are formed by nanophytoplankton (Laubscher et al. 1993).

It is thus clear that the phytoplankton communities characteristic of frontal zones and water masses have distinctive species composition and size distributions. However, the species composition and size distributions change over time as a result of a number of chemical and biological factors, including vertical stability of the water column, light limitation in well-mixed waters, grazing, and the availability of nutrients.

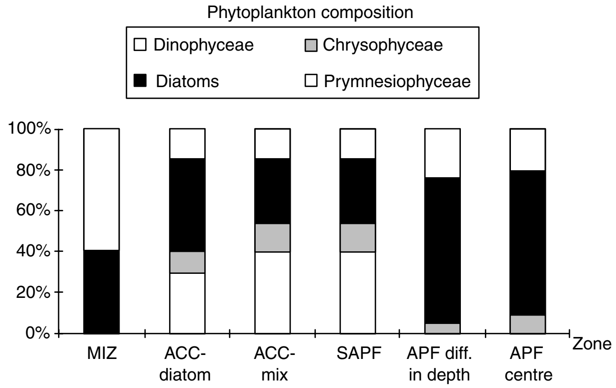


FIGURE 2.6 Phytoplankton composition within the different areas listed in Figure 2.5. (From Bracher, A.W., *Ber. Polarforsch*, 341, 39, 1999. With permission.)

2.4 LATITUDINAL ZONATION OF THE PLANKTONIC SUBSYSTEMS

2.4.1 Introduction

Table 2.1 compares the various relative factors operating in tropical and polar planktonic systems. Polar systems are characterized by high diatom abundance and low cyanobacteria and prochlorophytes. Other differences are marked. A pronounced difference is the effect of seasonality, which is marked in polar regions. This results in phytoplankton growth vertical fluxes from the surface layer and food web processes varying more on a seasonal cycle than on daily or annual cycles. At the low temperatures found in the Antarctic, a large temporal lag often exists between phytoplankton and mesozooplankton, which can allow the phytoplankton biomass to increase substantially (Cushing 1981). However, physical controls (e.g., limitation by available irradiance, either via seasonal variation in solar angle, vertical mixing by winds, or convection driven by ice formation, or simple presence of ice and snow as significant attenuators) are at times and places critical in the Southern Ocean, and the initiation of the blooms in spring is largely under physical control (Lancelot et al. 1998). Individual taxa vary along a north–south gradient. The Southern Ocean, particularly south of the Polar Front, is often dominated by heavily salicified diatoms, but locally and regionally large contributions of haptophytes, chrystophytes, and dinoflagellates often occur.

TABLE 2.1
Comparison Between Tropical and Polar Regions of Various Relative Factors Operating in Each System

Factor	Tropical Regions	Polar Regions
Temperature	High	Low
Seasonality	Low	High
Biological control of phytoplankton	High	Low
Maximum phytoplankton biomass	Low	High
Vertical export	Low	High
f-ratio	Low	High
Ambient macronutrient concentrations	Low	High
Abundance of diatoms	Low	Often high
Abundance of cyanobacteria and prochlorophytes	High	Low
Main source of iron	Atmospheric	Upwelling
Irradiance limitation	Rare	Frequent

Source: From Smith, W.O., Lancelot, C., *Ant. Sci.*, 16, 532, 2004. With permission.

Tréguer and Jacques (1992) have reviewed the latitudinal zonation pattern of the various plankton subsystems of the Southern Ocean. This zonation is marked by the presence of a number of frontal systems, as discussed in Chapter 1, Section 6.1. These frontal systems demarcate more or less concentric zones (Figure 2.7): the Antarctic Divergence (AD), the Seasonal Pack Ice Zone (SIZ) with its winter and summer limits, the Polar Frontal Zone (PFZ), the Subantarctic Convergence (SAC), and the Subtropical Convergence (STC). The main effects of the underwater topography on the localization of the fronts generate sharp nutrient gradients (e.g., Simon and Sarano 1978) as well as chlorophyll peaks at the shelf breaks (Hayes et al. 1984).

This zonal pattern is interrupted by two factors: (1) the presence of large embayments in the Ross Sea, Weddell Sea, and Prydz Bay, which may penetrate to 80°S and retain a part of the pack ice during the whole summer; and (2) a constriction between South America and the Antarctic Peninsula (Drake Passage).

As suggested by Tréguer and van Bennekom (1991), four major subsystems, excluding the Permanent Ice Zone, are to be considered south of the Polar Front (Figure 2.7): the Polar Frontal Zone (PFZ), the Permanently Open Zone (POOZ), the Seasonal Sea Ice Zone (SIZ), and the Coastal and Continental Shelf Zone (CCSZ). These subsystems are characterized by physical parameters, nutrient regimes, level and nature of primary production (including *f*-ratios), and the reaction of the first level to the upper trophic levels.

2.4.2 THE POLAR FRONTAL ZONE

Characteristic of this zone are the presence of strong ergoclines, sharp nutrient gradients (except for silicate with concentrations lower than 10 µm), and numerous mesoscale eddies (Park et al. 1991). Little is known about the striking features of the food web of this zone, however, the area is believed to be photosynthetically productive as attested by biomass accumulations in surface layers

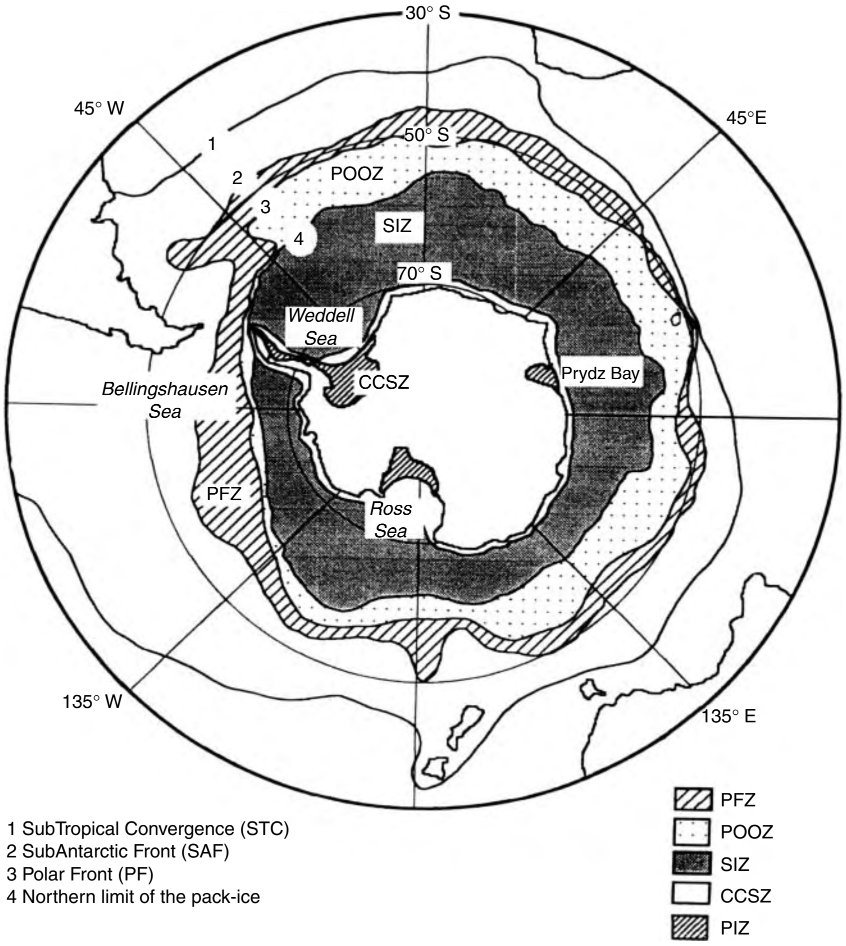


FIGURE 2.7 The four main subsystems in the Southern Ocean; frontal zones, and limits in surface waters. Permanent-ice zone (*hatched zone*); shelf break (*continuous line*); *!*. Subtropical Convergence; *PFZ* (Polar Frontal Zone) between *2* and *3*; *POOZ* (Permanently Open Ocean Zone) between *3* and *4*; *SIZ* (Sea Ice Zone), between *4* and the shelf break; *CCSZ* (Continental Shelf Zone), ice-free part of the continental shelf. (From Tréguer, P., Jacques, G., *Polar Biol.*, 12, 150, 1992. With permission.)

(Tréguer and van Bennekom 1991) and by silica-rich abyssal deposits (Jones et al. 1990). Although ammonium concentrations are usually not as high in surface layers as they are for SIZ and POOZ, concentrations as high as 1 µm have been reported below the photic zone, indicating considerable heterotrophic activity. Sediment trap data (Wefer and Fischer 1991) for the Atlantic sector confirm that this subsystem is relatively productive (estimate of primary production: about 89 g C m^{-2} yr^{-1}) compared to the rest of the Southern Ocean (<40 g C m^{-2} yr^{-1}).

2.4.3 Seasonal Sea Ice Zone (SIZ) and Coastal and Continental Shelf Zone (CCSZ)

These areas are frequently referred to as the Marginal Ice Zone (MIZ), which is defined as delimiting the influence of the input of low density meltwater from the receding pack ice; it can extend 50–250 km from the ice edge. Sullivan et al. (1988) have identified the parameters controlling the growth and losses of phytoplankton from the MIZ ecosystem. These are mostly related to meteorological conditions and have lagrangian and eulerian components, respectively, along the vertical and horizontal axes. The lagrangian component evidences active growth and decay of phytoplankton at the ice edge occurring over a time scale of weeks; light and vertical stability control growth, while vertical mixing, advective processes, grazing and sinking control phytoplankton biomass losses. The eulerian component represents horizontal movements of the bloom while the ice edge is retreating, eventually over large geographic areas (>10° of latitude) and over a time scale of months. It has been established since the beginning of the last decade (El-Sayed and Taguchi 1981) that primary production in marginal ice zones is significantly higher than in the open ocean zone, at least by a factor of about 2 (Smith and Nelson 1985a). Processes in this Marginal Ice Zone will be discussed in detail in Chapter 13.

At the beginning of spring, these subsystems are nutrient rich; concentrations >20 µM of nitrate, >1.5 µM of phosphate, and >40 µM of silicate are often measured in these waters. During the summer, only the CCSZ exhibits nutrient exhaustion at the ice edge. Very intense blooms of pennate diatoms have been observed in the inner Ross Sea, where chlorophyll *a* reaches concentrations of 6 mg m^{-3}. Comparable data have been reported for other coastal regions such as the Antarctic Peninsula (Huntley et al. 1991). High ammonium concentrations have been measured in marginal in zones, where values can be as high as 2–3 µM at the base of the photic layer, being ascribable to heterotrophic activity, mainly of protozoa (Goeyens et al. 1995).

2.4.4 The Permanently Open Ocean Zone (POOZ)

Although nutrient rich, the POOZ has been identified as an almost "oligotrophic" area (Jacques 1989). It is different from the SIZ and CCSZ in at least two striking features. First is the typically well mixed, permanently ice-free system of the Antarctic Ocean, as opposed to the SIZ (Sullivan et al. 1988). The second feature is the presence of a silicate gradient, from less than 10 µM in the northern part to >50 µM near the northern border of the SIZ; this gradient even becomes a sharp silicate front, as is the case in the Scotia Front approaches (Jones et al. 1990).

Research in this zone has received less attention than the research in the other zones. Research in the Indian Ocean (Fukuchi 1980) confirmed the oligotrophic nature of this zone in terms of phytoplankton biomass: about half of the stations sampled showed chlorophyll *a* concentrations 0.25 mg m^{-3}, with only 5% surpassing 1 mg m^{-3}. Apart from the Scotia Sea (Ronner et al. 1983), phytoplankton blooms rarely occur. Nutrients are never reduced to limiting levels.

2.4.5 Some North–South Transects Across the Zones

2.4.5.1 Indian Ocean

Odate and Fukuchi (1995) sampled a series of stations from 35 to 65°S. The transect crossed three fronts: the Subtropical Convergence, the Subantarctic Front, and the Polar Front, which divided the area into four distinct zones: (1) the Antarctic Zone (ANZ), equivalent to the Permanently Open Oceanic Zone (POOZ) in the scheme outline above; (2) the Polar Frontal Zone (PFZ); (3) the Subantarctic Zone (SAZ); and (4) the Subtropical Zone (STZ) (Figure 2.8). The phytoplankton abundance and picophytoplankton community structure in each water mass are summarized as follows (Table 2.2):

1. *ANZ*. The bulk chlorophyll was low (0.30 ± 0.32 µg l^{-1}), although an uneven horizontal distribution occurred and the bulk chlorophyll maximum was found below surface (75–129 m). Percent contribution of the pico-chlorophyll was low (23 ± 11%). Cell density of cyanobacteria was extremely low ($0.04 \pm 0.035 \times 10^3$ ml^{-1}) and other picophytoplankton ($3.5 \times 1.8 \times 10^3$ cell ml^{-1}). Vertical profiles of bulk chlorophyll showed a prominent subsurface chlorophyll maximum.
2. *PFZ*. The bulk chlorophyll was 0.30 ± 0.12 µg l^{-1} and its maximum was at the surface. Contribution of the pico fraction was 43 ± 11%. Cyanobacterial density ($1.9 \pm 2.3 \times 10^3$ cells ml^{-1}) was less than other picophytoplankton ($15 \times 1.6 \times 10^3$ cells ml^{-1}). The highest bulk chlorophyll occurred in the surface waters.
3. *SAZ*. The bulk chlorophyll was most abundant among the four distinct zones (0.93 ± 0.24 g l^{-1}), and the contribution of the pico fraction was less than half (41 ± 2%). Cell density of cyanobacterial density ($49 \pm 12 \times 10^3$cells ml^{-1}) was more than other picophytoplankton ($15 \pm 1.6 \times 10^3$ cells ml^{-1}). A drastic

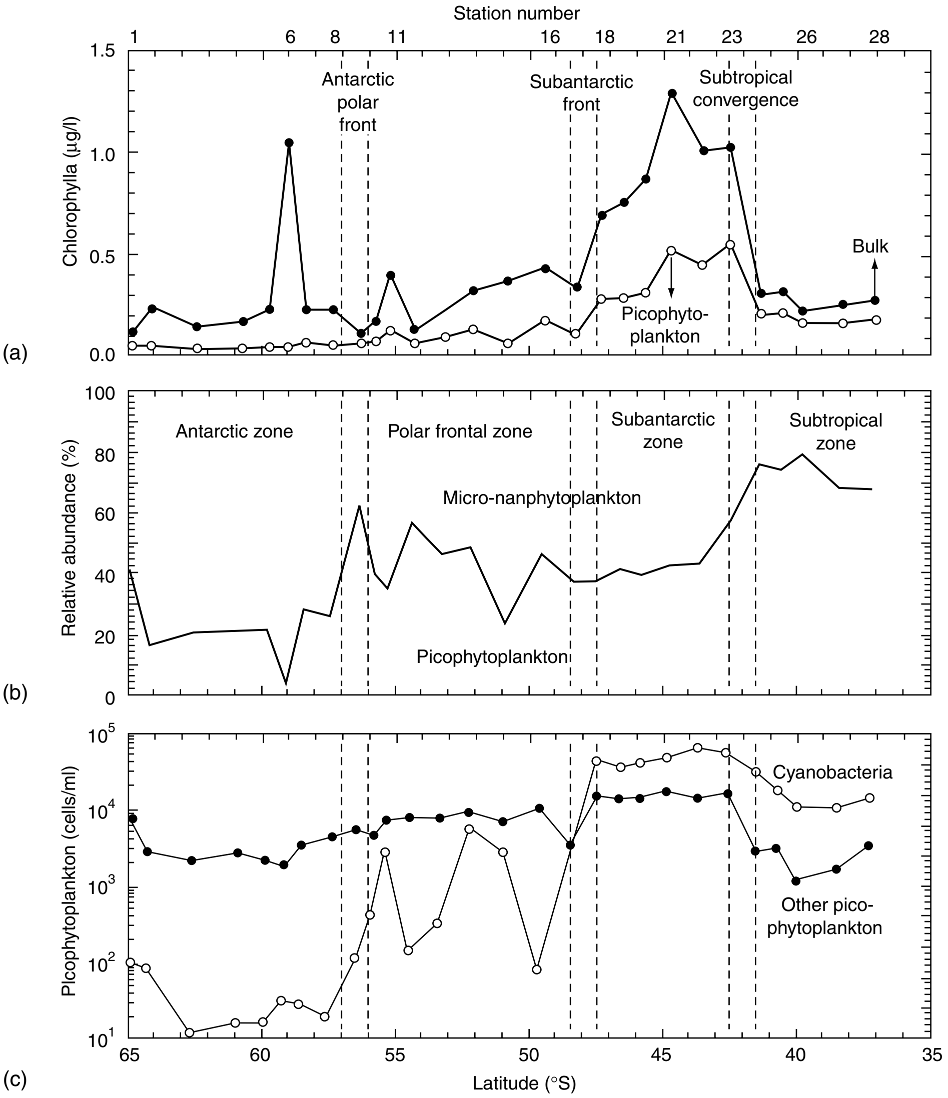


FIGURE 2.8 Surface distribution of chl *a* concentration in bulk (closed circles) and pico (open circles) fractions; (a) Percent contribution of the pico fraction; (b) Relative abundance of micro- nanophytoplankton; (c) Cell densities of cyanobacteria and other picophytoplankton. (From Odate, T., Fukuchi, M, *NIPR Symp. Polar Biol.*, 8, 90, 1995. With permission.)

TABLE 2.2
Summary of the Phytoplankton Abundance in the Surface Water along the Northward Cruise of *JARE* 33 (Mean Values (*1 SD*) shown)

Chlorophyll *a*			Phytotoplankton Cell Density			
Zone	**Bulk ($\mu g l^{-1}$)**	**Micro-Nano-phyto-Plankton ($\mu g l^{-1}$)**	**Pico-Plankton ($\mu g l^{-1}$)**	**Contribution of Pico-plankton (%)**	**Cyanobacteria ($\times 10^3$ cells l^{-1})**	**Other Phyto-plankton ($\times$ 10^3 cells l^{-1})**
Subtropical zone ($n=5$)	0.29 (0.04)	0.07 (0.02)	0.19 (0.03)	74 (5)	18 (9.1)	2.7 (1.1)
Subantarctic zone ($n=3$)	0.93 (0.24)	0.53 (0.12)	0.38 (0.11)	41 (2)	49 (12)	15 (1.6)
Polar frontal zone ($n=7$)	0.30 (0.12)	0.14 (0.06)	0.10 (0.04)	43 (11)	1.9 (2.3)	8.2 (1.9)
Antarctic zone ($n=8$)	0.30 (0.31)	0.24 (0.29)	0.04 (0.01)	24 (11)	0.041 (0.035)	3.5 (1.8)

Source: From Odate, T., Fukuchi, M., *NPIR Symp. Polar Biol.*, 8, 9, 1995. With permission.

change in the community structure of the picophytoplankton was found around the Subantarctic Front. The peak other picophytoplankton in the SAZ was two orders of magnitude higher than in the PFZ. The mean bulk chlorophyll was the highest among the water masses.

(4) *STZ*. The bulk chlorophyll was $0.29 \pm 0.04\ \mu g\ l^{-1}$, and the phytoplankton community was dominated by the pico fraction (74 ± 5%), in which the cyanobacteria was numerically more abundant ($18 \pm 9 \times 10^3$ cells ml^{-1}) than other picophytoplankton ($2.7 \pm 1.1 \times 10^3$ cells l^{-1}).

Mengesha et al. (1998) investigated the seasonal variation of the phytoplankton communities' structure and the nitrogen uptake regime along a transect at 63°E from 52 to 67°S. The transect passed through the Seasonal Sea Ice Zone (SIZ), the Permanently Open Ocean Zone (POOZ), and the Polar Frontal Zone (PFZ). While the study area can be considered to be oligotrophic (chl *a* stocks $< 59\ mg\ m^{-2}$), there was a large spatial variation of phytoplankton biomass and community structure.

The phytoplankton community in the SIZ showed higher biomass and was mainly composed of large diatom cells. However, in the POOZ the community had low biomass and was chiefly composed of nano- and picoflagellates. In the PFZ, although biomass was higher, the community structure was similar to that of the open-ocean zone. The results suggested that the variation in phytoplankton community on a larger scale structure resonates with gradients in water column stability and nutrient distribution.

Absolute nitrogen uptake rates were generally low, but their seasonal variations were highly significant. During the spring, the communities displayed high specific nitrate uptake (mean rate $= 0.0048\ h^{-1}$), and diatoms (in the SIZ) as well as nano- and picoflagellates in the POOZ and PFZ, were mainly based on new production (mean *f*-ratio = 0.69). The transition to summer was accompanied by a significant reduction in the nitrate uptake rate ($0.0071–0.0011\ h^{-1}$) and a shift from predominantly new to regenerated production (*f*-ratio 0.69 ± 0.39). Ammonium played a major role in the dynamics of phytoplankton nutrition. Despite a large contrast in community structure, the seasonal dynamics of the nitrogen uptake regime and phytoplankton community structure in all three subsystems were similar. Thus, the seasonal shift in nitrogen uptake regime can occur with, as well as without, marked changes in community structure.

2.4.5.2 South Pacific

DiTullo et al. (2003) investigated the distribution of phytoplankton pigments along a transect from 67° to the equator along 170°W (Figure 2.9). The transect crossed four fronts: the Subtropical Front, the Sub-Antarctic Front, the Polar Front, and the Southern Front, which divided the Antarctic Zone into AZ(n), equivalent to the Permanently Open Ocean Zone (POOZ), and the AZ(s), equivalent to the Sea Ice Zone (SIZ). The water masses from north to south were the Subantarctic Zone (ZAZ), the Polar Frontal Zone (PFZ), and the Antarctic Zone (AZ).

The highest concentrations of chlorophyll *a* occurred in the Polar and Subtropical Fronts (PF and STF, respectively) with concentrations exceeding $500\ \mu g\ l^{-1}$. In the STF, there was a distinct subsurface chl *a* maximum at 40 m, which gradually deepened northward to 120 m in the Subtropical Convergence Zone. Relatively high concentrations of fuxoxanthin and 19'-butanoyfucoxanthin occurred in the nutrient-rich waters south of the Subantarctic Front, and analyses indicated that diatoms, chrysophytes, pelagophytes, and haplophytes dominated the phytoplankton assemblage. North of the PF to the STF, where silicate concentrations were $< 1\ \mu M$, pelagophytes and coccolithophorids dominated the water column; diatoms were virtually absent, and *Phaeocystis*, prasinophytes, cryptophytes, and chlorophytes contributed significantly to the total algal biomass.

The Polar Front is an important area of biological production (Selph et al. 2001). This zone accumulates suspended organic matter (Nelson et al. 1989; Bidigare et al. 1995), and vertical stability maintains a favorable light environment for phytoplankton growth. During the summer, grazing by mesozooplankton can consume up to 21% of the daily phytoplankton production (Urban-Rich et al. 2001). The dominance of phytoplankton assemblage by chrysophytes decreased to less than 20% of the total chlorophyll *a* on the PF, with an increase in diatoms, pelagophytes, Hapto 3, and Hapto 4. While concentrations of nitrate and phosphate remained high, silicate concentrations decreased markedly (to less than 10 μM).The Polar Frontal Zone (PFZ) was characterized by extremely low silicate availability. North of the Polar Front, pelagophytes, Hapto 3, and Hapto 4 cells continued to increase, with a decline in the dominance of diatoms. However, diatoms still represented 10–30% of the total chlorophyll *a* in the low-silicate waters between 60 and 55°S.

The entire AZ had relatively high macronutrient concentrations. Stations north of the Sub-Antarctic Front (SF) had high biomass (Chl *a* $> 500\ \mu g\ l^{-1}$). The surface phytoplankton of the AZ consisted primarily of chrysophytes and diatoms, which together accounted for nearly 80% of the chl *a*. Hapto 4 and pelagophytes accounted for most of the remaining chl *a* biomass south of the PF.

2.4.5.3 Wedell-Scotia Sea Sector

Mathot et al. (1992) calculated daily rates of *gross* and *net* primary productivity along a transect from 57 to 67°S in the Weddell-Scotia Sea Sector of the Southern Ocean. Three distinct subareas were identified: the Closed Pack Ice Zone (CPIZ), the Marginal Ice Zone (MIZ), and the Open Ocean Zone off the ice edge (OOZ).

The CPIZ was characterized by the lowest average gross primary production ($0.36\ g\ C\ m^{-2}\ day^{-1}$). The MIZ, with a maximum mean value of $1.76\ g\ C\ m^{-2}\ day^{-1}$, had the highest value, while the OOZ had an intermediate mean value of $0.87\ g\ C\ m^{-2}\ day^{-1}$. Net primary production fluctuated in nearly the same proportions, averaging 0.55,

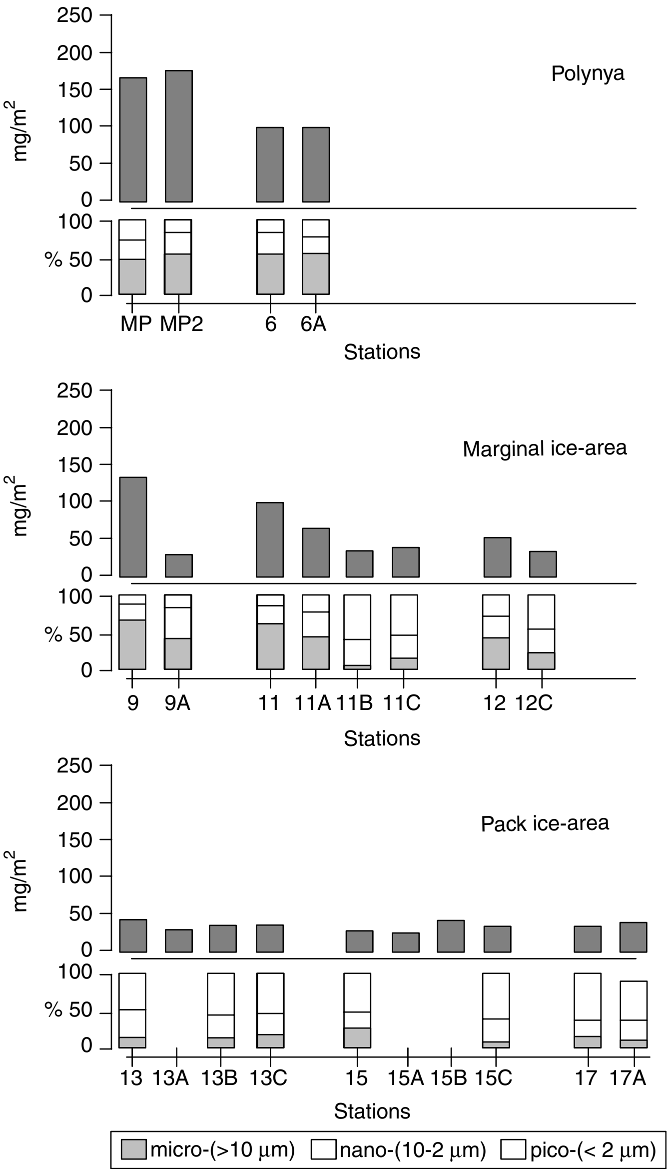


FIGURE 2.9 Variations in integrated values of total Chl *a* (μg l^{-1}) and percentage contribution of the different size fractions in replicated sets of stations in the three areas of the polyna, marginal ice zone, and pack-ice in the Ross Sea. (From Carrada, G. C. et al., *Ross Sea Ecology*, Faranda, F. M., Gugliemo, L., Ianora, A., Eds., Springer-Verlag, Berlin, 21, 1999. With permission.)

0.2, and 1.13 g C m^{-2} day^{-1} in the OOZ, CPIZ, and MIZ respectively, representing 53% of the total photo-assimilated carbon under heavy ice cover (CPIZ) and 64% in the other two areas. Available light, strongly dependent on ice cover, was shown to control the level of primary production in the sea ice associated areas, while protozoa grazing on phytoplankton determined the moderate primary production level of the "well-illuminated" OOZ area.

2.4.5.4 Ross Sea

Carrada et al. (1999) sampled a series of stations along 175°E stretching from 76.5 to 50°S. Three subsystems were identified: the polyna (PZ), the marginal ice zone (MIZ), and the pack-ice covered waters (PIZ). These three areas showed distinct differences in the size composition of the phytoplankton communities. Figure 2.9 illustrates the percentage composition of chl *a* of the micro- (>10 μm), nano- (10-2 μm), and total picophytoplankton (>2 μm). In the polyna, the microphytoplankton fraction was predominate. However, the relative abundance of the micro- and nanophytoplankton fractions was biased by the presence of large quantities of the palmelloid of *Phaeocystis antarctica*. In this area, the biomass was evenly distributed along the water column, as a consequence of the lack of stratification.

In the MIZ, the micro- and nanophytoplankton fractions were dominant. For this area, Saggiomo et al. (2000) report a phytoplankton community dominated by diatoms

(*Fragilariopsis curta* and *Pseudo-nistchia subcurta*) that increased their relative concentration to the south to 97%; this trend was concomitant with the gradual disappearance of *Phaeocystis*. In the MIZ and the PIZ, selective grazing over time by *Euphausia superba* resulted in the removal of meso- and microphytoplankton and a phytoplankton community dominated by picophytoplankton.

2.5 PHYTOPLANKTON BIOMASS

2.5.1 INTRODUCTION

When interpreting data on phytoplankton standing stock and primary production in the Southern Ocean, the limitations of the data base must be kept in mind. While data for regions such as the Drake Passage-Weddell Sea region, the Ross Sea, and the Indian Ocean south of Australia are relatively comprehensive, many other regions have been studied very little. In addition, the methods and techniques now used make it difficult to compare recent data with the results of earlier studies. Observations have often been made in isolation, both in space and time, as dictated by logistics and the overall scientific workload of the research vessels, and not by the biology of the plants (Heywood and Whitaker 1984). However, the situation has improved considerably in recent years. Anyone who has had experience in Antarctic waters can testify to the fact that phytoplankton blooms can develop very rapidly and can also be just as rapidly grazed down by zooplankton or dispersed by storms. Apart from observations made in coastal waters from shore stations, year-round observations are lacking, especially for the pack-ice region. The vast majority of the observations have been carried out over limited summer periods. In recent years, however, a number of expeditions have been undertaken to sample the phytoplankton in the late autumn, and a limited number of winter observations have been made. Seasonal progression of maximum productivity with latitude as demonstrated by Hart (1934, 1942), modified by sea state and wind force, could help explain the wide variation that has been found in phytoplankton biomass and production between areas with the same region of the Southern Ocean.

Early estimates of standing stock were made by counting phytoplankton (principally diatoms) cell numbers. This did not take into account the contribution made by the nano- and picophytoplankton, which, as we have seen, can be quite considerable. Estimates of phytoplankton standing crop are now made from chlorophyll *a* values by using standard chlorophyll *a* to carbon ratios. However, this ratio can vary by an order of magnitude between different physiological states of the same cell, or between species (Banse 1977). The results are expressed either as mg C m^{-3} or mg C m^{-2} integrated to a standard depth. This makes it difficult to compare studies that use these different measurements. To obtain more accurate information on phytoplankton biomass, we need to know concurrent zooplankton grazing rates and the loss of cells through sinking, senescence, and death—information that is not generally available. In a cruise off the Antarctic Peninsula, Gieskes and Elbracher (1986) found that between 10 and 80% of the chlorophyll *a* containing particles were smaller than 8 μm. In many samples, microscopic examination revealed that more than 50% of the nano-plankton-sized chlorophyll *a* containing particles were free-floating chloroplasts. Causes of the mechanical disruption of cells include mechanical effects on cells during storms and grazing by krill. Despite these deficiencies, however, comparative chlorophyll *a* levels are useful in overall comparisons, both geographically and seasonally. Chlorophyll *a* concentrations are expressed as values per cubic meter of the total water column beneath a square meter of the water surface.

2.5.2 SURFACE DISTRIBUTION OF CHLOROPHYLL BIOMASS

Chlorophyll biomass varies widely, both geographically and seasonally, throughout the Southern Ocean (Saijo and Kawashi 1964; El-Sayed and Mandelli 1965; El-Sayed 1970a; Fukuchi 1977, 1980; Bidigare et al. 1995; Kang and Lee 1995; Villafane et al. 1995; Kang et al. 2002; Kopczynska and Fiala 2003). Recorded values vary widely and range from 0.1 to 189 mg C m^{-3} and 4.0 to 3,600 mg C m^{-2}. Typical of this variability are the observations reported by Priddle et al. (1986a) for the seas around South Georgia, where the highest values for phytoplankton biomass were associated with stations off the southwest of the island, while the lowest chlorophyll levels were located to the southeast.

During the early summer, biomass values are generally high in the frontal zones, especially the Polar Front (Fukuchi and Tamura 1982; Sasaki 1984; Laubscher et al. 1993). In the late summer, the values are low, with the area of maximum biomass shited to the south of the Polar Front. Ice-edge blooms generate high biomass values (Comiso et al. 1990). Savidge et al. (1995) calculated the percentage contribution to the overall biomass from the Sub-Antarctic Front to the south. The specific contribution of the three zones was as follows: Polar Front, 5–10%; Marginal Sea Ice Zone, 20%; and the Antarctic Circumpolar Current (from the PF to the MIZ), 30%.

Fukuchi (1980) analyzed data on chlorophyll stocks in the Indian Ocean collected between 1965 and 1976. Surface chlorophyll *a* concentrations, measured at 631 stations in water south of 35°S, ranged from 0.01 to 3.01 mg m^{-3}. At about half of the stations, the values were less than 0.24 mg m^{-3}, while at only 29 stations were the values higher than 1.00 mg m^{-3}. The mean surface chlorophyll *a* concentrations recorded in the literature from oceanic waters of the Pacific, Atlantic, and Indian Ocean sectors range from 0.12 to 0.43 mg m^{-3}. These values are much lower than those reported from upwelling areas, but they are higher than those in the North Equatorial Current and the central Indian Ocean.

In contrast to the generally low-standing crop of phytoplankton in the oceanic waters of the Southern Ocean, elevated chlorophyll *a* levels have been reported from inshore waters, including west of the Antarctic Peninsula in the Gerlache Strait (El-Sayed 1968a); off the Antarctic Peninsula (Bidigare et al. 1995); in the inshore waters of Signy Island (Horne et al. 1969); near Kerguelen and Heard Islands (El-Sayed and Jitts 1973), near the Crozet Islands (Fiala et al. 2003), off Elephant Island (Villafane et al. 1993); at King George Island (Kang et al. 2002); and in the southern Ross Sea (El-Sayed et al. 1983; Saggiomo et al. 2000; Carrada et al. 1999). Exceptionally high values (i.e., greater than 25 mg m^{-3}) were reported by Mandelli and Burkholder (1966) during a phytoplankton bloom near Deception Island. In their studies of phytoplankton distribution and production in the southwestern Bransfield Strait, Holm-Hansen and Mitchell (1991) found that all deep stations north of the continental shelf break were low in phytoplankton biomass (>41 mg chl *a* m^{-2}), while at some stations in shelf waters the biomass exceeded 700 mg chl *a* m^{-2}. One of the most extensive and richest phytoplankton blooms recorded in the Southern Ocean occurred in the southwestern Weddell Sea (El-Sayed 1978); this bloom, composed almost entirely of the diatom *Thalassiosira tumida*, covered an area of 15,000 km^2 and had chlorophyll *a* concentrations of up to 190 mg m^{-3}. High phytoplankton biomass at different latitudes in the Weddell Sea in March have been reported by a number of investigators (El-Sayed and Taguchi 1981; Comiso et al. 1990; Estrada and Delgado 1990; Nothig et al. 1991).

Blooms of the colonial flagellate *Phaeocystis antarctica* are widespread, especially in coastal water and polynas. In McMurdo Sound, such blooms are an annual event occurring at the same time of the year (Knox 1986; Stoeckner et al. 1995) (see Chapter 12).

High chlorophyll concentrations have frequently been associated with frontal structures such as the Polar Front (Allanson et al. 1981; El-Sayed and Weber 1982; Yamaguchi and Shibata 1982; Lutjeharms et al. 1985; Bidigare et al. 1995; Sullivan et al. 1993) and in the Weddell-Scotia Confluence. El-Sayed (1983) reproduced a satellite (Nimbus 7 Coastal Colour Scanner) image from the region of the Polar Front in the Weddell Sea, and although it showed generally low values in the Polar Front region (0.05 mg chl *a* m^{-2}), it depicted a region of high pigment concentration squeezed between bands of low pigment concentration. In a study of the waters between 20 and 70°W, Hayes et al. (1984) found that high concentrations of chlorophyll *a* were usually associated with hydrographic and bathymetric features.

Villafane et al. (1996) investigated the distribution of phytoplankton organic carbon in the vicinity of Elephant Island. They determined that phytoplankton carbon represented 41–59% of the total particulate organic carbon; these percentages are very similar to those reported by Hewes et al. (1990) for diverse areas in Antarctic waters. Figure 2.10 depicts the distribution of phytoplankton carbon between the different phytoplankton categories over the period of 1990–1993. It can be seen that diatoms were dominant during 1990 and 1991. However, their numbers and biomass during 1992 and 1993 were very small, with flagellates being the dominant group. This change in phytoplankton abundance and in dominance by different taxonomic groups could be related in part to the fact that relatively high krill biomass occurred throughout the study area, and that krill concentrations apparently increased between 1990 and 1991 to 1992 and 1993 (Macaulay et al. 1990; Hewitt and Demer 1993). Since krill have a preference for microphytoplanktonic cells (Meyer and El-Sayed 1983), especially diatoms, it is to be expected that intense krill grazing could cause a change in cell size and composition of the phytoplankton from a microplanktonic to a nanoplanktonic assemblage.

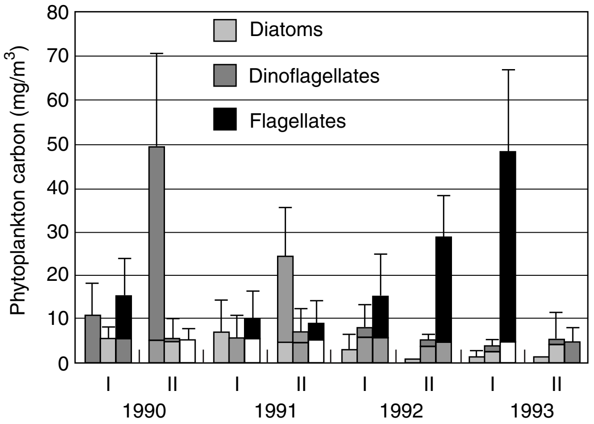


FIGURE 2.10 Mean phytoplankton carbon content (in mg C m^{-3}) at 5 m depth in the main taxonomic groups as determined by microscopical analysis. The thin lines represent one standard deviation. The roman numerals I and II indicate the two legs of each yearly cruise. (From Villifãne, V. E., Hebling, E. W., and Holm-Hansen, O., *Ant. Res. Ser.*, 70, 77, 1996. With permission.)

Kang and Lee (1995) investigated the composition and biomass of phytoplankton in the western Bransfield Strait during February. They found that phytoplankton cell abundance and carbon biomass integrated per m^2 for the upper 100 m ranged from 8.5×10^{10} to 5.9×10^{11} cells m^{-2} (average 2.68×10^{11} cells m^{-2}) and from 407 to 3,605 mg C m^{-2} (average 1.906 mg C m^{-2}). Although some 45 phytoplankton species were recorded (Kang et al. 2002), only 5 or 6 species accounted for 95% of the phytoplankton carbon. Averaged over the entire study area, unidentified autotrophic picoflagellates ($\sim$1.5 μm) were the most abundant species, accounting for about 41% of the total cell abundance. However, they accounted for only 6% of the total phytoplankton carbon because of their small cell size. In contrast to the picoflagellates, the larger-celled (>20 μm) diatom species such as *Rhizosolenia antennata* f. *semispina* was only 0.01% of the total cell abundance, but it accounted for 11% of the total phytoplankton carbon.

In their study of phytoplankton west of the Palmer Peninsula, Bidigare et al. (1995) found that in the Bellingshausen Sea Ice-edge Zone *Phaeocystis* was a significant biomass component because of its high numerical abundance. Other diatom species such as *Fragilariopsis* *cylindrus, Pseudonitzchia prolongatoides, Chaetoceros neglectum, and Ch. neogracile* were also abundant. Integrated *Phaeocystis* carbon in the upper 115 m of the water column ranged from 181 to 1,080 mg C m^{-2}, while the integrated carbon of the diatoms listed above ranged from 5.17 to 48.9 mg C m^{-2}. Although larger-celled diatom species were considered important biomass contributors due to their large cell volumes, in other ice-edge studies (Fryxell and Kendrick 1988; Kang and Fryxell 1993) *Phaeocystis* appeared to outcompete the larger-celled diatoms during the early spring in the ice-edge zone.

There have been a number of studies of the distribution of phytoplankton biomass in regions of fast ice adjacent to the Antarctic Continent. Fukuchi et al. (1984) measured chlorophyll *a* concentrations under the fast ice at five stations (10–675 m) near Syowa Station for a period of 13 months in 1982 and 1983. High chlorophyll *a* concentrations occurred between December and March, with other peaks taking place in late January. The maximum concentration recorded was 11.3 mg chl *a* m^{-3}, while the average stock in the water column was 1.05–6.72 mg m^{-3}, at least one order of magnitude higher than that reported from the open waters of the Southern Ocean. During 1983 and 1984, Satoh et al. (1986) also studied the seasonal change in chlorophyll *a* concentrations off Syowa Station. A winter minimum of 0.1 mg chl *a* was recorded from June to October, with a maximum concentration of 4.99 mg m^{-3} recorded in mid-February. The standing stocks of chlorophyll *a* in mid-January 1984 were less than half of those recorded in 1983. This was probably due to the thicker snow cover on the sea ice resulting in reduced light penetration. Iwanami et al. (1986) investigated summer chlorophyll *a* levels at the same site during the middle of the summer of 1984. At that time, the ice was continuously melting, resulting in a low salinity surface layer separated from the more saline water below by a well-defined pycnocline (the plane of separation between two layers of differing density) at a depth of about 2 m. Consequently, a subsurface chlorophyll *a* maximum developed. Integrated chlorophyll *a* stocks increased rapidly from 20.5 to 103.8 mg chl *a* m^{-2} within two weeks. In Lutzow-Holm Bay, Fukuchi et al. (1985a) recorded chlorophyll *a* levels of 0.54–0.73 mg m^{-3} under the fast ice on December 14, and 1.77–2.70 mg m^{-3} on January 3. The latter high values were probably correlated with the release of ice algae as the bottom ice melted; later concentrations in the open water after the ice breakout decreased rapidly. In Breid Bay on December 29 through 30, the following values were recorded: under the fast ice, 2.49–4.48 mg m^{-3}; at the edge of the fast ice, 4.62–4.99 mg m^{-3}; and in the open water, 1.62–2.82 mg m^{-3}. In mid-February, when the fast ice had disappeared, the chlorophyll *a* levels were 0.76–2.54 mg m^{-3}.

2.5.3 VERTICAL DISTRIBUTION OF CHLOROPHYLL

The vertical distribution of phytoplankton biomass in terms of chlorophyll *a* generally exhibits maximum values at subsurface depths, with decreasing chlorophyll values to a depth of 200 m, below which the chlorophyll concentration is generally negligible (El-Sayed 1970b; El-Sayed and Turner 1977; El-Sayed and Weber 1987). However, it is not uncommon for substantial amounts of chlorophyll to be found below the euphotic zone.

Heywood and Whitaker (1984) and El-Sayed (1987) have discussed the relationship between surface chlorophyll *a* values and subsurface maximum values and integrated values over the water column. Some authors (e.g., Fukuchi et al. 1984; Nast and Gieskes 1986; Weber et al. 1986) contend that the chlorophyll *a* measured near the surface is roughly indicative of the chlorophyll *a* distribution in the whole water column. However, El-Sayed (1970a) gave mean recorded chlorophyll *a* values for surface waters of the Atlantic and Pacific sectors of the Southern Ocean of 1.40 and 0.36 mg m^{-3}, respectively, while over the same time period the integrated values for the euphotic zone were 14.92 and 15.55 mg m^{-3}, respectively.

Bigidare et al. (1995) have figured data on the vertical distribution of chlorophyll *a* in waters west of the Antarctic Peninsula. The chlorophyll *a* profiles were homogeneously distributed in the upper 100 m layer at stations located in the Drake Passage, whereas chlorophyll *a* stratification was observed at stations close to Deception Island and coastal waters, showing a subsurface maximum at 30 m depth. The highest chlorophyll *a* concentrations—2.6 and 2.4 mg m^{-3}—were observed at 10 and 30 m depth. It is clear that stratification of the water column is the major factor determining the distribution of chlorophyll *a* throughout the water column.

2.6 PRIMARY PRODUCTION

2.6.1 INTRODUCTION

The absolute fixation rate of inorganic carbon into organic molecules is the gross primary production (P_g). When corrected for the respiration of the autotrophs (R), P_g reduces to net primary production (P_n):

$$P_g R = P_n$$

A major complication is that the microheterotrophs coexist with and share the same size range as autotrophs, and when attempting to measure biomass or metabolism of one it is extremely difficult to discriminate the biomass or metabolism of the other (Li 1986). If the respiration of all the heterotrophs (both macroscopic and microscopic) is subtracted from P_n, the residual is termed net community production (P_c).

Estimates of primary production depend on which measurement techniques are employed (Eppley 1980; Peterson 1980) (see Table 2.3). There are two kinds of indices for primary production. Incubation in vivo (seawater containing natural phytoplankton assemblages, contained in bottles) provides one such index of photosynthetic rate. For example, the assimilation of carbon may be measured by the uptake of the tracer ^{14}C or the evolution of oxygen by direct

TABLE 2.3
Methods for Estimating Primary Production in the Ocean and the Nominal Time Scales on which the Results Apply

Method	Nominal Component of Production	Nominal Time Scale
In vitro		
^{14}C assimilation	$P_{\Upsilon}(=P_a)$	Hours to 1 day
O_2 evolution	P_{Υ}	Hours to 1 day
$^{15}NO_3$, assimilation	P_{new}	Hours to 1 day
Bulk property		
Sedimentation rate below photic zone	$P_{new}(=P)$	Days to months (duration of trap deployment)
Oxygen utilization rare (OUR)	P_{new}	Seasonal to annual
Net O_2, accumulation in phvtie zone	P_{new}	Seasonal to annual
NO_3 flux to photic zone	P_{new}	Hours to days
Upper limit optimal energy		
Conversion of photons absorbed by phyto-plankton pigments	P_{Υ}	Instantaneous to annual
Lower limit		
Depletion of winter accumulation of NO_3 above seasonal thermocline		Seasonal

The components P_g (gross primary production), P_n (net primary production) and P_c (P_n respiration of all heterotrophs) refer to a scheme based on carbon; P_T. (total production), P_r (regenerated production) and P_{new} (new production) to one based on nitrogen. Sedimentation rate refers to the gravitational flux of organic particles leaving the photic zone, not the (much smaller) flux arriving at the sediment surface.

Source: After Platt et al., 1909.

titration. Changes in the bulk properties of the water column give other indices of primary production. They include change in the dissolved oxygen content of the photic zone, the rate of sedimentation of organic particles, the consumption of oxygen below the photic zone by the decomposition of the sedimenting material (the oxygen utilization rate, OUR), and the vertical flux of nitrate into the photic zone (Platt et al. 1993).

Primary production is generally estimated by the ^{14}C uptake method of Steeman-Nielsen (1952). While there has been much debate as to exactly what is measured by this method (Dring and Jewsen 1979), it is currently the only technique sensitive enough to measure the low rates of production frequently encountered. However, the results of ^{14}C experiments are often difficult to interpret, and a number of workers consider that in general the method underestimates primary production (see Gieskes et al. 1979). Bearing this in mind, the next section discusses production values that have been determined by the ^{14}C method.

2.6.2 Spatial Distribution of Primary Production

Since the magnitude of primary production is a function of the phytoplankton biomass and growth rates it is not surprising that most of the primary productivity data show a good correlation with the distribution of the phytoplankton standing crop. For instance, low values of primary production rates reported from the Drake Passage, the Bellingshausen Sea, and the oceanic waters of the Southern Ocean in general are typical of oligotrophic waters (<1 g C m^{-2} day^{-1}) (El-Sayed 1985, 1987). On the other hand, high values have been recorded in coastal regions in the vicinity of the Antarctic Continent and the off-lying islands, in the ice-edge zone, and in polynas (see Chapter 13). El-Sayed (1967) recorded a value of 3.2 g C m^{-2} day^{-1} in the Gerlache Strait, and Mandelli and Burkholder (1966) reported 3.6 g C m^{-2} day^{-1} near Deception Island. Horne et al. (1969) found a peak productivity of 2.8 g C m^{-2} day^{-1} in the inshore waters of Signey Island, while Jacques (1983) reported a maximum value of 5.2 g C m^{-2} day^{-1} from the Indian Ocean sector. In their Bransfield Strait studies, Holm-Hansen and Mitchell (1991) found low rates of primary production (mean 0.34 g C m^{-2} day$^{-1)}$ in oceanic waters, in contrast to shelf waters in December, where rates exceeded 3.0 g C m^{-2} day^{-1}. In the Drake Passage and the South Atlantic Ocean, Xiuren et al. (1996) recorded primary production levels of 0.26–0.62 mg C m^{-2} h^{-1}. Arrigo and McClain (1994), from data obtained by the coastal zone colour scanner (CZCS), identified an intense phytoplankton bloom covering more than 108,000 km^2 in the western Ross Sea in early December. The bloom developed inside the Ross Sea polyna, and primary productivity was calculated at 3.9 g C m^{-2} day^{-1}. This was up to four times the values measured during mid-January in situ studies. Production yields over the spring and summer were estimated at 141–171 g C m^{-2}, three to four times the values previously reported from the western Ross Sea. Saggiomo et al. (2000) measured integrated total daily phytoplankton production levels in the western Ross Sea ranging from 131 to

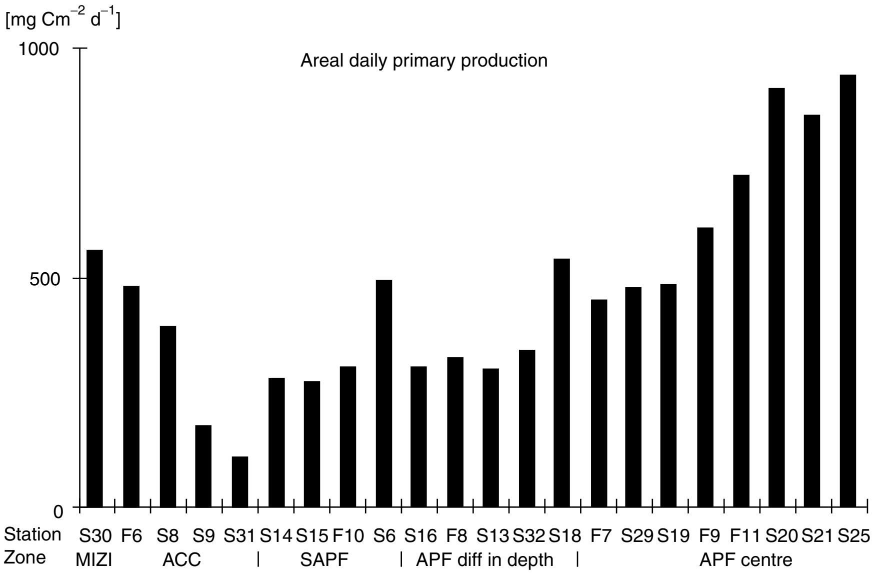


FIGURE 2.11 Areal daily primary production rates at all stations sampled in the Southern Ocean during ANT Xii2 (See Figure 2.6 for the definitions of the various zones). (From Bracher, A.W., *Ber. Polarforsch.*, 341, 39, 1999. With permission.)

2,992 mg C m^{-2} day^{-1}. The highest values were measured in the polyna and the Marginal Sea Ice Zone.

Bracher et al. (1999) have figured the aerial daily primary production in the zonal regions of the Southern Ocean (MIZ, ACO, SAPF, and APF) (Figure 2.11) during ANT XIII 2. It can be seen that the level of production differs between the various regions, with the highest values occurring in the center of the Polar Frontal region.

When von Bodungen et al. (1986) studied phytoplankton production during spring in the Antarctic Peninsula area, three distinct and persistent zones were encountered: Zone I, which had a low biomass comprising flagellates and diatoms in the Drake Passage; Zone II, with a high to moderate biomass of *Phaeocystis* and diatoms in the northern and central Bransfield Strait; and Zone III, with a moderate biomass (*Thalassiosira* spp. in the process of forming resting spores) in the vertically homogeneous waters on the northern Antarctic Peninsula shelf. The rates of primary production for Zones I, II, and III averaged 230, 1,660 and 830 mg C m^{-2} day^{-1}, respectively.

Brockel (1985) measured phytoplankton production for three size classes (<20 μm, 20–100 μm, and >100 μm) in the southeastern Weddell Sea in February and March of 1983. Total primary production ranged between 80 and 1,670 mg C m^{-2} day^{-1}, with an average of 570 mg C m^{-2} day^{-1}, nearly 70% of which was contributed by the <200 μm size fraction. Production was in the range of higher values reported by other investigators for the same region, e.g., a January to March range of 160–580 (El-Sayed and Mandelli 1965), 350–1,560 (El-Sayed 1978) and 58–170 (von Brockel 1981). Around the Antarctic Peninsula and the southern Weddell Sea, von Brockel (1981) found that the very small phytoplankton (<20 μm) contributed between 60 and 90% of the total primary production.

Aristegui et al. (1996) investigated phytoplankton primary production and oxygen consumption at four stations in the coastal waters of the Antarctic Peninsula: (1) shelf waters of the Antarctic Peninsula, (2) Gerlache Strait; (3) Hanusse Bay near the polar circle; and (4) Deception Island. ^{14}C uptake values varied from 279 to 1,525 mg C m^{-2}, with the highest values observed in Hanusse Bay (Table 2.4). Although there was a good quantitative agreement between the oxygen and carbon measurements, total daily water column integrated carbon incorporation measured by radiocarbon uptake in the particulate fraction underestimated net community production measured by the oxygen method by up to 29–54% (using a photosynthetic quotient of 1.5). Unaccounted-for exudation of dissolved organic carbon during the ^{14}C uptake experiments may explain this discrepancy. Respiratory carbon losses by microorganisms (largely phytoplankton) ranged between 19 and 50% of gross production, with the highest values corresponding to the more productive stations. The results show that microbial respiration is an important part of the carbon flux of coastal Antarctic plankton. Unless it is considered in carbon flux, models in marine food webs may be seriously underestimated.

Robinson et al. (1999) carried out an investigation similar to that of Aristegui et al. (1996) in East Antarctica, measuring the rates of plankton community production and respiration determined from in vitro changes in dissolved organic carbon and dissolved oxygen and the incorporation of ^{14}C in December through February of 1984 (Figure 2.12). The breakout of the seasonal fast ice was associated with a succession of dominant phytoplankton from *Cryptomonas* to *Phaeocystis* to a diatom assemblage. Gross production reached 33 mmol C m^{-3} day^{-1} and, ^{14}C incorporation peaked at 24 mmol C m^{-3} day^{-1} on January 23, at the

TABLE 2.4
Depth-integrated Values of ^{14}C Uptake by Phytoplankton and Gross (GP) and Community Respiration (R) Calculated by the Oxygen Method

	Station	$Z_{EZ(m)}$	Range (m)	^{14}C Uptake (mg C m^{-2})	GP (mg O_2 m^{-2})	GP (mg C m^{-2})	R (mg O_2 m^{-2})	R (mg C m^{-2})	R/GP (O_2) (%)	R/GP (C) (%)
Shelf waters of Antarctic Peninsula	S1	58	0–30	316	2,700	600	188	71	6.8	10.3
			0–60	419						
Gerlache Strait	S2	35	0–30	279	1,571	393	236	89	15.0	22.6
			0–60	308						
Hanussee Bay	S3	30	0–30	1,303	8,194	2,209	2,269	851	27.7	41.5
			0–60	1,525						
Deception Island	S4	15	0–30	620	4,133	1,033	1,385	520	33.5	50
			0–60	631						

GP, R, and ^{14}C measurements refer to daylight incubations (~13 h). Respiratory losses of GP in oxygen (O_2) units and carbon (C) are calculated. A photosynthetic quotient of 1.5 and a respiratory quotient of 1 (mol:mol) were used to transform oxygen to carbon. Z_{EZ}: depth of the euphotic zone at each station.

Source: From Aristegui, J. et al., *Mar. Ecol. Prog. Ser.*, 132, 198, 1996. With permission.

chlorophyll *a* maximum (22 mg chl *a* m^{-3}). Dark community respiration reached its maximum (13 mmol m^{-3} day^{-1}) four days later. Photosynthetic rates calculated from ^{14}C incorporation were significantly lower (17–59%) than rates of gross production.

Until the early 1960s, it was believed that the Southern ocean was very rich in primary production, based on the obvious assumption that the maintenance of the observed large stocks of whales, seals, birds, and fish required correspondingly high levels of the basic primary production in Antarctic waters, the phytoplankton. In later years, it became clear that in the Southern Ocean primary productivity is low in large areas (El-Sayed 1984), where nanophytoplankton cells (<20 μm) may sometimes comprise more than 50% of the phytoplankton biomass (von Brockel 1981; Koike et al. 1996) and more than 90% of the primary production (von Brockel 1985). Also in these areas, the food webs structure is much more complex, with the larger part occupied by food webs without krill (Hempel 1985b).

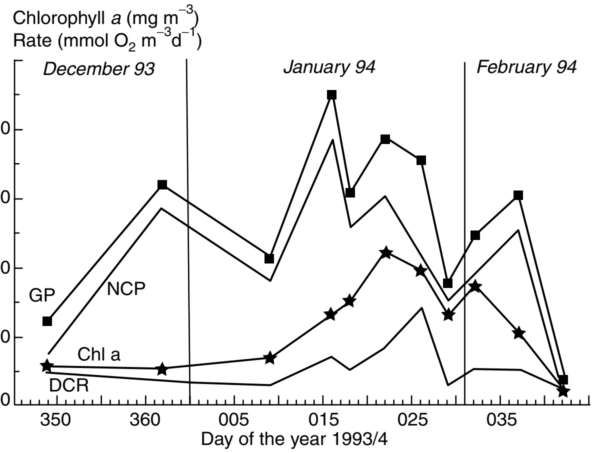


FIGURE 2.12 Gross production (GP[O_2]), net community production (NCP[O_2]) and dark community respiration (DCR[O_2]) (mmol O_2 m^{-3} day^{-1}) and chl *a* (mg chl *a* m^{-3}) measured at 3- to 4-day intervals between December 1993 and February 1994. (From Robinson, C., Archer, S.D., Williams, P.J. leB., *Mar. Ecol. Prog. Ser.*, 27, 189, 1999. With permission.)

Today, it is obvious that primary productivity in the Southern Ocean is spatially and temporarily highly variable (Sullivan et al. 1993); however, compared to other regions, maximum phytoplankton growth rates are generally low (<0.6 day^{-1}) due to low temperatures (Sakshug and Slagstad 1991). As described above, during the spring and summer phytoplankton blooms are frequently observed in coastal regions, near the ice edge, in polynas, and at frontal zone systems. High levels of the major nutrients in surface waters are maintained by the combined effects of wind stress and thermohaline circulation, resulting in circumpolar surface divergence and upwelling (e.g., Nelson et al. 1987). Despite this, the main body of the Antarctic Circumpolar Current is characterized by low levels of biomass and primary productivity, <0.5 mg chl *a* m^{-3} and 300 mg C m^{-2} day^{-1}, respectively (e.g., Holm-Hansen et al. 1977; El-Sayed 1978; Sakshaug and Holm-Hansen 1984; Holm-Hansen and Mitchell 1991). Therefore, these regions of the Southern Ocean, like the subarctic Pacific and the equatorial Pacific, can be termed "high-nutrient, low-chlorophyll" areas. Here, phytoplankton do not exhaust phosphate and nitrate in the surface waters.

It is also clear that primary production is highly variable, especially in the pack-ice zone. As we have seen, phytoplankton blooms, often intense, and sometime short lived, do occur here, especially in the spring. If these are missed in sampling programs, primary production in these areas may be underestimated.

2.6.3 VERTICAL DISTRIBUTION OF PRIMARY PRODUCTION

Maximum photosynthetic activity generally occurs at depths corresponding to a photosynthetically available radiation (PAR) of between 500 and 100 μE m^{-2} sec^{-1} (Bodungen 1986). Carbon fixation, however, has been measured in samples well below the euphotic zone. For example, El-Sayed and Taguchi (1981) and El-Sayed et al. (1983) report that the primary production below the euphotic zone in the Ross and Weddell Seas was nearly one-fourth of the total water column production. However, in the Atlantic and Indian Ocean sectors, carbon fixation below the euphotic zone did not exceed 3–10% of that in the euphotic zone (El-Sayed and Jitts 1973; El-Sayed and Weber 1982).

Figure 2.13 depicts the vertical distribution of primary production for two ice-free stations and one covered with about 70% of ice floes in the southwestern Weddell Sea (Brockel 1985). It can be seen that the 1% light level occurs between 20 and 30 m, indicating that the water column was strongly stratified. The nanophytoplankton were substantial contributors to the overall production.

Based on in situ primary productivity experiments conducted by El-Sayed during *Eltanin* cruises 38, 46, and 51 in the Pacific and Atlantic sectors, a mean primary productivity value of 0.134 g C m^{-2} day^{-1} was calculated (El-Sayed and Turner 1977). The mean value is considerably lower than those values reported for phytoplankton blooms. The following conclusions can be drawn from the studies carried out thus far on primary production in the Southern Ocean: (1) the productivity of these waters varies by at least one or two orders of magnitude; and (2) Antarctic waters, in general, exhibit high productivity levels mainly in coastal waters and especially at the receding ice edge. As El-Sayed (1984) points out, given the fact that the ocean south of the Polar Front contains a circumpolar phytoplankton population, one that is more or less adapted to cold temperatures and that enjoys an abundant nutrient supply and lives in a fairly uniform environment, with sufficient light for photosynthesis (at least during the spring and summer), it is somewhat surprising that the phytoplankton are not only patchily distributed but very low in diversity, approaching that of an oligotrophic ocean over vast areas. According to Holm-Hansen and Huntley (1984), the nutrient levels should be able to support a phytoplankton biomass of at least 25 μg chl *a* l^{-1}, but it seldom attains this density except for the blooms referred to above.

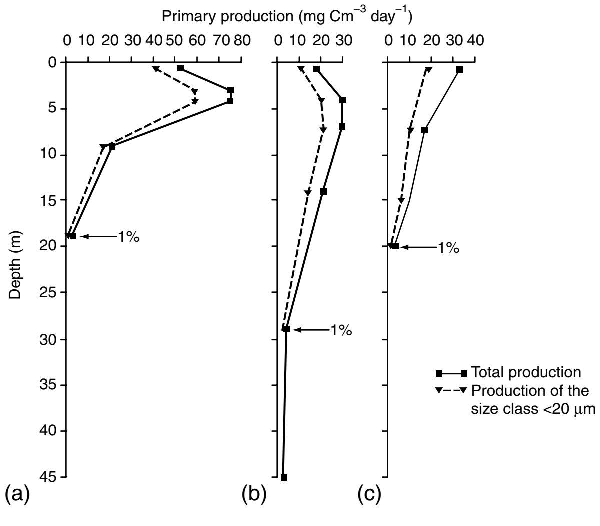


FIGURE 2.13 Vertical distribution of primary production for two typical ice-free stations (a and b), and a third station (c) covered to about 70% with ice-floes in the southeastern Weddell Sea. (From von Brockel, K., *Polar Biol.*, 4, 75, 1985. With permission.)

2.7 SEASONAL AND GEOGRAPHIC VARIATION OF PHYTOPLANKTON BIOMASS AND PRIMARY PRODUCTION

At present, there is a relative dearth of long-term phytoplankton data from the Southern Ocean, and the information collected on seasonal cycles based on data from single stations, or from single depths, may not be representative (El-Sayed 1987). For example, a deep chlorophyll *a* maximum may be missed entirely if surface samples are used to reconstruct the seasonal cycle of phytoplankton biomass (Harris 1980). Further, large-scale advection may modify the seasonal cycle as observed at a single point if the seasonal cycle differs between water masses. These complications should be kept in mind when examining the seasonal variability of the phytoplankton.

In spite of the methods that Hart (1934, 1942) used, his data on the seasonal variability of Southern Ocean phytoplankton are still the most complete. He demonstrated that the onset of the period of maximum production changes from early spring to late summer or early winter with increasing latitude (Figure 2.14). His data also showed that the period of maximum production decreased in duration with increasing latitude and, further, that annual differences in hydrographic conditions could affect the timing and magnitude of these peaks and the species that were active during the period. These early observations have been corroborated by many subsequent investigators. In Figure 2.14, the marked similarities between El-Sayed's findings (1971a, 1971b) and those made by Hart in the "Northern Zone" are clear.

The objective of many Southern Ocean phytoplankton studies has been to describe "key" or "indicator" species that would delineate specific water masses. Most of such papers dealing with ecological considerations have reported either a short list of the dominant species of the phytoplankton (e.g., Theriot and Fryxell 1985) or a long list of all species identified in the water samples (Cassie 1963). Usually these studies are based on a limited number of stations, where each station was sampled only one time. However, despite the many investigations carried out since the pioneer studies of Hart (1934, 1942), there are no data to suggest that any specific phytoplankton species is strictly confined to particular water masses or to specific regions in water south

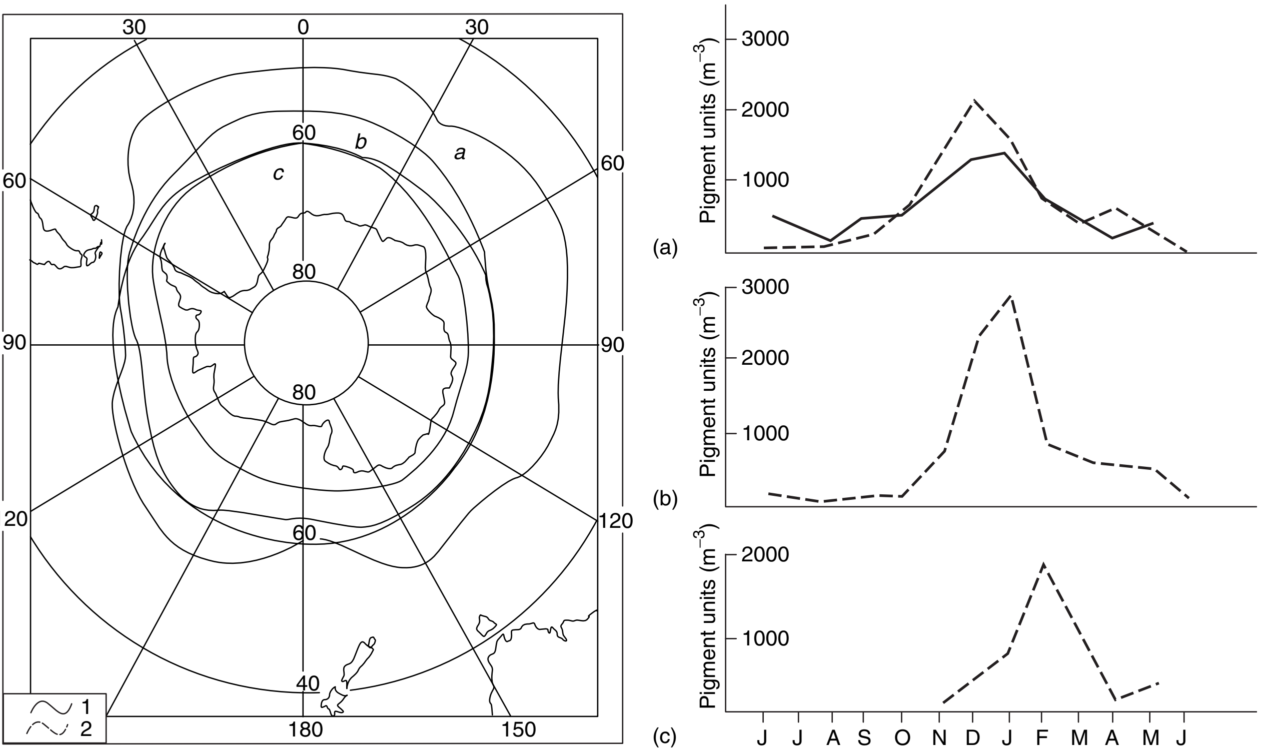


FIGURE 2.14 Left: Phytoplankton zonation in the Southern Ocean, delineated by solid lines (a) Northern Zone (ca 50°00′S–55°50′S); (b) Intermediate Zone (ca 55°50′S–66°00′S). The dotted lines delineate corresponding zooplankton zones. (Modified from Voronina 1984). Right: Seasonal variation in plant pigment concentrations with latitude: (s) Northern Zone; (b) Intermediate Zone; (c) Southern Zone (After Hart's (1942) *Discovery* data). (From El-Sayed, S. Z., *Comp. Biochem. Physiol.*, 90B, 489, 1988b; modified from Vorinina (1984). With permission.)

of the Polar Front. There is, however, much spatial variability in the abundance of phytoplankton and the relative concentrations of the different species.

A number of studies have addressed the question of spatial and temporal variability of phytoplankton composition and biomass over extended periods. Villafane et al. (1993) investigated the spatial and temporal variability of the phytoplankton in the vicinity of Elephant Island during 1990 through 1993. They found much intra-annual variability, with a trend of increasing biomass from January and February (Leg I) to February and March (Leg II), except in the 1993 studies. There was also a change in the phytoplankton composition between the two legs. During 1990 and 1991, the increase was mostly due to diatoms; during 1992, the increase was mostly to an increase in flagellates, while during 1993 there was a decrease in total biomass between the two legs, with diatoms decreasing so that dinoflagellates dominated the biomass during the second leg. This resulted in dramatic changes in the distribution of phytoplankton carbon among the diatoms, dinoflagellates, and flagellates. Such dramatic changes cannot be ascribed to seasonal events involving changes in incident solar radiation or water temperature. These changes probably resulted from grazing pressure and changes in the depth of the Upper Mixed Layer.

The great variation of phytoplankton biomass, distribution, and taxonomic composition recorded in these and other studies suggests that the physical and chemical characteristics of the different water masses in Antarctic waters are not sufficiently different to enable them to be characterized by specific phytoplankton species or taxonomic groups. The variability both spatially and temporarily is more likely to be related to the changing environmental characteristics of any water mass, which will create favorable growing conditions for certain species or groups of phytoplankton. There are many possible sources of such variability (both spatially and temporarily) in water characteristics, including wind stress and duration, extent of ice cover, rate of ice melt, magnitude of freshwater input from land runoff or melting icebergs, variations in the strength of upwelling, and change in flow patterns of currents. The following three considerations emerge from the studies discussed above (Villafane et al. 1993): (1) a description of the composition of phytoplankton species determined over one short period of time, where there is no seasonal coverage of the area, cannot be very useful in delineating hydrographic features; this implies that there are no ecologically relevant "indicator" species of phytoplankton that can be used unequivocally to indicate specific water masses; (2) selective grazing of zooplankton must be considered as a possible process of modifying the species composition of the phytoplankton; and (3) to improve our understanding of the variability of phytoplankton in Antarctic waters, it is necessary to achieve a better understanding of the autecology of the dominant species or groups of phytoplankton, so that floristic composition of the phytoplankton may be interpreted in the context of the ever-changing physical-chemical and optical factors that characterize the upper water column.

As we have seen, phytoplankton blooms are characteristic of coastal waters and frontal systems. Such blooms may be dominated by diatoms, dinoflagellates, *Phaeocystis*, or coccolithophorids. They may be short lived or persist over varying periods. Frontal systems are characterized by the enhancement of phytoplankton biomass and productivity (Allanson et al. 1981; Fukuchi and Tanimura 1982; Lutjeharms et al. 1985; Laubscher et al. 1993; Froneman et al. 1997; Bathmann et al. 1997; Clementson et al. 1998; Fiala et al. 1998; Hense et al. 2000; Kopczynska et al. 2001). In particular, the subantarctic region (between 40 and 50°S), with its fronts south of Australia and Africa, the latter including the dynamic frontal area of the Crozet Basin, is considered a zone of elevated biological production and increased oceanic CO_2 sink (Poison et al. 1993). Physical, chemical, and biological factors viewed as responsible for algal accumulation at fronts include the enhancement of in-situ production based on renewal of nutrients due to cross frontal mixing, increased water column stability, and mechanical accumulation of cells and biomass by converging fronts (Heywood and Priddle 1987; Kopezynska 1988; Franks 1992; Laubscher et al. 1993). A study by Clemenston et al. (1998) on the interaction of physics and chemistry with phytoplankton communities in the Australian sector of the Subtropical Convergence showed that the factors responsible for elevated production include high surface nitrates unlikely to be depleted, wind-mixing supplying nitrates, and salinity gradients leading to water column stability.

The stations of only a handful of researchers provide data on phytoplankton dynamics: Fukuchi et al. (1985a, 1985b) in Lutzow-Holm Bay; Tokarczyk (1986) in Admiralty Bay, King George Island; Domanov and Lapiski (1990) in Admiralty Bay; Kang and Kang (1997) and Kang et al. (2002) in Marion Cove, King George Island; Clarke et al. (1998a) at Signy Island; and Kang et al. (2002) in Marion Cove, King George Island. In the latter study, Kang et al. found that in Marion Cove the abundance of microalgae and carbon biomass exhibited clear seasonal variation. Annual mean total microalgal abundance in surface waters was 2.42×10^4 cells l^{-1}. Microalgal abundance showed a multimodal distribution of standing crop. Microalgae started to bloom in October and increased abruptly during November. In the months of November and December, more than 45% (average 3.5 mg m^{-3}) of chlorophyll *a* was present, dominated by microplanktonic diatoms (>20 μm) such as *Fragilaria striatula, Licmophora belgacae,* and *Achanthes groenlandica*. Nanoplankton microalgae also increased during the summer. The increase in the diatoms was mainly due to the re-suspension of benthic microalgae by wind and tidal currents in spring and summer. In contrast, microalgal assemblages in winter were characterized by the dominance of pico- and nanoplantonic microalgae (<20 μm) such as *Phaeocystis antarctica*, *Navicula glaciei,* and *N. perminuta*. In October, the nanoflagellates *Cryptomonas* spp. started to increase in abundance, and they continued increase until December. Thus, microalgae as the carbon source for the benthic animals underwent changes seasonally with respect to abundance and species composition.

It is clear that there are considerable differences in phytoplankton composition and biomass between coastal and oceanic regions. These differences will be discussed further in Chapter 13.

2.8 FACTORS AFFECTING PRIMARY PRODUCTION

2.8.1 INTRODUCTION

Despite its generally high nutrient levels, only low-standing stocks of phytoplankton have been found in the Southern Ocean (El-Sayed 1984; Holm-Hansen 1985). The phytoplankton biomass in the most productive ice-edge regions is relatively modest, even during the austral spring (Sullivan et al. 1988), and nutrient levels are still above depletion after phytoplankton blooms (Hayes et al. 1984; Sakshaug and Holm-Hansen 1984). A number of factors have been hypothesized to control phytoplankton productivity in the Southern Ocean (Cullen 1991): nutrient effects (e.g., ammonia, silicate, iron, and other trace metals), physical limitation (via irradiance, temperature, turbulent mixing, and ice cover), and biological interactions (loss processes such as herbivorous grazing and sinking). The relative importance of each factor undoubtedly varies with time and space in the large Southern Ocean, and the reason for the high-nutrient, low-chlorophyll conditions remains unresolved.

Forty-five years ago, Hart (1934) reviewed the possible factors limiting the production of phytoplankton in the Southern Ocean. He concluded that of the major nutrients only silicate was likely to be limiting, but then only in certain areas. He thought it was the physical features of the environment (light intensity and duration, ice cover, surface water stability, and currents) that exerted the "strongest influence upon phytoplankton production in the far south." Since then, there has been considerable progress in our understanding of algal physiology and ecology, and there has been an increasing number of physiological and ecological studies dealing with Antarctic phytoplankton. In the last two decades in particular, there have been a number of reviews of the factors governing the ecology and productivity of Antarctic phytoplankton (for reviews, see Fogg 1977; Holm-Hansen et al. 1977; El-Sayed 1978, 1984, 1985, 1987, 1988a, 1988b; Jacques 1983; Heywood and Whitaker 1984; Priddle et al. 1986a; Sakshaug and Holm-Hansen 1986; Bianchi 1992; Sullivan et al 1993; Bidigare et al. 1996; Savidge et al. 1996; Moline et al. 1997; Bracher 1999; Innamotati et al. 2000; Di Tuillo et al. 2003). Of the many chemical, physical, and biological factors that might limit phytoplankton productivity in the Southern Ocean, the availability of macro- and micronutrients, temperature, solar radiation, water column stability and zooplankton grazing are considered to be the most important.

2.8.2 MACRONUTRIENTS

Numerous observations of the concentrations of nitrate, phosphate, and silicate have been made in the Southern Ocean, starting with the *Discovery* investigations (Deacon 1937; Clowes 1938; Hart 1942). These observations have shown that the concentrations are high in the surface waters, and that they remain so throughout the year (Holm-Hansen et al. 1977; Whitaker 1982; Jacques 1983; El-Sayed 1984; Hayes et al. 1984; Tréguer and Jacques 1992; Goeyens et al. 1991; Bianchi et al. 1997; Mengesha et al. 1998; Reay et al. 2001). The results of a series of enrichment experiments in the Southern Ocean between 20 and 70°W carried out by Hayes et al. (1984) suggested that the availability of nitrate, phosphate and silicate, trace metals, and vitamins exerted no control over phytoplankton production. Even at the peak of phytoplankton growth, the concentration of nutrients generally remains well above limiting values. El-Sayed (1978) measured 2.49 g-at $\mathrm{l^{-1}}$ NO_2–N, 2.02 g-at PO_4–P, and 18.00 g-at SO_2–S, during a dense phytoplankton bloom in the Weddell Sea.

However, seasonal depletion of surface nutrient concentrations does occur in the summer and appears to be geographically widespread (Jennings et al. 1984) Still, even in mid-summer the surface concentrations of nitrate, phosphate, and silicate generally remain high enough (>25, >1.75, and 30 μM, respectively) to ensure that the phytoplankton are not nutrient limited. On the other hand, a number of studies have revealed that significant nutrient depletion can take place in certain circumstances. Satoh et al. (1986) found that in Prydz Bay, where there were high concentrations of chlorophyll *a* ($>2.0\ \mathrm{g\,l^{-1}}$) in the upper water layer, in the zone of the phytoplankton bloom, nutrients were depressed (<1.0 g-at P $\mathrm{l^{-1}}$, <10 g-at Si $\mathrm{l^{-1}}$, and 16 g-at N $\mathrm{l^{-1}}$). Off of Davis Station, Perrin et al. (1987) found that the concentrations of nitrate, phosphate, and silicate increased

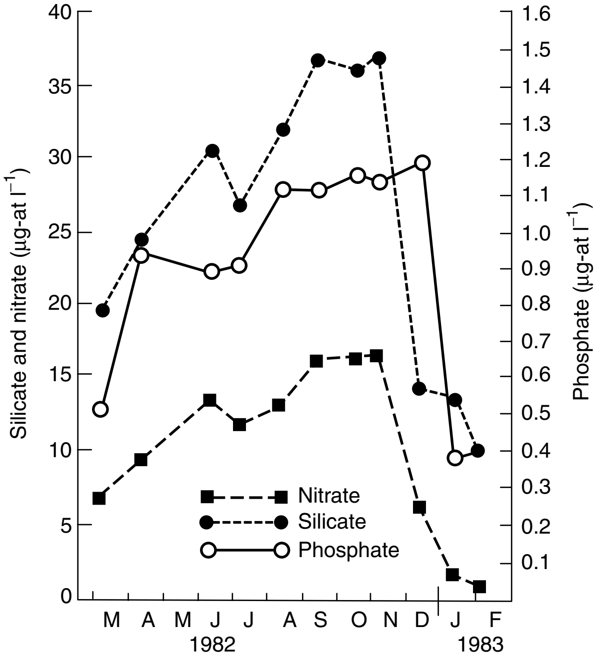


FIGURE 2.15 Seasonal changes in the averaged concentrations of nitrate, silicate, and phosphate in the water column 1 km off Davis Station (68°35′S; 77°50′E). (From Perrin, R.A., Marchant, H.J., *Hydrobiologia*, 146, 33, 1987. With permission.)

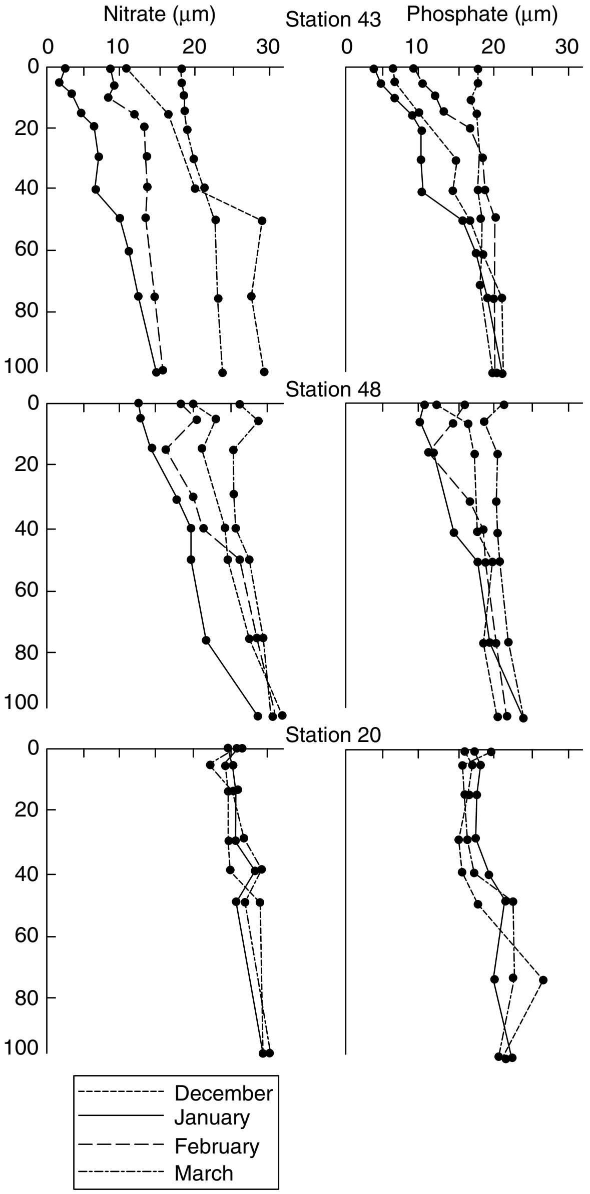
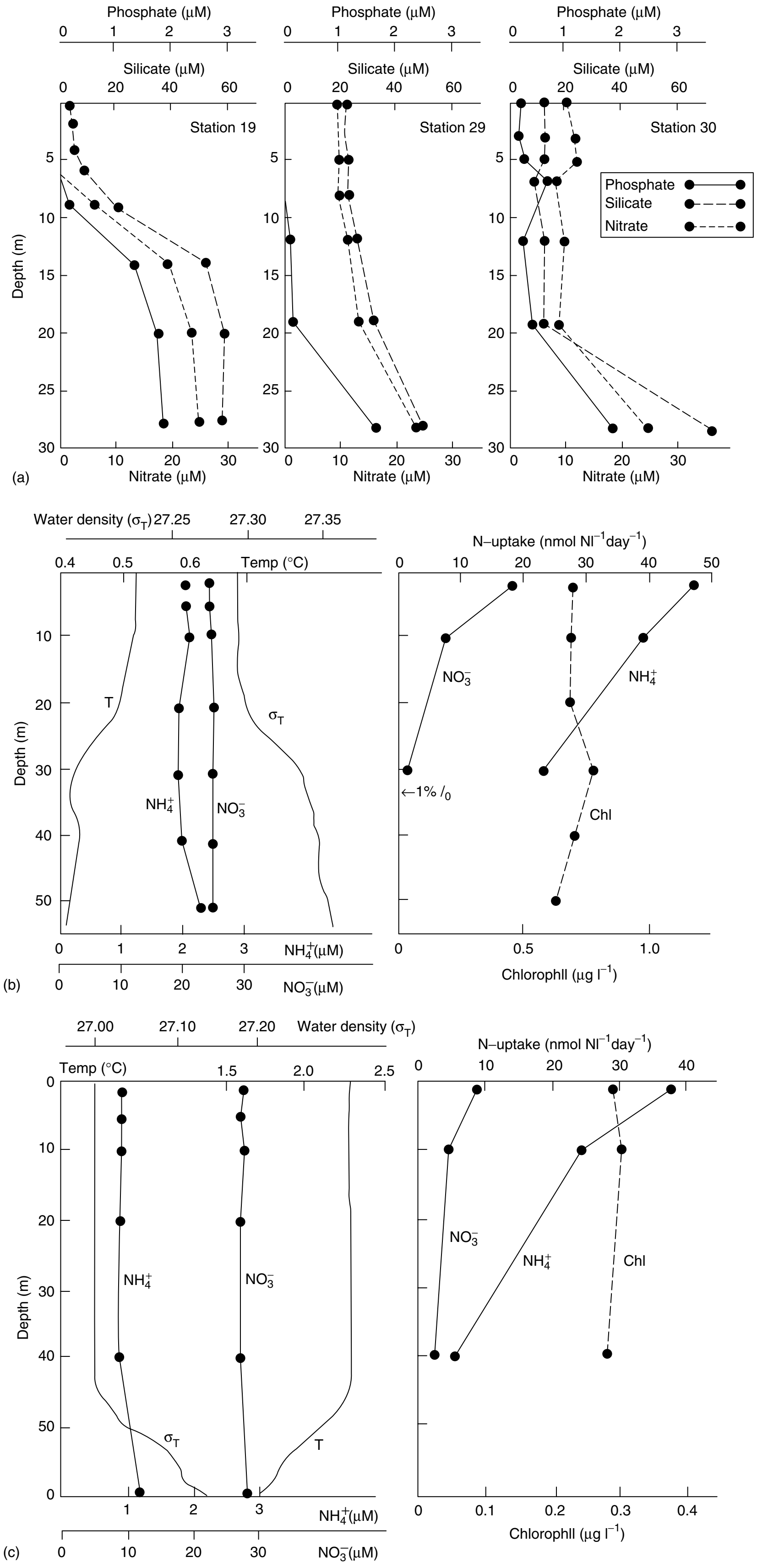


FIGURE 2.16 Inorganic nitrogen (NO+NO) and phosphate concentrations in the southwestern Bransfield Strait and adjacent waters at stations with high biomass (Sta. 43), intermediate values for biomass (Sta. 48), and low biomass (Sta. 20). Data are for the months of December, January, February, and March. There were no data from Sta. 20 in December as it was covered by sea ice. (From Holm-Hansen, O., Mitchell, G.G., *Deep-Sea Res.*, 38, 961,1991. With permission.)


Phosphate (μM)
Silicate (μM)
Nitrate (μM)
Depth (m)
Station 19
Station 29
Station 30
Phosphate
Silicate
Nitrate
(a)
Water density (σ$_T$)
Temp (°C)
T
σ$_T$
NH$_4^+$
NO$_3^-$
NH$_4^+$(μM)
NO$_3^-$(μM)
N–uptake (nmol Nl^{-1}day^{-1})
←1% I$_0$
Chl
Chlorophll (μg l^{-1})
(b)
(c)

throughout the year until December, when the concentrations of silicate and nitrogen fell sharply, followed a month later by reductions in phosphate concentrations (Figure 2.15). Inorganic nitrogen and phosphate concentrations in the upper 100 m of the water column at three stations in the southwestern Bransfield Strait, which are representative of stations with high, intermediate, and low-phytoplankton biomass (Stations 43, 18, and 20, respectively) are shown in Figure 2.16 (Holm-Hansen and Mitchell 1991). At Station 43, nutrients dropped to low levels (1.9 mmol m^{-3} inorganic nitrogen, 0.37 mmol m^{-3} phosphate) in January and increased during February and March to relatively high concentrations. At Station 20, there was very little seasonal depletion, while at Station 18 nutrient levels were observed to be between those of the two other stations.

During a *Phaeocystis* bloom encountered by El-Sayed et al. (1983), however, nitrate concentrations were still high, with euphotic zone concentrations averaging 17 g-at l^{-1}. Within the high biomass core of a very intensive ice-edge phytoplankton bloom in the western Ross Sea (Nelson and Smith 1986), uptake by phytoplankton depleted both nitrate and phosphate to analytically undetectable concentrations at some individual stations within the bloom (Figure 2.17). Apart from these exceptions, the concentrations of nitrate, phosphate, and silicate generally exceeded 4, 0.1 and 10 μM, respectively—concentrations high enough to allow most planktonic algae to take up nutrients at their maximum experimental rates (Nelson et al. 1989). It could therefore be concluded that nutrient availability is seldom, if ever, a significant limiting factor to the phytoplankton in the Southern Ocean.

There is, however, some evidence that under certain conditions nutrients could be limiting. In a series of experiments in Borge Bay, Signey Island, Whitaker (1977a, 1977b) found that the addition of phosphates and nitrates, either separately or in combination, indicated that PO_4–P was rate limiting below 0.59 g-at l^{-1} for a natural mixed population of phytoplankton dominated by the diatom *Thalassiosira antarctica*. At that time, the summer minimum of PO_4–P was 0.34 g-at l^{-1}. According to Walsh (1971) and Allanson et al. (1981), the pattern of silicate distribution indicates that silicates may be the most limiting of the major nutrients to phytoplankton growth.

Still, it may not be the total quantity of nitrogen, phosphorus, and silicate that is important but rather the uptake preferences for a particular molecular species of the inorganic nutrients in relation to the proportions of these species in the environment (Priddle et al. 1986b). An analysis by Priddle et al. (1986b) has indicated the importance of silicate and its ratio to phosphorus in interpreting phytoplankton dynamics near South Georgia. Very high measured concentrations of nitrogen are usually nitrate. However, N-uptake experiments with Antarctic phytoplankton have shown that ammonia, or occasionally urea (where measured), is the preferred nitrogen substrate, with between 50 and 80% of all nitrogen assimilated by Antarctic phytoplankton being in the form of ammonium (Slawyk 1979; Olson 1980; Koike et al. 1981, 1986; Biggs 1982; Gilbert et al. 1982; Ronner et al. 1983; Probyn and Painting 1985), and with the nanophytoplankton showing a higher uptake of ammonia than the microphytoplankton. On the other hand, Colos and Slawyk (1986) concluded that nitrate could account for most of the primary production of the Southern Ocean south of the Polar Front.

Experiments by Koike et al. (1986) in the southern Scotia Sea in February 1981 determined that up to 93% of the phytoplankton nitrogen was at that time assimilated in the form of ammonium, with an overall mean of 78%. Time-course experiments showed that the uptake of nitrate and ammonium overnight amounted to approximately 15 and 50%, respectively, of daytime values. Over the shallow waters of the Scotia shelf, most of the ammonium uptake was associated with the nanophytoplankton. Figure 2.17b and c show profiles of nitrogen uptake rates, together with profiles of nutrients and water density. It can be seen that the coastal waters (Figure 2.17b) had more ammonium than the offshore waters (Figure 2.7c). Uptake rates decreased with depth. Probyn and Painting (1985) have found evidence of nitrogen resource partitioning between algae of different size classes. The average ammonium uptake as a percentage of total nitrogen uptake amounted to 62% for the nanophytoplankton and 75% for the picophytoplankton. In the eastern Scotia Sea, Ronner et al. (1983) found that the summer phytoplankton production subsisted on ammonium (83%), with a lower incorporation of nitrate (14%) and nitrite (1%).

In general, ammonium represents only a small fraction (2–10%) of the inorganic nitrogen pool (Biggs et al. 1983). It is possible that the phytoplankton switch to nitrate nutrition where ammonium levels are low, although Priddle et al. (1986a) found no evidence of this in their studies off of South Georgia. However, Probyn and Painting (1985) used ^{15}N-labeled substrates to measure nutrient preferences of phytoplankton at five Southern Ocean stations and found that high relative uptake of nitrate, particularly by cells >15 μm, occurred at stations with low ammonium and urea concentrations.

FIGURE 2.17 (a) Vertical profiles of nitrate, phosphate, and salicic acid concentrations at 3 stations (Sta. 19, 29, and 30) in an ice-edge phytoplankton bloom in the western Ross Sea. Stations 19 and 20 were the only ones at which nitrate and phosphate were depleted to undetectable concentrations within the surface layer. The profiles of Station 30 are more typical of the general condition within the bloom; while there was clear depletion of nutrient concentrations within the surface layer, the lowest concentrations observed were well above analytical detection limits. (From Nelson, D.M., Smith Jr., W.O., *J. Geophys. Res.*, 36, 1389, 1986. With permission.), (b) Depth profiles of physical, nutritional, and biological properties at a coastal station near Elephant Island in the southern Scotia Sea., (c) Depth profiles of the physical, nutritional, and biological properties at an offshore station in the southern Scotia Sea. (From Koike, I., Holm-Hansen, O., Briggs, D.C., *Mar. Ecol. Prog. Ser.*, 30, 105, 1986. With permission.)

Mengesha et al. (1998) investigated the seasonal variation pf the phytoplankton community structure and nitrogen uptake in the Indian Ocean sector of the Southern Ocean. Absolute nitrogen uptake rates were generally low, but their seasonal variations were highly significant. During spring, the communities displayed high specific nitrate uptake (mean rate $= 0.0048\ h^{-1}$), and diatoms (in the seasonal ice zone), as well as nano- and picoflagellates (in the Permanently Open Ocean Zone and the Polar Frontal Zone) were mainly based on new production (mean f-ratio $= 0.69$). In this period, the availability and relative contributions of ammonia and urea were small, and specific nitrate uptake rates were, respectively, ~ 3 and ~ 5 times higher than the ammonium and urea uptake rates. The transition to summer was accompanied by a significant reduction in nitrate stocks and uptake rate and a shift from predominantly new to regenerated production (f-ratio $= 0.69$–0.39). Ammonium played a major role in the dynamics of phytoplankton nutrition, with a significant (three- to sevenfold) increase in the ammonium stock. Ammonium uptake rates exceeded nitrate uptake rates, confirming the conclusions of Smith and Nelson (1990) that Antarctic phytoplankton can increase their ammonium uptake capacity when provided with higher ambient ammonium.

Thus, in areas of seasonally contrasting growth conditions and heavy selective grazing pressure such as in the MIZ of the Weddell Sea, the seasonal shift in nitrogen uptake regime is paralleled by changes in community structure. In contrast, under certain conditions of persistently favorable (e.g., CCSZ and SIZ) or unfavorable conditions, the nitrogen uptake regime shifts with little change in community structure. Mengesha et al. (1998) concluded that the seasonal shift in nitrogen uptake regime can occur with or without a shift in community structure.

Reay et al. (2001) investigated the impact of low temperatures on nutrient uptake in the vicinity of South Georgia. Phytoplankton from 15 stations were incubated at ambient temperature, and while specimens from 2 stations were investigated at elevated temperatures (ambient plus 3°C, and ambient plus 6°C). Rates of growth, nutrient depletion, ^{15}N-nitrate, and nutrient interaction were all studied. Microalgal growth rates showed a strong positive relationship to temperature elevation, indicating that the ambient temperatures were suboptimal for the phytoplankton community as a whole. Ratios of silicate uptake to chlorophyll *a* increase were high at ambient temperatures and showed a strong negative relationship with temperature elevation. Nitrate uptake rates, measured by ^{15}N-nitrate incorporation, showed a consistent trend of an increased uptake rate at elevated temperatures. Specific nitrate depletion rates, ^{15}N-nitrate uptake rates, and the f ratio all showed an inverse relationship to increasing ammonium concentration. In addition to the microalgal response, the specific affinity of bacteria was significantly reduced at suboptimum temperatures. Thus, the ambient temperature is important in the maintenance of the high-nutrient, low-chlorophyll conditions that are common in the Southern Ocean.

Tréguer and Jacques (1992) have reviewed the dynamics of nutrients and phytoplankton and the fluxes of carbon, nitrogen, and silicon in the Antarctic Ocean. This review focuses on the different subsystems discussed in Section 2.4, the Coastal and Continental Shelf Zone (CCSZ, $0.9\ M\ m^2$), The Sea Ice Zone (SIZ, $16\ M\ m^2$), and the Permanently Open Ocean Zone (POOZ, $14\ M\ m^2$).

2.8.3 MICRONUTRIENTS

A range of mineral micronutrients (Mo, Mn, Co, Zn, Cu, V, B, Mg, Fe) have been shown to be important in plant growth. In addition, a number of organic substances, especially vitamins, are implicated. Volkovinskii (1966) found a positive correlation between phytoplankton production and levels of magnesium and molybdenum in the Weddell Sea. El-Sayed (1968b) concluded that cobalt, zinc, copper, and vanadium may be important, as may be iron (Fogg 1977). Carlucci and Cuhel (1977), after a studying the significance of vitamins B_{12}, thiamine, and biotin in the Indian Ocean sector, concluded that most of the phytoplankton did not require vitamins. However, it is possible that the availability of vitamins could alter the species composition of the phytoplankton without altering the overall rate of phytoplankton production. It is also possible that the availability of trace or micronutrients could be altered by pack ice and iceberg meltwater, thus affecting the productivity or species composition of the waters in the vicinity of pack ice and icebergs. The role of trace elements and organic substances in the ecology of the Southern Ocean would appear to be a profitable research area.

Of the minor elements, iron appears to be of importance to phytoplankton production in the Southern Ocean. This will be discussed in the following section.

2.8.4 IRON

In 1990, Martin et al. (1990a, 1990b) hypothesized that Antarctic phytoplankton suffer from iron deficiency, which prevents them from blooming and using up the plentiful supply of nutrients that are present. They found that the highly productive waters of the Gerlache Strait ($3\ g\ C\ m^{-2}\ day^{-1}$) have an abundant supply of iron ($7.4\ nmol\ kg^{-1}$), which facilitates phytoplankton blooming. In contrast, in the offshore Drake Passage waters ($0.1\ g\ C\ m^{-2}\ day^{-1}$), the dissolved iron levels are so low ($0.16\ nmol\ kg^{-1}$) that the phytoplankton could use less than 10% of the available nutrients. Recent observations have shown that concentrations of dissolved iron in Southern Ocean waters are in the range of 0.08–8 nM. Although the biological availability of operationally defined dissolved iron (< 0.2 or 0.4 nM) to phytoplankton is not clearly elucidated, the experiments of Takeda and Watanabe (1997) on the growth response of Antarctic phytoplankton to iron enrichment suggest that Antarctic phytoplankton species may respond differentially and significantly to changes in iron level. Broad differences among phytoplankton in their adaptations to iron availability have been identified. It has also been shown that growth rates of oceanic phytoplankton are less limited by iron concentration than those of coastal species. However, Takeda and Watanabe (1997) found no differences in their response to iron enrichments between isolates from the open ocean and marginal ice waters. A number of investigators (e.g., Takeda and Watanabe 1997; Timmermans et al. 1998, 2001) have shown that large and small diatoms respond differently to iron availability and enrichment. Iron enrichment led to growth enhancement of the largest size class of phytoplankton (de Baar et al. 1995; Timmermans et al. 1998; Boyd et al. 2000), in particular the chain-forming species (de Baar and Boyd 2000). Timmermans et al (1998) concluded that through bottom-up (i.e., ecophysiological) control, iron plays an important role in the Pacific region of the Southern Ocean. They consider that iron stress may result in low numbers of small-sized phytoplankton and thus reduced numbers of zooplankton. There is also evidence that a combination of silicate and iron stress prevents diatom dominance north of the Polar Front.

Brandini (1993) investigated the impact of iron enrichment on the summer plankton community in Admiralty Bay, King George Island, under stable water column conditions when iron occurred in non-limiting concentrations. The phytoplankton were numerically dominated by nanoflagellates and small pennate diatoms. The protozoa were dominated by tintinnids and heterotrophic dinoflagellates. Although the light/nutrient regime was optimal for autotrophic growth, the grazing pressure of microzooplankton precluded phytoplankton biomass accumulation, maintaining low chlorophyll *a* concentrations. The results of Brandini's investigations showed clearly that fertilization of the natural environment with iron does not necessarily increase phytoplankton biomass when the microbial network is the dominant community and the grazer response of such a community is unchecked.

In spite of the evidence discussed above, the conclusions have been challenged by other workers (e.g., Dugdale and Wilkerson 1990; Broecker 1990). The iron hypothesis was tested in a series of experiments in the Weddell and Scotia Seas encompassing different water masses and various phytoplankton communities, biomass, and dynamic spring and summer conditions (Baar et al. 1996; Timmermans et al. 1998). Iron always stimulated chlorophyll *a* synthesis and nutrient assimilation. However, the controls also steadily outgrew typical chlorophyll *a* and particulate organic carbon (POC) levels in ambient waters. This strongly suggested that despite the enhancement of phytoplankton growth, iron was not the major factor controlling phytoplankton growth in the Weddell and Scotia Seas. Banse (1990) points out that iron limitation might apply only to the larger diatoms. In the oligotrophic waters of the Southern Ocean, as we have seen, the phytoplankton is dominated by smaller pico- and nanophytoplankton. Thus, it seems that the role of iron in phytoplankton growth in the Southern Ocean is not yet fully resolved.

2.8.5 NUTRIENT CYCLING IN THE SOUTHERN OCEAN

The limiting elemental resource for plant production in most oceanic regions is believed to be nitrogen (Carpenter and Capone 1983), which is supplied in various chemical forms from a variety of sources. Thus, primary production can be partitioned according to the source and oxidation state of the nitrogen substances utilized (Dugdale and Goering 1967). This partition is based on whether the nitrogen is supplied by regeneration from organisms within the euphotic zone (regenerated production, P_r) or from outside the photic zone (new production, P_{new}). In the open ocean, the dominant contribution to the externally supplied nitrogen is in the form of nitrate (Fogg 1982), whereas regenerated production depends only on reduced nitrogen compounds, in particular ammonia. The sum of P_{new} and P_r is referred to as the total production, P_T. Total production is the nitrogen equivalent of gross production (P_g), in the sense that it represents the sum total of the nitrogen assimilation of the photoautrophs. However, according to Platt et al. (1989), since there is no evidence that phytoplankton re-mineralize nitrogen, a case can be made for equating P_T with P_g. Figure 2.18 shows a schematic diagram of the principal fluxes for new and regenerated production.

"Regenerated production" is intimately related to the rates of re-mineralization of organic matter by biological and chemical processes in the euphotic zone. The microbial processes that are involved in this process will be discussed further in Chapter 13. "New production," on the other hand, is maintained by the supply of nitrogen by advection and turbulence from deeper waters. Studies assessing the roles of "new" nitrogen (in the oxidized form as nitrate) and "regenerated" nitrogen (in the form of ammonium) have given conflicting results depending on the type of system studied (e.g., open ocean, ice-edge bloom, or coastal waters), and the time of the year. Ammonium appears to play an important role in the nutrition of Antarctic phytoplankton in the open ocean and is generally present in substantial amounts throughout the euphotic zone. Concentrations have been found to increase from 0.1 μM in the late winter to early spring (Olson 1980) to over 1.0 μM in late summer and autumn (Gilbert et al. 1982; Ronner et al. 1983). Investigations, mostly in offshore waters (Slawyk 1979; Olson 1980; Gilbert et al. 1982; Ronner et al. 1983) have shown that Antarctic phytoplankton generally derive at least 50% of their nitrogen from ammonium. In an investigation of the coastal waters in the Scotia Sea in February and March 1981, Koike et al. (1986) found that, in spite of the high concentration of nitrate present (19–21 μM), up to 93% of the phytoplankton was assimilated in the form of ammonium. Over the shallow waters of the Scotia Arc close to Elephant Island, most of the ammonium was associated with nanophytoplankton, which actively assimilated both ammonium and nitrate, while the microphytoplankton assimilated mostly nitrate.

In contrast, Nelson and Smith (1986) found in their above-mentioned study of phytoplankton bloom dynamics in the western Ross Sea ice edge that ammonium

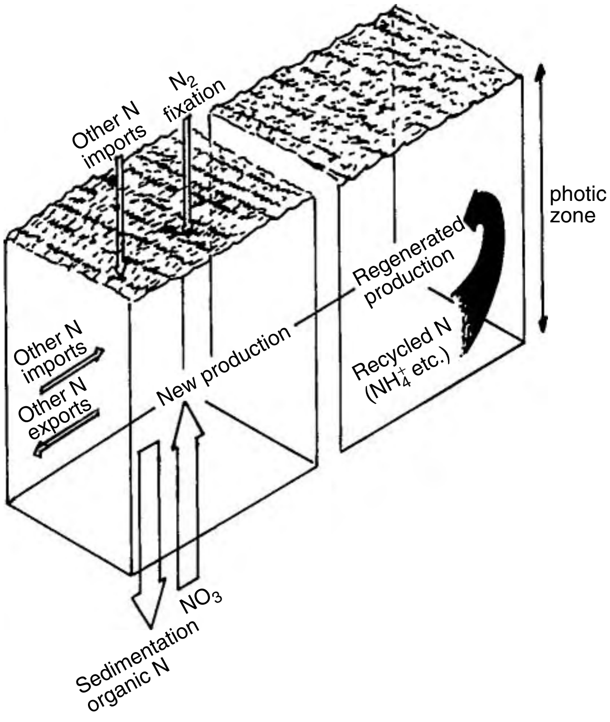


FIGURE 2.18 Schematic diagram of the principal fluxes for new and regenerated primary production. The sole support for the regenerated production is reduced nitrogen supplied within the photic zone by the excretion of organisms. New production depends on nitrogen supplied from outside the photic zone, of which the dominant flux is the delivery of nitrate from below. In the steady state, this vertical flux is balanced by the downward flux of nitrogen in sedimenting particles. Over a period of a year, current evidence shows that in the open ocean, new production is very roughly from one-third to one-half of the regenerated production, but may deviate considerably from this figure over short time and space scales. (From Platt, T., et al., *Mar. Ecol. Prog. Ser.*, 52, 77, 1989. With permission.)

concentrations within the bloom were frequently below detection limits (<0.1 μM), and nearly always less than 0.25 μM. Rates of nitrate uptake were high enough to satisfy approximately 65% of the phytoplankton nitrogen demand estimated from C-primary productivity and particulate organic carbon-nitrogen ratios. The mean rate of biogenic silica production within the bloom was 38 mmol Si m^{-2} day^{-1}, which is an order of magnitude higher than previous estimates for the Southern Ocean remote from the ice edge (Nelson et al. 1989). The significance of the observed high rates of nitrogen uptake and biogenic silica production in the ice-edge phytoplankton blooms will be discussed further in Chapter 13.

To date, there are comparatively few data available on microbial re-mineralization of inorganic nutrients in the Southern Ocean, but it appears that nitrogen, and probably phosphate, are recycled rapidly in the euphotic zone. Ronner et al. (1983) consider that nitrogen may be recycled approximately eight times before it is lost from the euphotic zone. Although a number of studies suggest rapid recycling of nutrients through the microbial community (Ronner et al. 1983; Holm-Hansen et al. 1982; Le Jehan and Tréguer 1985), levels of ammonium ions remain low in the Southern Ocean, indicating that it is rapidly used by the phytoplankton.

Holm-Hansen et al. (1982) posed the question, “What is the source of ammonia in Antarctic waters?” Since ammonium is not detectable in deep-water upwelling, upwelling could not be the source. Very small amounts originate from the atmosphere or the melting of ice. Thus, it appears that nearly all of the ammonium must originate from in situ processes occurring in the euphotic zone. It has been suggested that a maximum 2% of the ammonium flux could be accounted for by the grazing effects of microplankton greater than 200 μm, so it can be concluded that over 90% of the ammonium results from the activities of microbial organisms.

2.8.6 TEMPERATURE

Early workers (e.g., Gran 1932; Hart 1934) thought that Antarctic phytoplankton were fully adapted to the prevailing low temperatures of the Southern Ocean. Since then, however, temperature has been commonly listed as one of the major factors influencing phytoplankton production (e.g., Saijo and Kawashi 1964; Tilzer et al. 1986). In the Southern Ocean, surface water temperatures reach as low as −1.8°C, with a maximum summer temperature of around 4.0°C. It is increasingly accepted that the majority of oceanic phytoplankton in the Southern Ocean are psychrotolerant, rather than psychrophilic, with temperature optima for growth and photosynthesis far in excess of any environmental temperature encountered (Tilzer et al. 1986). In low-temperature environments, active uptake of inorganic nutrients such as nitrate, silicate and, in particular, iron may be reduced.

The effects of temperature on photosynthetic carbon uptake have been investigated for a number of phytoplankton species (Bunt 1968a; Whitaker 1977b; Neori and Holm-Hansen 1982; Jacques 1983; Hoepifner 1994; Tilzer et al. 1985, 1986; Tizler and Dubinsky 1987; Priscu et al. 1987; Reay et al. 2001). The species studied constantly showed maximum uptake of inorganic carbon at temperatures in the range of 7–12°C, well above the ambient temperature range. Neori and Holm-Hansen (1982), in experiments conducted in the Scotia Sea and northwestern Weddell Sea, concluded that temperature limited primary production rates at times when light intensity was saturating the photochemical apparatus of the cell. Since the phytoplankton are saturated by light intensities that are approximately 10–15% of that generally incident on the sea surface, it can be assumed that temperature will be a rate-controlling factor in the upper 10–12 m of the water column (Figure 2.19) (El-Sayed 1988a). Fukuchi et al. (1986) observed variable positive or negative relationships between temperature and chlorophyll in the zones of the Subtropical Convergence, the Subantarctic Front, and the Antarctic Convergence. This variable relationship has also been noted by Hayes et al. (1984) and Taniguchi et al.

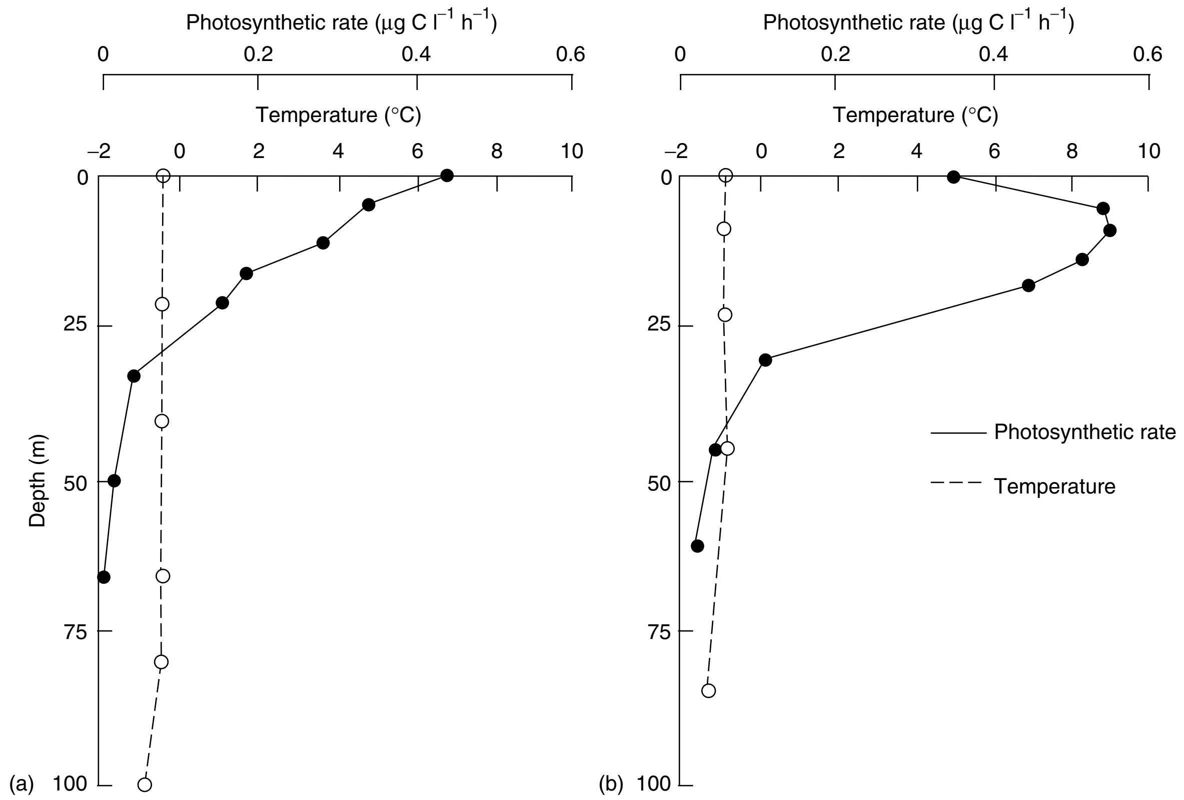


FIGURE 2.19 Vertical distribution of photosynthetic rate and temperature in the Ross Sea during *Eltanin* cruise, January–February 1972: Station 14 (a), where PAR (photosynthetically available radiation) was 32 cal cm^{-2} (1/2 light $day)^{-1}$; Station 16 (b), where PAR was 22 cal cm^{-2} (1/2 light $day)^{-1}$. (From Holm-Hansen, O. et al., *Adaptations Within Antarctic Ecosystems*, Llano, G. A., Ed., 11, 1977. With permission.)

(1986). Tilzer et al. (1986) studied carbon-fixation rates of Southern Ocean phytoplankton incubated at various irradiances and temperatures. They found that the rates of both light-saturated and light-induced-photosynthesis were temperature dependent in the range of −1.5 to 5.0°C, with values for Q10 of 4.2 and 2.6, respectively. Above 5°C, no temperature enhancement could be detected. The authors concluded that Antarctic marine phytoplankton had not developed mechanisms to overcome the inhibiting effects of low temperature on photosynthesis, although the temperature optimum for photosynthesis was low in comparison to that for phytoplankton from lower latitudes.

Phytoplankton from the southwest Atlantic sector of the Southern Ocean were incubated by Reay et al. (2001) at ambient temperature and two elevated temperatures (ambient plus 3 and ambient plus 6°C). Rates of growth, nutrient depletion, ^{15}N-nitrate, and nutrient interaction were also studied. Microalgal growth rates showed a strong positive relationship to temperature elevation, indicating ambient temperatures were suboptimal for the phytoplankton community as a whole. Ratios of silicate uptake to chlorophyll *a* increase were high at ambient temperatures and showed a strong negative relationship with temperature elevation. Nitrate-uptake rates, measured by ^{15}N-nitrate incorporation, showed a consistent trend of increased uptake rate at elevated temperatures. Specific nitrate-depletion rates, ^{15}N-nitrate uptake rates, and *f* ratio all showed an inverse relationship to increasing ammonium concentration. Similarly, in a previous study Reay et al. (1999) demonstrated that the specific affinity of a range of bacteria and marine microalgae for nitrate is significantly reduced at suboptimal temperatures. The results of these studies imply that ambient temperature, in addition to direct iron limitation, is important for the maintenance of the high-nutrient, low-chlorophyll conditions common in the Southern Ocean.

Temperature optima for growth (measured as the increase in cell numbers or biomass), as opposed to carbon fixation, may be closer to ambient temperatures, and growth rates at ambient temperatures may exceed predicted values, such as those established by Eppley (1972). Recorded specific growth rates for Antarctic phytoplankton are of the order of 0.1–0.3 doublings per day in the Ross Sea (Holm-Hansen et al. 1977), between 0.4 and 0.6 doublings per day in the southern Indian Ocean (Jacques and Minas 1981), and 0.51–2.10 in the Indian Ocean south of Africa (Miller et al. 1985). The maximum rate of 2.10 doublings per day was higher than the previously recorded maximum of 0.7 doublings per day (El-Sayed and Taguchi 1981). The mean of 1.23 doublings per day found by Miller et al. (1985) is also significantly higher than other recorded means, and it exceeds Eppley's (1972) theoretically predicted maximum growth rate for phytoplankton at 1.0°C (0.91 doublings per

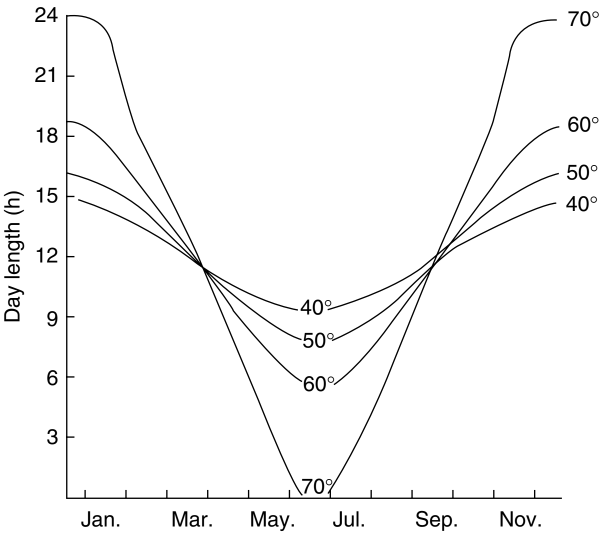


FIGURE 2.20 Latitudinal variation in day length over the year and hence in the daily incident radiation in the Southern Ocean.

day). There is thus a wide variation in recorded growth rates with evidence both in favor of and against the hypothesis that the low temperatures of Antarctic waters do limit algal growth rates. It would appear that under certain conditions growth rates are limited, while under others the low temperatures do not consistently limit phytoplankton biomass production, thus suggesting that phytoplankton photosynthesis in Antarctic waters may show *some* adaptive response to low ambient temperatures.

2.8.7 LIGHT AND PHOTOSYNTHESIS

Variations in available light, intensity, duration, and spectra are important factors in influencing phytoplankton growth in the Southern Ocean (Smith and Sakshaug 1990). Total incident radiation is a function of latitude, with higher latitudes experiencing more drastic variations (Figure 2.20). Regions within the Antarctic Circle (66°S) will experience a period of complete darkness in winter (60 days at 75°S, 100 days at 80°S). This variation in light intensity is illustrated in Figure 2.21, which plots the mean values of radiant energy (with average cloudiness), together with values of primary production and standing crop of phytoplankton collected in Antarctic waters. It is evident that phytoplankton biomass and primary production are directly related to the amount of energy received. During the summer months, the amount of light energy reaching the water column will depend on the sun or the transparency of the atmosphere. Near the Antarctic coast, skies are often lightly clouded or clear. Here, incident light may reach up to 2,500 μmol photons m^{-2} sec^{-1} on a summer day, and total daily fluxes exceed those of tropical latitudes (Holm-Hansen et al. 1977). Photoinhibition phenomena may frequently occur under this light condition. On the other hand, over the open ocean low pressure systems develop continuously,

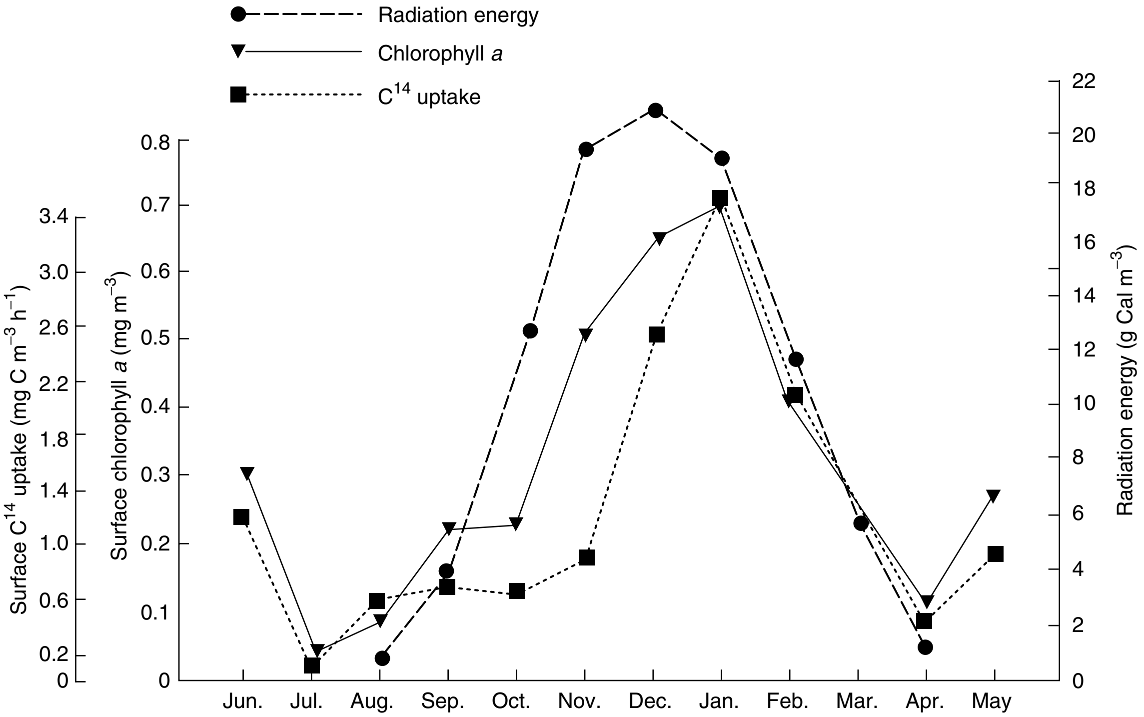


FIGURE 2.21 Monthly variation of radiant energy (with average cloudiness) at Maudheim Station (71°03′S, 10°56′W) compared with monthly changes in surface chlorophyll *a* and C^{14} uptake in Antarctic waters. (From El-Sayed, S. Z., *Symposium on Antarctic Ice and Water Masses*, 35, 35, 1971a. With permission.)

resulting in persistent cloud cover that attenuates 40–90% of the light.

Under clear sky conditions, it is the progressive changes in daylight and solar zenith angle (Figure 2.22A) that determine seasonal changes in daily integrated irradiance (Figure 2.22B) reaching any given location. However, at the Palmer Station LTER Station B (Moline and Preslen 1997) from late spring through the summer of 1991 and 1992, incident Q_{par} was routinely less than the theoretical limit (Figure 2.23B). On average, only $73 \pm 29\%$ of daily Q_{par} reached the study site (Figure 2.23C). Fluctuations in daily integrated Q_{par} could vary by two to three times within a day or two of each other. On the time scale of a few weeks, integrated Q_{par} appeared to reflect the somewhat periodic nature of Antarctic storms and their associated increased cloud cover. During a storm event during the last week in January, only 28% of daily Q_{par} reached the study site. As in other studies (Holm-Hansen and Mitchell 1991), incident Q_{par} was occasionally higher than the calculated maximum for clear skies, and is thought to be due to the reflection from snow and ice cover.

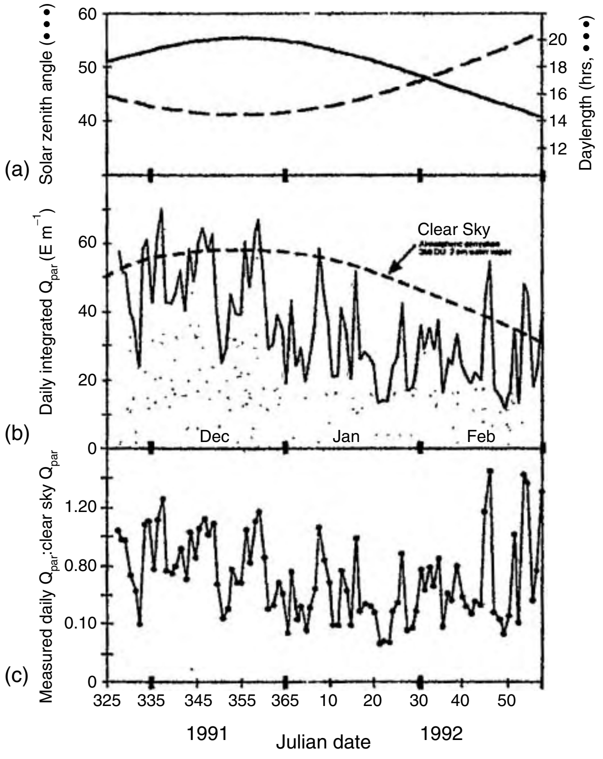


FIGURE 2.22 (A) Seasonal changes in midday solar zenith (*dashed line*) and daylength (*solid line*) at the latitude (54°S) for Palmer LTER; (B) Comparison of the seasonal changes in the measured (*shaded area*) and the theoretical maximum (clear sky, *dashed line*) daily integrated Q_{par} (E m^{-2} day^{-1}) for Palmer Station during the late austral spring and summer of 1991–1992; (C) Seasonal changes in the above-water ratio of measured clear-sky flux of daily integrated Q_{par} Palmer LTER Sta b. (From Moline, M.A., Preslen, B.B., *Polar Biol.*, 17, 42, 1997. With permission.)

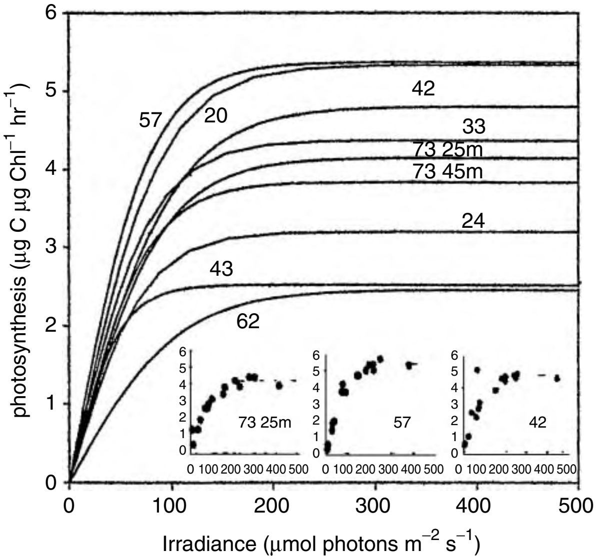


FIGURE 2.23 Photosynthesis versus irradiance for phytoplankton from Stations 20, 24, 33, 42, 43, 57, 62, 73, (depth 25 m) and 73 (depth 45 m). (From Sakshaug, F., Slagstad, D., *Symposium on Polar Marine Ecology*, Sakshaud, E. and Hopkins, C. E., Eds., 1991. With permission.)

Superimposed upon the annual pattern of incident radiance are a number of other factors influencing the availability of light energy to the phytoplankton. First, the sun's height above the horizon is relatively lower for more of the year than in temperate and tropical latitudes. This low angle of incidence increases the reflection from the sea surface. The period of effective submarine light is also reduced. Second, the Southern Ocean is particularly stormy, affecting surface reflection as well as producing bubbles that considerably reduce transmission through the surface waters (Powell and Clarke 1936). Light variation induced by turbulent mixing (Falkowski and Winick 1981) operates on a highly variable time scale. In experiments designed to study the effects of fluctuating light regimes, it was found that cells grown under alternating periods of light and dark, stimulating the conditions of vertical mixing, had a higher rate of productivity than algae grown in continuous light. This increased efficiency of light utilization in an environment characterized by fluctuating light conditions is probably an adaptation that enables the algae to overcome such restraints and attain a higher productivity than expected. Third, 56% of the Southern Ocean is covered with ice during the winter. Most of this breaks up, drifts north, and melts during the summer—but approximately 17.5% of the sea ice remains as fast or pack ice. The ice, and especially the snow cover, reduces considerably the amount of radiation entering the water column and changes its spectral quality (Hoshiai 1969; Whitaker 1982; Palmisano et al. 1985b) (see Chapter 3). This may amplify by 10,000 times the annual variation in the amount of light that enters the water column. The combination of these varying factors is reflected in the extreme seasonality of phytoplankon growth in the Southern Ocean.

The amount of light penetrating the water column depends on the absorption by suspended particles. While non-alga (inorganic particles) light absorption in the Southern Ocean is particularly low die to minimal terrestrial influx (Mitchell 1992), phytoplankton pigment concentration within the water column influences not only light intensity but also the spectral composition of the underwater light, as well (Tilzer et al. 1994).

As detailed in Table 2.5, a number of parameters are used to measure the relationships between light and photosynthesis. Dower et al. (1996) investigated phytoplankton biomass, P–I relationships, and primary production in the Weddell Sea during the austral autumn. P–I parameters in Antarctic waters exhibit a "bewildering variability" (Figure 2.23; Sakshaug and Slagstad 1991). Dower et al. (1996) recorded maximum photosynthetic rates (Pbmax) of $x = 1.25$ mg C mg chl a^{-1} h^{-1} similar to those found in other autumn and winter studies ($x = 1.19$ mg C mg chl a^{-1} h^{-1}) (Brightman and Smith 1989). The initial slope of the P–I curve, x^{B}, falls within the range 0.019–0.074 mg C mg chl a^{-1} h^{-1} (μmol m^{-2} sec^{-1})$^{-1}$, which is similar to the slopes recorded by Brightman and Smith (1989) under winter conditions. The light intensity required to saturate photosynthesis (I_{k}) appears to vary considerably in different systems under different environmental conditions. During studies carried out in March 1977 and 1980, Jacques (1983) found I_{k} to be between 13 and 46 μmol m^{-2} sec^{-1}, which suggests that the phytoplankton was shade adapted. Dower et al. found a mean I_{k} of 32.2 μmol m^{-2} sec^{-1} (range 20–45 μmol m^{-2} sec^{-1}), while winter photosynthesis-irradiance experiments showed more variation, with a higher mean of 60 μmol m^{-2} sec^{-1} at the surface and 40 μmol m^{-2} sec^{-1} at 50 m (Brightman and Smith 1989). In lower latitudes and more temperate regions, I_{k} often exceeds 300 μmol m^{-2} sec^{-1} (Nelson and Smith 1991; Dower and Lucas 1993). On the whole, P^{B}max is higher during spring and summer, while x^{B} does not show much variation (Rivkin and Putt 1987; Brightman and Smith 1989). Variability in I_{k} at high latitudes has been coupled with variability of P^{B}max, which is higher during spring and summer, while x^{B} does not show much variation (Rivkin and Putt 1987; Brightman and Smith 1989). Variability in I_{k} at high latitudes has been coupled with variability in P^{B}max, which has been attributed to temperature effects (Harrison and Platt 1986). Lack of agreement between different studies can be explained by the use of differing methodologies, community structure, phytoplankton size classes, and other factors (Sakshaug and Slagstad 1991).

The inhibition coefficient B is high, ranging from 0.0005 to 0.0258 mg C mg chl a^{-1} h^{-1} (μmol m^{-2} sec^{-1})$^{-1}$. Because of low submarine irradiance due to decreasing daylight and predominantly overcast conditions, the significance of photoinhibition in polar regions is negligible, especially in terms of daily integrated production (Skashaug and Slagstad 1991). The net photocompensation irradiances (I_{n}) chosen by Dower et al. (1996) for calculating the critical depth was based on information in the literature that shows I_{n} to range from 0.1 to 35 μmol m^{-2} sec^{-1} (see Raymont 1980; Smith 1987; Nelson and Smith 1991). The compensation light intensity of polar phytoplankton is lower than that of temperate and tropical phytoplankton because of its physiological adaptation to low light intensities and the resultant low respiration rates (El-Sayed et al. 1983; Palmisano et al. 1985c; Smith 1987; Tilzer and Dubinsky 1987). The relationships between the mixing depths, Z_{mix} and $Z_{c,r}$ is important. If Z_{mix} is deeper than $Z_{c,r}$, cells will spend time in an unfavorable light environment; alternatively, production will be enhanced if Z_{mix} is shallower than $Z_{c,r}$, as cells will be

TABLE 2.5
Parameters Used to Measure the Relationships Between Light and Photosynthesis

a^*	In vivo spectral average optical absorption cross-section normalized to chlorophyll a (m^2 per mg chlorophyll)
$a^*(\lambda)$	In vivo cross-section absorption coefficient of phytoplankton cell normalized to chlorophyll a (m^2 mg^{-1} chl a)
AN	Assimilation number (μg C μg chl a^{-1} h^{-1})
Chl	Chlorophyll a concentration (μg chl a l^{-1})
E	Irradiance (μmol q m^{-2}sec^{-1})
E_{k}	Light intensity at which photosynthesis approaches saturation (μmol q m^{-2}sec^{-1})
K_{c}	Specific vertical attenuation coefficient for downward irradiance per unit chlorophyll a (m^2 mg^{-1} chl a)
K_{d}	Attenuation coefficient of downward irradiance (m^{-1})
OD	Optical density
PAR	Photosynthetically available radiation between 400 and 700 nm
P	Photosynthesis [μg C (μg chl a^{-1})h^{-1}]
P_{max}	Maximal photosynthetic rate at light saturation [μg C (μg chl a)$^{-1}$ h^{-1}]
x	Initial slope of the photosynthesis curve [μg C (μg chl a)$^{-1}$h^{-1} (μmol q m^{-2} sec^{-1})$^{-1}$]
β	Coefficient corrected for path length amplification with the glass filter
λ	Wavelength (nm)
ϕ	Quantum yield (mol CO_2 mol q^{-1})
ϕ_{max}	Maximum quantum yield (mol O_2 mol q^{-1})

mixed in a constantly favorable light environment. Stabilization of the water column by meltwater, solar insolation, and reduced wind speeds in summer are critical in raising Z_{mix} to the level of $Z_{c,r}$. During winter, wind stress creates considerable water column instability, thus deepening the upper mixed layer. Simultaneously, the light environment deteriorates, so that $Z_{c,r}$ becomes shallower than Z_{mix}.

It is thus clear that the Antarctic phytoplankton are subjected to highly variable light regimes that can fluctuate on a variety of time scales. There is evidence that the phytoplankton of the pack ice zone are adapted to the low light levels caused by the presence of ice. Holm-Hansen and Mitchell (1991) found that the summer populations in the southwestern Bransfield Strait were low-light adapted, as they showed low $P_{\max}$ values (1.1 mg C mg chl a^{-1} h^{-1}), low saturating light values I_{k} (18 μE m^{-2} sec^{-1}), high initial slope of the fitted curve to plotted assimilation numbers, AN (0.06 (mg C mg chl a^{-1} hr^{-1}/μE m^{-2} sec^{-1})), and a compensation point for net activated fixation of CO_2 of 1.0 E m^{-2} sec^{-1}. The $P_{\max}$ was higher than those reported by Tilzer et al. (1986), but similar to the mean value reported for the same region by Brightman and Smith (1989) and to the values reported for Arctic waters (Harrison and Platt 1986). The observed AN is higher, and I_{k} is lower, than the values of Tilzer et al. (1986), Sakshaug and Holm-Hansen (1986), and Brightman and Smith (1989). Holm-Hansen and Mitchell's (1991) AN value, however, was based on in situ observations, and the algae in their study were low-light adapted.

In their study of the effect of radiant energy on the photosynthetic activity of Antarctic phytoplankton, Holm-Hansen et al. (1977) found a high degree of correlation between the intensity of the solar radiation and the photosynthetic rates in the euphotic zone. When the incident light was high, photosynthetic rates were low in the surface waters; these rates increased with depth. In contrast, when incident light was low, photosynthetic rates remained constant in the upper waters of the euphotic zone or were higher in the surface waters (Figure 2.23). These results were most likely due to photoinhibitation. The threshold for photoinhibition for Antarctic phytoplankton was calculated to be in the range of 40–50 cal m^{-2} (half light day)$^{-1}$. Sakshaug and Holm-Hansen (1986) have shown that the photochemical apparatus of Antarctic phytoplankton is "saturated" at between 100 and 180 E m^{-2} sec^{-1}, depending on the depth from which the sample was taken. As the incident light flux (on a sunny day) is about 1,500 μE m^{-2} sec^{-1}, it is evident that the phytoplankton in the surface waters will be either "saturated" by the ambient flux or photoinhibited. Jacques (1983) contends that during such times the phytoplankton are unable to use the available light optimally in the euphotic zone.

Particularly important is the effect of temperature on the compensation-point light intensity (Heywood and Whitaker 1984). The compensation-point light intensity is that point at which the production of carbon exactly balances carbon loss through metabolic processes (as indicated by respiration). Cell growth occurs when light levels are above the compensation-light intensity. At the low temperature of the Southern Ocean, the rate of respiration (or carbon loss) is suppressed more than the photosynthetic rate (carbon gain). The result is an increase in net production for a given light intensity, and the compensation-point light intensity is correspondingly lowered Tilzer and Dobinsky (1987) studied the effects of temperature and day length on Antarctic phytoplankton growth. Based on the results, they suggested that, with ample light energy supply during the long summer days in Antarctic waters, potential daily growth rates are not severely affected by the prevailing low temperatures. They also concluded that if the energy supply is restricted by short days and deep water column mixing, subsequent reduced respiration rates would allow the algae to survive.

Tilzer et al. (1986) in studies of phytoplankton photosynthesis in the Bransfield Strait and the Scotia Sea found that photosynthetic capacity (photosynthesis per unit of chlorophyll *a* at optimum light) and maximum quantum yield of photosynthesis (moles of carbon dioxide assimilation per mole light quantum absorbed) on average were smaller by factors of seven and four, respectively, than in phytoplankton at lower latitudes. They concluded that, because the utilization efficiency of incident radiation was reduced in the Antarctic by both reduction in the photosynthetic capacity and lower light-limited quantum yields, the phytoplankton can utilize incident light only inefficiently, even in situations where biomass accumulation is high.

2.8.8 VERTICAL MIXING AND STABILITY OF THE WATER COLUMN

A number of investigators (Baarud and Klem 1931; Sverdrup 1953; Pingnee 1978; Mengsha et al. 1998; Bracher 1999) have drawn attention to the importance of the water column's stability in controlling primary production and hence phytoplankton biomass. The length of time that the phytoplankton cells remain within the euphotic zone depends on the extent of vertical mixing (Lewis et al. 1984). Sverdrup (1953) demonstrated theoretically that phytoplankton blooms will only occur when the depth of the mixed layer is less than the critical depth (the depth at which waters can be mixed without stopping phytoplankton growth). The critical depth in the Southern Ocean is generally between 150 and 200 m (Jacques and Minas 1981). The surface water of the Southern Ocean is characteristically well mixed, with little vertical structure in the distribution of inorganic nutrients. Mixed layer depths in the Southern Ocean are often difficult to define in the absence of a pycnocline, but usually they are greater than 100 m. Euphotic depth (the depth to which 1% of the incident radiation penetrates) varies from 20 to 100 m over much of the Southern Ocean (Walsh 1971; Gilbert et al. 1982; Priddle et al. 1986a, 1986b). It would therefore seem that Sverdrup's critical depth hypothesis could not explain low phytoplankton production in the Southern Ocean (Jacques 1981). However, El-Sayed (1987) postulated that turbulence within the euphotic zone played an insignificant role in preventing large increases in phytoplankton biomass in the Southern Ocean. Sakshaug and Holm-Hansen (1984) reported that for ten stations in the Scotia Sea when chlorophyll *a* was >2.0 mg m^{-3}, the pycnocline was situated at 20–40 m. They speculated that 50 m may be the maximum pycnocline depth for a bloom to develop. Thus, the presence of a homogeneous (i.e., isothermal) water column extending to depths of 50–100 m during most of the year hinders the development of a bloom and contributes to the prevalence of low primary production in Antarctic waters. It is of interest that the *Discovery* investigations found that the depth to which wind action was generally effective in overturning the water column in the open ocean (i.e., the depth of frictional resistance) (Ekman 1928) ranged from 60 to 80 m, and that the water was generally fairly uniform to a depth of 80 m, especially after storms (Deacon 1937). Heywood and Whittaker (1984) observed a discontinuity layer at 112 m after a two-day storm at latitude 55°S (in the sector between 20 and 30°E), and Nast and Gieskes (1986) reported a deep mixed layer (up to 200 m) north of Elephant Island as a result of high wind forces.

The underwater light field, which phytoplankton encounter, is influenced by the upper mixed layer (UML) depth, which is associated with the vertical stability of the water column. In the Southern Ocean, density stratification is caused by differences in salinity rather than temperature. Strongly stratified regions have only been observed around land masses, in the MIZ, and in an area of high stability at sloping frontal edges (Orsi et al. 1995). Waters with shallow and rather stable ULMs were found to be essential for the formation of Antarctic phytoplankton blooms (El-Sayed 1984; Smith and Nelson 1985a, 1985b; Legendre 1985; Perissinotto et al. 1990; Laubscher et al. 1993; Bracher et al. 1999). In shallow UMLs, phytoplankton are held above the critical depth, which, compared to conditions at lower latitudes, have been suggested to be deeper in the Antarctic Ocean than under conditions of higher water temperatures; this has been inferred from the observation that respiration rates exhibited smaller temperature dependence than light-saturated photosynthesis (Tilzer and Dubinski 1987). In contrast, weak vertical stability of surface water prevents phytoplankton from remaining in the optimum light zone long enough for extensive production (Jacques 1989).

The development of shallow ULMs within the two blooming areas, MIZ and APF, are caused differently. In the Marginal Ice Zone (MIZ) during the seasonal cycle sea ice forms and melts. The melting of the sea ice in spring and summer produces low-salinity water. If this is not dispersed, the surface water produces a stable layer subject to high irradiance in which rapid growth can occur (Savidge et al. 1996). The Antarctic Polar Front (APF) is the boundary of two main water masses, where warm waters from the mid-latitudes meet colder waters from the Antarctic area; the region is a site of substantial mesoscale activity, and meanders and eddies are typical (e.g., Gille and Kelly 1996).

The vertical stability induced by meltwater has also been suggested as a significant process in initiating and sustaining near-ice phytoplankton blooms. Mitchell and Holm-Hansen (1991) in their multidisciplinary grid survey of the southwestern Bransfield Strait over the period of December through March observed massive persistent mid-summer phytoplankton blooms (>10 mg chl *a* + phaeopigments m^{-2}) where there were shallow mixed layers (ULMs) of <20 m caused by meltwater stabilization. Stations with low phytoplankton biomass had deep ULMs (>20 m) with small density gradients. The role of such melting and its impact on phytoplankton production will be considered in detail in Chapter 13.

Bottom topography may, on a regional basis, play an important role in inducing vertical mixing. This was first suggested by Hart (1934) and corroborated by El-Sayed and Jitts (1973) at a station in close proximity to Banzare Bank, which was notable for its extremely high stocks of phytoplankton and zooplankton. Lutjeharms et al. (1985) describe the occurrence of high levels of primary productivity and chlorophyll *a* concentrations, from a cruise between Africa and the Antarctic continent, at sea surface fronts wherever such fronts have the characteristic of a convergence. Information gathered by the Coastal Zone Colour Scanner of the Nimbus 7 satellite off of South Africa showed a clear relationship between the horizontal shear edges of currents and biological enhancement. Lutjeharms et al. (1985) recognized two types of fronts (Figure 2.24): vertical convergence zones and horizontal shearing zones. In the former, conditions favorable to increased primary productivity may be created by an increase in density stratification in the upper layer, enhancing vertical stability and causing retention of the phytoplankton in the euphotic zone. Higher-than-average values of chlorophyll *a* and primary production have been reported from the vicinity of the Polar Front (El-Sayed and Weber 1982; Allanson et al. 1981; Yamaguchi and Shibata 1982). It is of interest that Kennett (1977) contends that the high rates of siliceous biogenic sedimentation at the Polar Front may be indicative of substantial primary production in the surface waters of this region. However, the continuous advection of phytoplankton into the frontal zone may be a mechanical means of increasing chlorophyll *a* concentrations without necessarily increasing primary production. A number of investigators (Grinley and Lane 1979; Allanson et al. 1985; Grinley and David 1985) have reported chlorophyll *a* levels, primary production, and zooplankton biomass in the lee of islands such as the Marion and Prince Edward Islands. Wind shear, when coupled with island effects on the structure of the West Wind Drift, causes vortex fields to be set up in the lee of the island, with consequent upwelling Figure 2.24.

2.8.9 GRAZING

In the Southern Ocean, euphausiids (particularly *Euphausia superba*) may constitute a substantial proportion of the zooplankton biomass, and consequently their grazing can have a significant impact on the phytoplankton. Being primarily herbivorous, Antarctic krill would be expected to exert considerable grazing pressure on the phytoplankton.

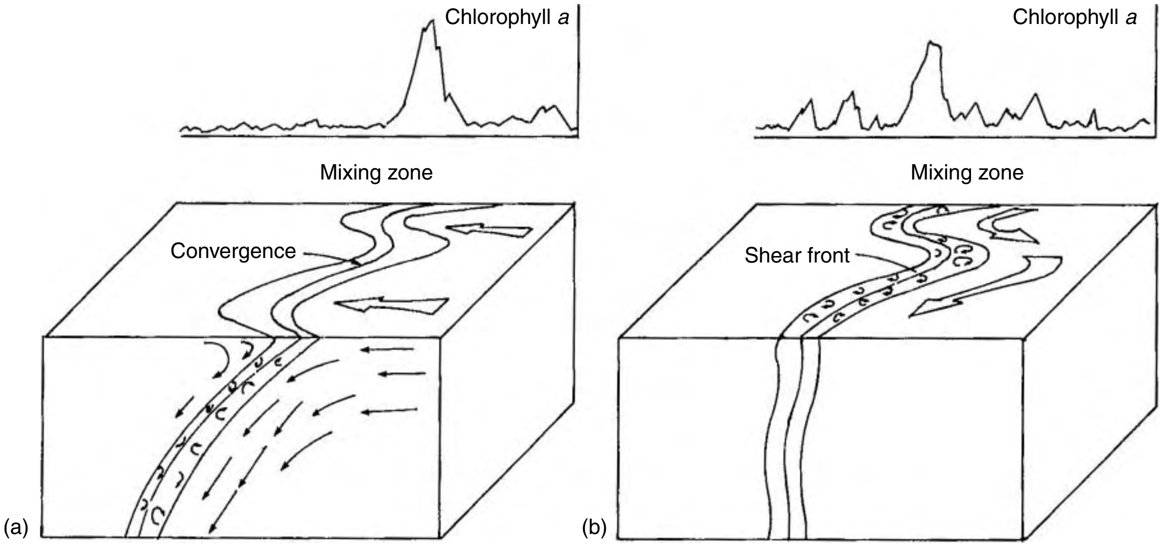


FIGURE 2.24 Schematic illustration of the two types of dynamic ocean fronts found in the Southern Ocean, and the distribution of chlorophyll *a* concentrations at the sea surface across them: (a) a vertical convergence zone; (b) a horizontal shear front. (From Lutjeharms, J.R.E., Walter, N.M., Allanson, B.R., *Antarctic Nutrient Cycles and Food Websw*, Siegfried, W.R., Condy, P.R., Laws, R.M., Springer-Verlag, Berlin Heidelberg, 11, 1985. With permission.)

As krill exhibit a preference for large cells, especially chain-forming diatoms (Pavlov 1969; Meyer and El-Sayed 1983), it is expected that extensive grazing by krill could result in changes in the species composition of the phytoplankton community, with a relative increase in the smaller nano- and picophytoplankton (Quenton and Ross 1985; Priddle et al. 1986a). In areas where high concentrations of *E. superba* have been found, low phytoplankton stocks have been encountered; this inverse relationship has been attributed to the effects of sustained grazing pressure (Uribe 1982; El-Sayed 1984; Whitaker 1982). Weber and El-Sayed (1986a) concluded that while over the range of 4–20 km the variability in phytoplankton biomass was largely determined by physical processes, the steepness of the flourescence spectrum relative to the temperature spectra, together with consistent coherence between phytoplankton and krill profiles, suggested that krill herbivory was important in determining the distributional patterns and composition of the phytoplankton on a smaller scale around Elephant Island in November 1983. Nast and Gieskes (1986) found a significant co-occurrence of high krill densities with low chlorophyll concentrations, pointing to an inverse phytoplankton–zooplankton relationship. Price (1989) in mesocosm studies demonstrated that krill density within a phytoplankton bloom was higher by an order of magnitude than the control density within half an hour after algal introduction. von Bodungen et al. (1986) estimated the grazing loss of phytoplankton by krill at 45% of the primary production over a period of three weeks. However, large-scale surveys of phytoplankton standing stocks indicated that the build-up of blooms during the spring was not controlled by krill grazing. A distinct decline in large spring phytoplankton blooms before the occurrence of high krill densities has been noted by Witek et al. (1985). von Bodungen et al. (1986) have suggested that mass sedimentation of spring populations, triggered by the deterioration of the physical environment rather than by grazing, was responsible for the decline in phytoplankton biomass. This is in contrast to other studies in which grazing has been reported as an important factor in controlling phytoplankton biomass build-up in the spring (Quentin and Ross 1985; Priddle et al. 1986a; Villafane et al. 1995).

While the overall proportion of the standing crop of phytoplankton that is consumed by krill is low—around 3% per day in two studies (Miller et al. 1985; Priddle et al. 1986a)—the local impact of krill swarms may be considerable (Rakusa-Suszczewski 1982; Uribe 1982; Holm-Hansen and Huntly 1984). Heywood et al. (1985) conducted a winter study at South Georgia and found that the standing stock of krill around the island was much lower than expected. At that time, the phytoplankton concentrations were concomitantly higher (Morris and Priddle 1984) than those found in previous studies (Hart 1934, 1942; El-Sayed 1967), suggesting that the normal winter decline in phytoplankton could be attributed to removal by grazing exceeding replenishment by growth. It should be noted that coincidence of high phytoplankton standing crop and high krill density has also been reported (Weber and El-Sayed 1985a; Mujica and Asencio 1983); however, it is possible that krill had only recently moved into an area of high phytoplankton density. Nast and Gieskes (1986), in discussing the relationship between krill and phytoplankton densities, concluded that "whereas the negative correlation between chlorophyll *a* and krill abundance seems to be valid on the mesoscale, a positive correlation between the high krill mass in the Scotia Sea and enhanced phytoplankton food sources may also exist."

The impact of krill grazing on phytoplankton community species composition and biomass will be considered in more detail in Chapter 5. However, in many areas of the Southern Ocean other grazing herbivores, especially copepods and salps, are dominant. Their impact on phytoplankton will be evaluated in detail in Chapter 4. Heavy selective grazing on phytoplankton by various herbivorous zooplankton (protozoans, copepods, salps, and krill) can lead to a shift in species composition and a reduction in the mass of the larger bloom-forming phytoplankters. Chaolum et al. (2001) investigated the summer feeding activities of zooplankton in Prydz Bay. The ingestion rates of the copepod *Calanoides acutus*, measured by the gut flourescence method, were about 14.6–45.0 μg C ind^{-1} day^{-1}. Using the same method, Dubischer and Bathmann (1997) estimated lower values of 0.82–3.97 μg C ind^{-1} day^{-1} in the Atlantic sector in October and November, and Drits and Pasternak (1993) measured values of 5.0–5.3 μg C ind^{-1} day^{-1} during the summer. The previous results in Prydz Bay of 5.25 ± 2.28 μg C ind^{-1} day^{-1} (Swadling et al. 1997) using a ^{14}C-methylamine tracer method were also less than those measured by Chaolum et al. (2001). Similar to Chaolum et al. (2001), Schnack (1985b) obtained results of between 4.5 and 31.1 μg C ind^{-1} day^{-1} in the Antarctic Peninsula region. Chaolum et al. (2001) found that ingestion rates of *Metridia gerlachei* accounted for 6.4–26.1 μg C ind^{-1} day^{-1}. Schnack (1985b) reported higher values for this species, at 10.2–45.8 μg C ind^{-1} day^{-1}.

Another important grazer component of Antarctic pelagic ecosystems are the salps. The gut pigment contents of the salp *Salpa thompsoni* measured by Choalum et al. (2001) ranged between 0.14 and 1.27 μg pigment ind^{-1}, among the lowest found in previous investigations. For the same body size, Perissinotto and Pakhomov (1998) determined a value of 0.08–2.5 μg pigment ind^{-1}, and Dubischer and Bathman (1997) estimated a value of 2.0–2.7 μg pigment ind^{-1}. The ingestion rate for *S. thompsoni* yielded from culture experiments was about 215 μg ind^{-1} day^{-1}. The rates were higher than the values (about 100 μg C ind^{-1} day^{-1}) reported by Dubischer and Bathmann (1997) using the same approach, but were lower than the result from the gut-flourescence method. *S. thompsoni* exhibited a relatively high grazing impact (72%) at one station. This implied that salps were an important phytoplankton consumer in the northern part of the investigation area, especially where swarming occurs. Such high grazing impact was also reported in previous studies (Dubischer and Bathmann 1997; Perissinotto and Pakhomov 1998). Perissinotto and Pakhomov (1998) measured exceptionally high *S. thompsoni* grazing rates in the Lazarez Sea at the onset of a phytoplankton bloom (0.27–0.8 μg chl *a* l), with up to 160 μg of plant pigment consumed per day by an individual salp measuring 7–10 cm.

In contrast to the larger zooplankton such as the krill, the microzooplankton are grazers on the smaller diatoms and the nanophytoplankton. Chaolum et al. (2001) concluded that the grazing impact of microzooplankton accounted for 10–65% of the standing stock of phytoplankton and 34–100% of the potential daily primary production (Table 2.6). Previous investigators in the Southern Ocean have reported similar high values. Mathot et al. (1992) reported that the microzooplankton grazing impact on phytoplankton was 10% of primary production under ice but up to 30% in the ice-melt area. Along a transect in the Bellingshausen Sea, microzooplankton was estimated to graze between 21 and 27% of phytoplankton production (Burkill et al. 1995). In studies in the vicinity of South Georgia, Ward et al. (1995) estimated that the herbivorous zooplankton consumed between 25 and 56% of the primary production. Other estimates include those of Schnack et al. (1985), at 1% in the Bransfield Strait and 55% in the Drake Passage; and of Huntley et al. (1991), at 1–5% in December/January and 9–72% in February/March in a spring bloom in the Gerlache and Bransfield Straits. According to the review of Garrison (1991b), 41% of the primary production could be consumed by microzooplankton in the Southern Ocean, while Morales et al. (1993) gives a value of less than 30%. Studies of zooplankton grazing in the Southern Ocean suggest that grazers are not food limited, and that losses due to vertical flux and phytoplankton respiration or excretion generally exceed those due to zooplankton

TABLE 2.6

Grazing Impact of Microzooplankton Based on the Dilution Technique in Prydz Bay in Austral Summer (December/January) 1998–1999 (*k* Phytoplankton Growth Coefficient, *g* Microzooplankton Grazing Coefficient, P_i Initial Phytoplankton Stock Removed, P_p Potential Primary Production Grazed)

Station	Sampling Depth (m)	Temperature (°C)	Chlorophyll *a* ($\mu g l^{-1}$)	*k* (day^{-1})	*g* (day^{-1})	P_i (% day^{-1})	P_p (% day^{-1})	r^2
F	2	−2.0	0.29	1.20	1.06	65	94	0.60
III-2	2	−1.0	0.33	2.60	0.37	31	34	0.72
III-13	2	1.5	4.10	0.11	0.11	10	100	0.80

Source: From Chaolum, L., Zhang, S. G., Peng, Ji., *Polar Biol.*, 24, 897, 2001. With permission.

grazing (Schnack et al. 1985; Hopkins 1987; Huntley et al. 1991; Ward et al. 1995).

Another component of the zooplankton that has the potential to affect phytoplankton stocks is the protozooplankton. This includes dinoflagellates, choanoflagellates ciliates, tintinnids, and amoeboid forms. While many of these are primarily bactivorous, others, especially ciliates and dinoflagellates, have been shown to consume diatoms and other phytoplankton (Smetacek 1981a, 1981b; Jacobsen and Anderson 1986; Buck et al. 1987. The impact of the protozooplankton on the pelagic ecosystem will be considered in detail in Chapter 14 of Section 6.

Smetacek et al. (2004) have recently reviewed the role of grazing in structuring the Southern Ocean pelagic system and biogeochemical cycles. Many studies have shown that mortality due to grazing decreases with cell size. This has important implications for the structure of Southern Ocean pelagic ecosystems. Smetacek et al (2004) contrast the iron-limited, silica-sinking open ocean system with the iron-replete, carbon-sinking phytoplankton bloom system.

While pico- and nanoflagellates contribute the bulk of the phytoplankton biomass in the iron-limited Southern Ocean, microplankton diatoms ($>20\ \mu m$) are a universal feature. They are highly diverse in shape and size and comprise over 100 species from a broad range of the common diatom genera. In restricted regions along fronts where iron, albeit at low concentrations, is introduced to the surface in upwelling water, diatom biomass can exceed that of the microbial phytoplankton by a factor of two or three or more (Tremblay et al. 2002; Smetacek et al. 2002). About six species from disparate genera tend to contribute the bulk of the biomass. They are all giants of their respective genera and are of eye-catching appearance due to their extravagant use of silica (Si:N$>$2). They can dominate the diatom biomass in the Polar Frontal Zone at Si concentrations of <5 mmol m^{-3}, indicating that high ambient concentrations are not a prerequisite for making thick frustules (Smetacek et al. 2002). Prominent species are *Fragiliaropsis kerguelensis, Thalassiothrix antarctica, Thalassionema nitzschia, Corethron pennatum* (formerly *criophilium*), *Chaetoceroa* spp., especially of the subgenera *Phaeoceros* and *Hylochaetae*, *Thalassiosira lentiginosa*, and *Pseudo-nitzschia* spp. It is these giant diatoms that contribute to the large vertical flux of silica. Salps and copepods graze on the regenerating system comprising pico- and nanophytoplankton. In the iron-replete system, high growth rates of weakly silicified diatoms and *Phaeocyctis* result in the buildup of blooms that fuel the food chain of the giants (i.e., diatoms, krill, whales) that drive the carbon pump. The vertical flux of carbon comprises diatom cells, phytodetritus, or feces of crustacean zooplankton with much lower Si–C ratios than in the iron-limited system.

Froneman and Bernard (2004) investigated phytoplankton growth rates and grazing impact in the Polar Frontal Zone south of the Prince Edward Islands. In the absence of any grazers, net growth rate of the phytopankton was positive and ranged between 0.209 and 0.403 day^{-1}. Protozooplankton, dominated by nanoflagellates, dinoflagellates, and ciliates (Froneman and Balarin 1998) were identified as the most important consumers of the phytoplankton biomass. Their grazing impact was equivalent to $<10\%$ of the integrated phytoplankton biomass (Bernard and Froneman 2003). This high impact of the microheterotrophs can be attributed to the inability of the larger metazoans ($>200\ \mu m$) to graze efficiently on the small phytoplankton cells due to feeding constraints (Fortier et al. 1994).

2.9 GROWTH RATES

Ultimately, the growth rate of the phytoplankton is dependent on the rate at which the phytoplankton cells fix carbon dioxide. As we have seen in Section 2.8, primary production is influenced by many physical, chemical, and biological factors, including the availability of macro- and micronutrients, temperature, solar radiation, water column stability, and zooplankton grazing. The irradiance regime is critical, affecting phytoplankton growth mainly through irradiance and photoperiod. The algae in turn respond by adaptation, provided that the change in light is not too large or abrupt. Photoadaptation involves alterations of the properties of the photosynthetic apparatus of the cells, characteristics of respiration, and overall chemical composition, and the net effect is to minimize the impact of variations in the light regime on the growth rate. Some polar phytoplankton species can grow at a nearly constant growth rate for a 4- to 25-fold variation in irradiance, provided there is time to adapt to each irradiance (Sakshaug and Holm-Hansen 1986; Gilstard 1987). Variations in daylength also have an impact on growth rates; the growth rate is almost linearly proportional to daylength for short days but varies negligibly between 19 and 24 h of daylength (Sakshaug and Andresen 1986; Gilstard 1987).

The physiological state and the adaptation of the algae to environmental conditions such as light and nutrients are expressed in the ability of the algae to absorb and utilize light. Investigations in different areas of the Southern Ocean have shown that photosynthesis versus irradiance relationships (P versus E) show considerable variation between different studies, between stations, and with depth. In the Bellingshausen and Amundsen Seas, Stambler (2003) investigated irradiance curves. The light intensity at which photosynthesis approaches saturation (E_k) varied between 59 and 105 μmol m^{-2} sec^{-1}. These values are similar to those published by Figuerias et al. (1998) for Bransfield Bellingshausen water, and by Lorenzo et al. (2002) for the southern Bellingshausen Sea. These low E_k are typical of low-light adapted cells and are due to low temperature (Cota et al. 1992; Falkowski and Raven 1997).

The quantum yield is the photosynthesis stored radiation as a fraction of the photosynthetically usable (absorbed) radiation, i.e., the number of moles of oxygen evolved divided by the moles of quanta absorbed (Falkowski and Raven 1997). These quantum yields are highly variable between different regions of the Southern Ocean.

In oligotrophic and eutrophic regions, the maximum yield is about 0.8 mol C mol^{-1} quanta. Maximal quantum yields, $Q_{\max}$, of phytoplankton from the South Scotia Sea and Bransfield Strait was shown to vary between 0.0024 and 0.028 (Tilzer at al. 1985). In the Atlantic sector of the Southern Ocean, $Q_{\max}$ ranged from 0.006 to 0.035 at the surface and from 0.02 to 0.093 at the 1% light depth (Bracher et al. 1999).

Phytoplankton growth rates in the waters of the Southern Ocean have been considered to be low due to a combination of the effects from light (El-Sayed and Mandelli 1965) and temperature (Neori and Holm-Hansen 1982; Wilson et al. 1986). Two indices are used in describing algal growth rates: the assimilation number (AN), i.e., the number of micrograms of carbon fixed per liter per day divided by the number of micrograms of chlorophyll *a* per liter (μg Cm^{-2} day^{-1} (μg chl *a* l)$^{-1}$); and the number of doublings per day. Figure 2.25 shows some typical profiles of AN and the number of doublings per day for stations in the Pacific sector (Holm-Hansen et al. 1977). The observed growth

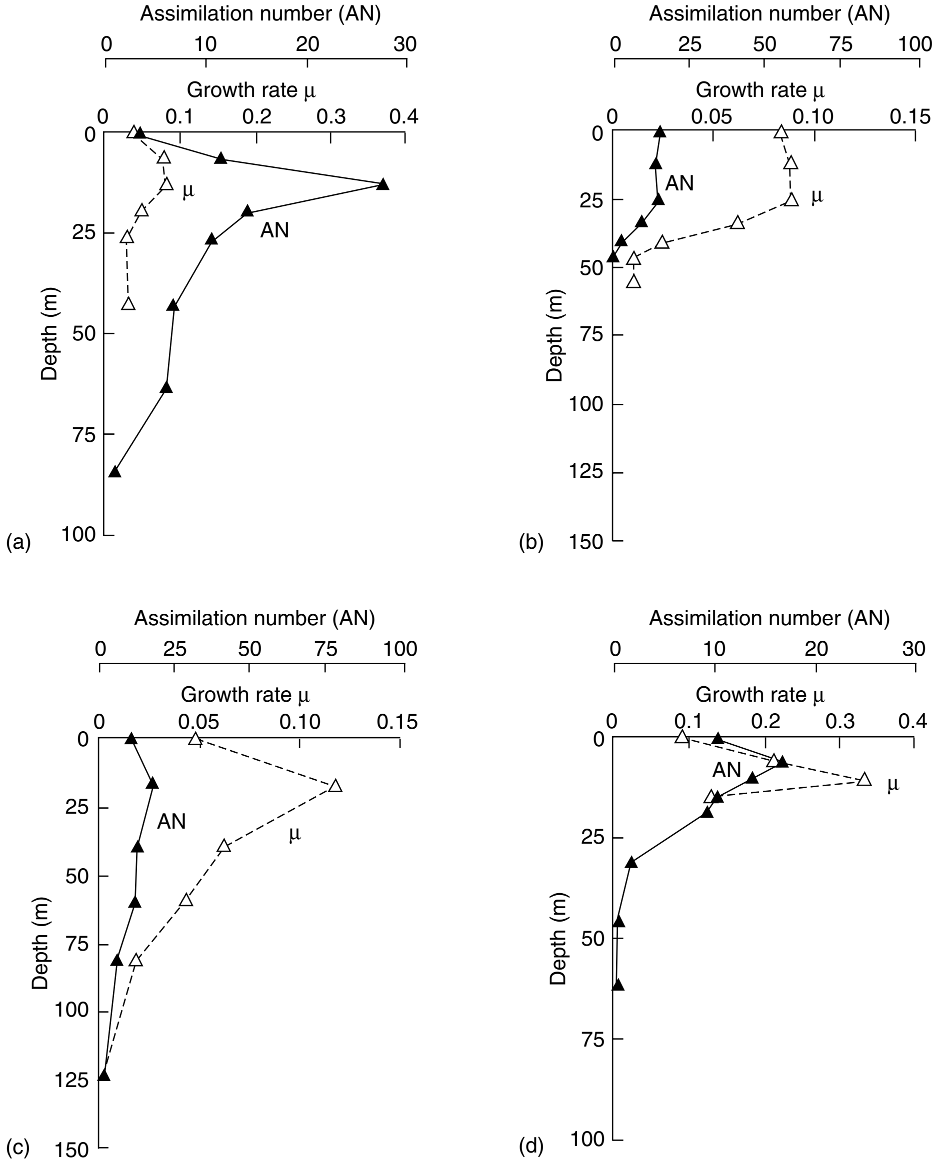


FIGURE 2.25 Vertical distribution of assimilation number (AN, g C l^{-1} μg chl *a* l^{-1}) and specific growth rate or doubling time from stations on *Eltanin* cruises 38, 46, and 51. (a) Station characteristic of subantarctic waters. Euphotic zone, 43 m; photosynthetically active solar radiation 160 cal m^{-2} half-light-day^{-1}. (b) Station characteristic of Antarctic Convergence waters. Euphotic zone 60 m; photosynthetically active solar radiation 62 cal m^{-2} half-light-day^{-1}. (c) Station characteristic of Antarctic waters. Euphotic zone 145 m; photosynthetically active solar radiation 157 cal m^{-2} half-light-day^{-1}. (d) Station characteristic of Antarctic (Ross Ice Shelf) waters. Euphotic zone 30 m; photosynthetically active solar radiation 72 cal m^{-2} half-light-day^{-1}. (From Holm-Hansen, O., et al., *Adaptations Within Antarctic Ecosystems*, Llano, G., Ed., Smithsonian Institution, Washington, D.C., 11, 1977. With permission.)

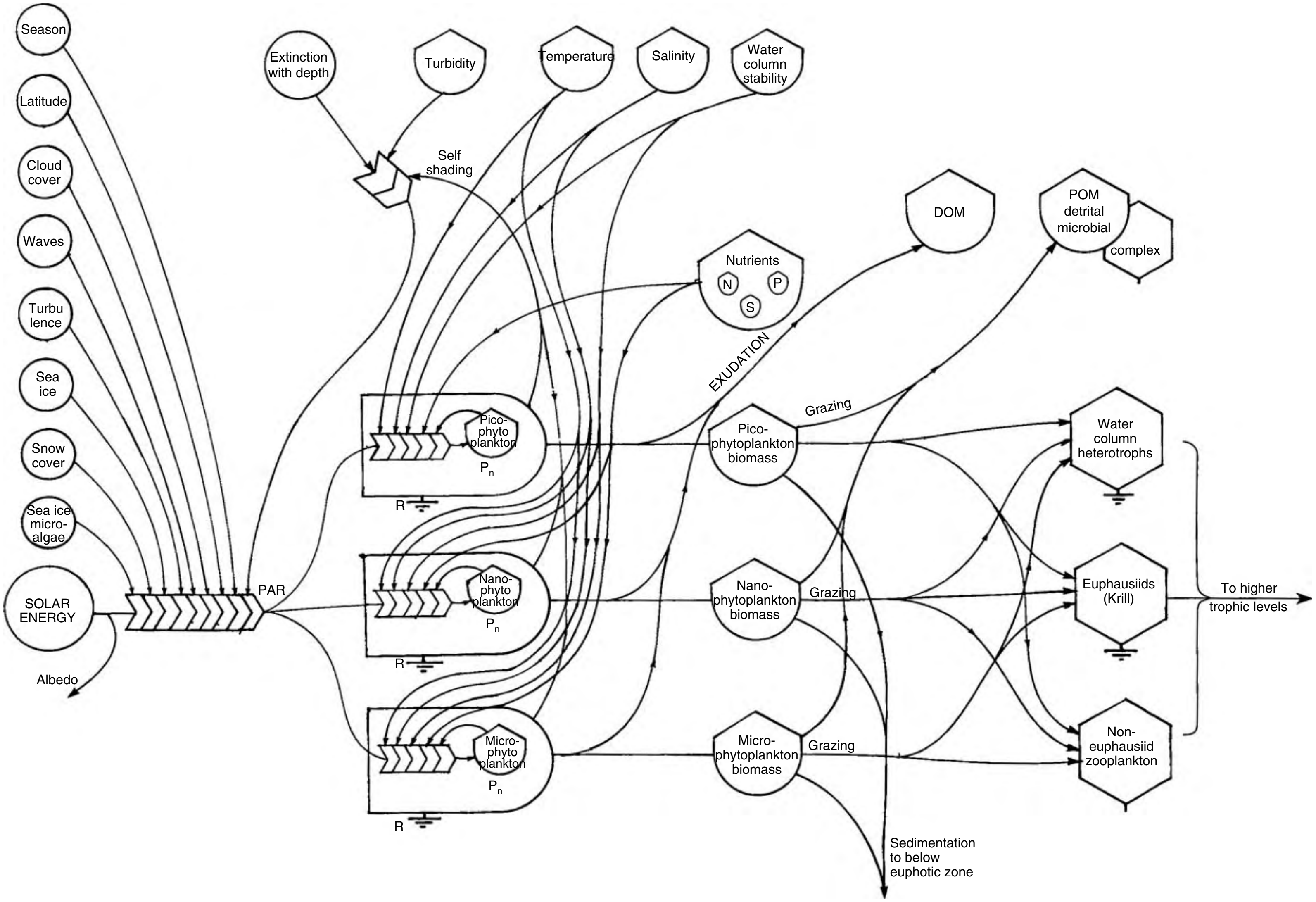


FIGURE 2.26 Simplified model of the forcing functions and environmental variables influencing phytoplankton production and biomass in the Southern Ocean.

rates in this study were low (0.05–0.33 doublings per day). Profiles of growth rates show low growth rates in surface waters, with rates increasing with depth until a maximum was reached at between15 and 40 m, below which values again decreased.

Sommer (1989) found that the maximal growth rates of 15 Antarctic phytoplankton species ranged from 0.32 to 0.72 day^{-1} and showed only a weak dependence on cell size. These values are usually higher than those reported by Spies (1987) for congeric but unidentified species from the Weddell Sea. However, the light intensities used by Spies may not have been saturating. Thus, although the growth rates recorded were lower than those for phytoplankton from warmer waters, doubling in the range recorded by Spies would lead to relatively rapid population increases.

2.10 HETEROTROPHIC NUTRITION

While most microalgae satisfy their carbon requirements through the photochemical reactions of photosynthesis, some are nutritionally opportunistic and can supplement their autotrophic metabolism by phagotrophy or osmotrophy (Droop 1974; Hellebust and Lewin 1977). Rivkin and Putt (1987) found that diatoms isolated from benthic, planktonic, and sea ice microbial communities in McMurdo Sound assimilated ambient concentrations of dissolved amino acids and glucose both in the light and the dark. Amino acid uptake rates were up to 250 times greater than those of glucose. The amino acids were incorporated into proteins and other complex polymers at rates of assimilation and patterns of polymer synthesis similar to those of light-saturated photosynthetic incorporation of inorganic carbon. Thus, the diatoms are able to use exogenous amino acids to synthesize essential macromolecules. It is therefore probable that the assimilation of dissolved organic substances could supplement light-limited growth during the austral spring and summer and could potentially support heterotrophic growth through the aphotic polar winter.

2.11 A MODEL OF PHYTOPLANKTON PRODUCTION

Figure 2.26 is a simplified model illustrating the forcing functions and environmental variables that influence primary production and phytoplankton biomass. The photosynthetically available radiation (PAR) in the Southern Ocean at any one point in time or depth within the water column is determined by a complex of factors, including cloudiness, turbulence, wave action, season (day length), latitude (affecting the angle of incidence of the sun's rays), sea ice (thickness, percentage cover), depth of snow on the ice, degree of development of the sea ice microalgae, extinction with depth (influenced by the turbidity of the water), and self-shading, especially when dense blooms develop.

Net production (P_n) is determined by the interaction of PAR, the physiological state of the algae, including the degree of inhibition by high light intensity and the degree of adaptation to low light intensity, temperature, salinity, the stability of the water column, and the kind and availability of nutrients. The major nutrients are nitrate, ammonia, and silicate. Availability of nitrate ("new" N) is determined by water circulation patterns (especially upwelling), turbulence, and the stability of the water column (Figure 2.27). On the other hand, concentrations of ammonia ("regenerated" N), which is often the preferred nutrient, especially by the pico- and nanophytoplankton, is the result of primarily microbial processes in the euphotic zone (see Chapter 14) and excretion by zooplankton.

Table 2.7 gives an interaction matrix of the model forcing functions and environmental variables that influence

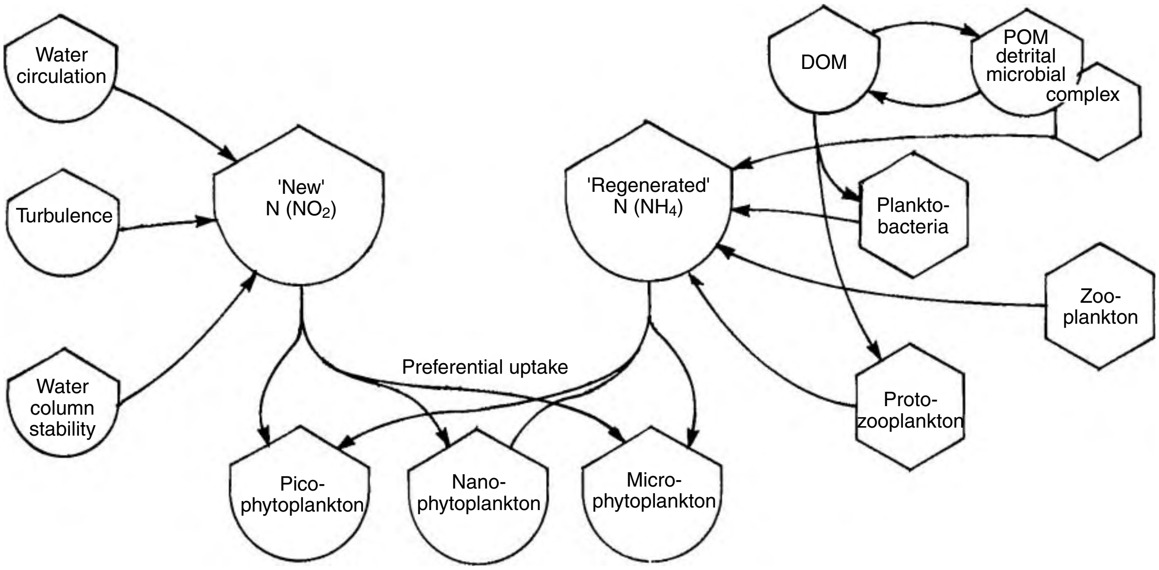


FIGURE 2.27 Model of the variables influencing the concentration of nitrogen on the surface waters of the Southern Ocean.

TABLE 2.7
Matrix of Model Forcing Functions and Environmental Variables Influencing Water Column Primary

	Solar Radiation	Season	Latitude	Cloud Cover	Waves	Turbulence	Water Circulation	Turbidity	Sea Temperature	Salinity	Water Column Stability	Sea Ice Formulation	Sea Ice Melting and Breakout	Sea Ice Snow Cover	Sea Ice Microalgae	Nutrients	Grazing	Sedimentation
Solar radiation		x	x						x			x	x	x	x			
Season	x		x	x	x	x			x		x	x	x	x	x		x	x
Latitude	x	x		x				x	x			x	x	x	x	x	x	
Cloud Cover	x	x	x															
Waves	x	x				x		x			x	x	x	x				
Turbulence	x	x			x		x				x					x		x
Water circulation		x	x			x			x	x	x				x	x	x	
Turbidity	x																	
Sea temperature		x	x				x			x	x	x	x					
Salinity			x				x		x	x	x	x	x					
Water column stability		x			x	x	x	x	x	x						x	x	x
Sea ice formulation	x	x	x						x	x					x	x	x	x
Sea ice melting and breakout	x	x	x		x	x		x	x	x	x			x	x	x	x	x
Sea ice snow cover	x	x	x												x			
Sea ice microalgae	x	x	x													x	x	
Nutrients						x	x				x				x			
Grazing		x													x			x
Sedimentation		x													x		x	

Source: After Knox (1990).

phytoplankton production. It can thus be seen that primary production is determined by a complex interaction between the variables listed in the matrix. Overall, seasonality is the dominant influence, with its impact on the light regime and weather, especially the wind strength and the prevalence and frequency of storms. While a number of studies have explored the impact of some of these variables, the complexity of their interaction has yet to be elucidated.

Mitchell and Holm-Hansen (1991) developed a model of the Antarctic phytoplankton crop in relation to the mixing depth. This model was based on mixing depth and pigment-specific light attenuation and in situ photosynthesis–irradiance relationships. It indicated that the depth of the upper mixed layer (Z_{ULM}) can be used to predict the upper limit of phytoplankton crop size. Assuming that nutrients do not limit crop size, a best fit of the model observations indicated that specific loss rates were approximately 0.3–0.35 day^{-1}, and that massive blooms only occur if Z_{ULM} is <25 m. Mitchell and Holm-Hansen considered that in most studies grazing, particularly the contribution of the protozooplankton, has been underestimated. Further such modeling studies are needed.

3 Sea-Ice Microbial Communities

CONTENTS

3.1 INTRODUCTION

The geographical and seasonal distributions of the Antarctic sea ice, its zonal characteristics and pack ice movement have been described in Chapter 1. This chapter focuses on the microbial communities that develop in association with the sea ice, and their relationships with the pelagic communities. Diatoms have been known from the sea ice for more than 150 years. They were first described from the Arctic by Ehrenberg (1944, 1953) and from the Antarctic by Hooker (1847).

Early work on sea-ice microlagae was principally of a taxonomic nature, although Vanhoeffen (1902) provided the earliest description of the seasonal cycle for ice diatoms. However, it was not until the early 1960s that Bunt and his coworkers (Bunt 1963, 1964a, 1964b, 1967, 1968a, 1968b, 1969; Bunt and Wood 1963; Bunt et al. 1968; Bunt and Lee 1970) carried out a detailed study of the community composition, primary productivity, and physiology of the sea-ice microalgae in McMurdo Sound. Since that time there have been many studies of sea-ice communities in various parts of the Southern Ocean, notably by Hoshiai and his coworkers at Soyawa Stations (Hoshiae and Kato 1961; Hoshiai 1969, 1972, 1981a, 1981b, 1985; Watanabe 1988; Watanabe et al. 1990), Burkholder and Mandelli (1965) in the vicinity of Palmer Station, Whitaker (1977a, 1977b, 1982) at Signy Island, Ackley et al. (1978a, 1978b, 1979) in the Weddell Sea, and McConville and his coworkers in East Antarctic (McConville and Wetherbee 1983; McConville et al. 1985). However, more recently the most substantial contribution to our understanding of the ecology and phytology of sea-ice communities has been made by Sullivan and his coworkers working in McMurdo Sound (Sullivan and Palmisano 1981, 1984; Palmisano and Sullivan 1982, 1983a, 1983b, 1985a; Sullivan et al. 1982, 1984, 1985; Grossi et al. 1984, 1987; Kottmeier et al. 1984, 1986, 1987; Palmisano et al. 1984, 1985a, 1985b, 1985c, 1985d, 1987a, 1987b, 1988; Grossi 1985; Grossi and Sullivan 1985; Sullivan 1985; Palmisano 1986; Kottmeier and Sullivan 1987, 1988, 1990; Soohoo et al. 1987; Lizotte and Sullivan 1991a, 1991b, 1992; Arrigo et al. 1995). Comprehensive reviews of sea-ice microbial communities are to be found in Horner (1986), Horner et al. (1988, 1992), Legendre et al. (1992), Karl (1993), Palmisano and Garrison (1993), Brierley and Thomas (2002), and Thomas and Dieckman (2003).

3.2 SEA ICE AS A HABITAT

Because of the extent and seasonal patterns of formation, break-up and melting, sea ice is a dominant forcing function in the ecology of the Southern Ocean. The upper surface provides a habitat for a number of seabirds and mammals, while the ice itself, especially part in contact with the water, constitutes a unique habitat for microalgae and bacteria. They, in turn, provide a food resource for the associated microfauna, meiofauna, and cryopelagic fauna of the surface water layer immediately below the ice (Figure 3.1).

Sea ice is a complex habitat. Its chemical characteristics are a function of ice formation and growth, various physical processes of deformation, and season and age of ice (Clarke and Ackley 1984; Garrison 1986b; Eicken 1992). The understanding of these processes has been based on studies of the structural composition of the ice and measurements of chemical parameters, such as salinity (see Lange 1988 and Eicken and Lange 1989 for concise overviews). The basic structural types include frazil ice, platelet ice, congelation ice, and snow ice. The relative composition of ice in floes varies throughout the ice-covered regions and is determined primarily by physical properties (Weeks and Ackley 1982; Clarke and Ackley 1984; Lange 1988; Eicken and Lange 1989; Garrison 1991a).

The overriding constraints on the biological activity in the ice are space, temperature, salinity, and, for primary production, the quantity and quality of the light transmitted through the ice. Sea-ice microalgae, in general, are photoacclimated and have the potential to photosynthesize in low light conditions. The physiology of the dominant sea-ice organisms are well acclimated to a dynamic salinity regime and can cope with both hyper- and hyposaline stress (Eicken 1992; Kirst and Wiencke 1995; Thomas and Dieckmann 2002).

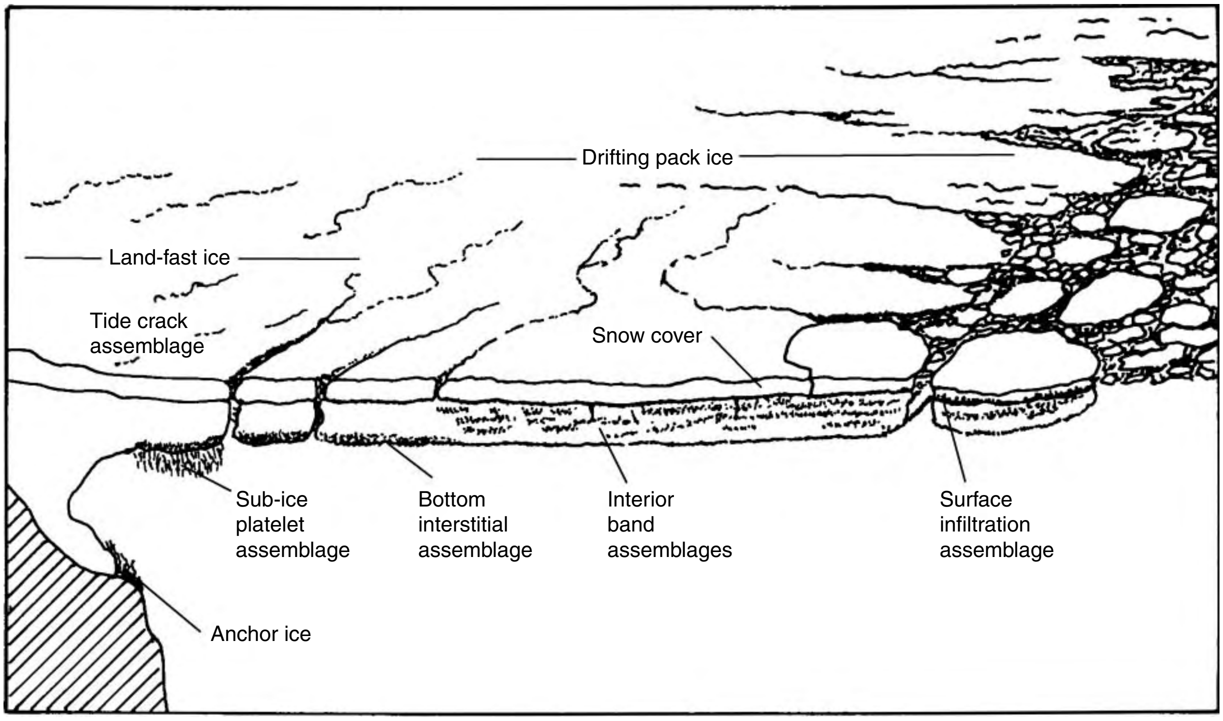


FIGURE 3.1 Microalgal habitats associated with sea ice. Modified from Garrison et al. (1987); based on Whitaker (1977) and other sources.

3.2.1 ICE FORMATION AND STRUCTURE

Once the surface layer of the sea reaches freezing point, additional heat loss produces slight supercooling of the water and ice formation. Initial ice formation occurs at or near the surface of the water in the form of small platelets and needles, termed *frazil ice*. This type of ice often contains high concentrations of biological material (Garrison et al. 1983, 1987, 1989). Studies by Ackley and his coworkers (e.g. Weeks and Ackley 1982; Clarke and Ackley 1984; Gow et al. 1987; Lange et al. 1989) have shown that ice floes from the pack ice region usually contain large amounts of frazil ice as a result of the dynamic physical regime of the pack ice region. Continued freezing results in the formation of *grease ice*, a soupy mixture of unconsolidated frazil crystals. Once the ice formation exceeds 30–40%, the transition to a solid cover begins. In the presence of a wave field, the transition is marked by the formation of *pancakes*, rounded masses of semi-consolidated slush 0.3–3.0 m in diameter. These pancakes eventually consolidate and become welded together to form a composite ice sheet.

A second type of ice is *congelation* (sometimes called *columnar ice*), which grows at the ice–water interface in response to conductive heat losses along the temperature gradient in the ice. In this form, the crystals are orientated with their *c*-axis (the principal axis of symmetry) horizontal and growth occurs perpendicular to the axis, producing interlocking columns approximately 1–2 cm in diameter (Lewis and Weeks 1971). This forms a partly permeable crystal structure with numerous small brine pockets and channels, many less than 100 μm in diameter (Palmisano and Sullivan 1983b). Larger brine channels are formed during the early stages of freezing, but these later become filled with congelation ice (Lewis and Weeks 1971). When large pockets of trapped brine drain down to the ice–water interface, the resultant plume can produce an ice stalactite that may be as much as 6 m in length (Dayton and Martin 1971). As congelation ice is formed, particulate material is rejected from the ice matrix (Clarke and Ackley 1984) so that young congelation ice typically has a lower content of incorporated biological material than frazil ice. Studies at McMurdo Sound by Gow et al. (1982) have shown that landfast ice floes were primarily composed of congelation ice. Recent studies indicate that coastal ice from other localities may contain variable amounts of frazil, platelet, and congelation ice (Watanabe 1988; Eicken and Lange 1989; Lange et al. 1989).

Frazil ice also forms in the water column, as well as at the surface. As had been demonstrated for McMurdo Sound, two types of ice crystals are formed within the water column: extremely small crystals and large ice platelets 10–15 cm in diameter and 0.2–0.3 cm in thickness (*platelet* ice) (Dayton et al. 1969). Platelet ice can form at considerable depths in the water column as water flowing from under ice shelves rises and undergoes supercooling (Maykut 1985; Dieckmann et al. 1986). Ice platelets formed by this process float upwards and often accumulate under established ice floes and fast ice and may form layers up to 5 m thick (Barry 1988; Lange 1988; Knox 1990).

Sea ice is commonly overlain by snow that can vary considerably in depth. Regions near the coast that receive blowing snow from katabatic and other offshore winds may accumulate a layer of snow up to 6 m thick (Keys 1984). Along leads in the pack ice and at the ice edge, the snow–water interface may become flooded with sea water. This flooding may form a layer of infiltration ice along the snow–ice interface (Meguro 1962). Pools may form on the surface of the sea ice either by thawing of the ice (McConville and Wetherbee 1983), a combination of flooding and melting, or by flooding alone. These provide additional habitats for microbial growth.

Sea ice in the Pack-Ice Zone periodically breaks up under the influence of storms and can move considerable distances, driven by wind and surface currents, before refreezing into solid pack during calm periods. This contrasts with shore-fast ice that occurs along most of the coastline of the Antarctic continent. This ice forms early in the winter and either breaks up in the late summer or remains for two or more years, forming multiyear ice that may by up to more than 10 m thick. It may be anchored to the bottom at the shoreline. Although rigidly anchored, it may move tens of meters in response to thermal and mechanical stress. Its extent is determined primarily by sea bottom and shoreline topography and is highly variable. Where it joins the land or the ice sheets, tidal rise and fall create a series of parallel tide cracks through which the seawater passes easily (Figure 3.1). These cracks accumulate snow and platelet ice, and often frazil crystals form, providing a nutrient-rich well-illuminated environment for microbial growth (Whitaker 1977a; Rawlence et al. 1987; Waghorn and Knox 1988).

In contrast to the Arctic, where surface meting is responsible for most of the disappearance of the pack ice in the summer (Maykut 1985), the disappearance of the Antarctic pack is due almost entirely to melting at the ice–water interface. Gordon (1981) estimated that no more than half the energy for this melting could be derived from the relatively warm deep water below the Southern Ocean pycnocline. The remainder must come from shortwave radiation absorbed by the upper ocean, either through leads in the pack ice or near the ice edge.

3.2.2 PHYSICAL AND CHEMICAL PROPERTIES

Many of the important physical and chemical properties of the microenvironment within the sea ice are determined by freezing-point relationships. When ice forms from sea water (at $-1.9°$ and a salinity of 35), dissolved salts are excluded from the ice crystals and accumulate within the ice matrix as brine cells or inclusions (Weeks and Ackley 1982; Maykut 1985). Brine is rejected from the sea ice when freezing begins and is constantly lost over time, so bulk salinity (salinity measured on a melted ice sample, including trapped brine) is a function of ice age (Maykut 1985). The salinity of the enclosed brine is determined by the in situ temperature, while the volume of the ice occupied by the brine varies directly as a function of temperature. Salinity profiles through sea ice in McMurdo Sound revealed high salinity at the top, decreasing near the middle, and rising again toward the bottom (Weeks and Lee 1982). This pattern is probably due to the rapid formation of near-surface ice trapping larger amounts of salt; the much slower rates of freezing beneath this layer, and the gradual migration of brine as density currents down the ice column. Thus the microbiota can be subjected to widely varying salinity concentrations. In the Weddell Sea, salinity was lower in the upper layers with a maximum in the middle, indicating only a partial migration of brine (Ackley et al. 1979).

Air temperatures in the ice-covered regions are usually below freezing (see Vincent 1988), and a large temperature differential may exist between the atmosphere and seawater, resulting in a vertical gradient in temperature and parameters affected by temperature through the ice floes (Figure 3.2). The temperature regime within ice is difficult to predict because snow cover can serve as an insulating layer to buffer temperature fluctuation in the underlying ice floe (Figure 3.2). The importance of temperature-induced gradients in ice may vary with latitude (Garrison and Close 1993); air temperatures at McMurdo Sound (77°S) frequently reach −42°C (Littlepage 1965), whereas at lower latitudes (e.g., Palmer Station on the Antarctic Peninsula at 64°S) winter lows are rarely below −10°C.

Nutrient concentrations within sea ice are not well known; they are difficult to measure and techniques have yet to be developed for their in situ determination within the brine channels. Early data collected by Bunt and Lee (1970) indicate that McMurdo Sound frazil ice contains high levels of nutrients. The interstitial waters had 7.07 mmol m^{-3} of nitrate and 2.6 mmol m^{-3} of dissolved reactive phosphorus. These values, as well as salinity (31), pH (8.03) and temperature (−1.75°C) were comparable with the seawater below. However, higher in the ice column where there is less exchange with the underlying seawater the nutrient levels were lower, probably due to microbial growth. In the Weddell Sea (Clarke and Ackley 1984) silicate and nitrate concentrations, particularly in the older ice, indicated nutrient depletion by the ice biota. Additionally, in some ice cores, high nitrate values suggested the presence of populations of nitrifying bacteria.

Solar radiation is attenuated in passage through snow ice and microbial communities, resulting in changes in both the quantity and quality of light (Figure 3.3) (Sullivan et al. 1984; Palmisano et al. 1987a). Strong attenuation of the longer wavelengths cause the spectral composition of the light to undergo rapid changes as it passes through the ice. Measurement of downwelling radiation beneath first-year ice show energy maxima occurring at 470 and 480 nm wavelength bands (Maykut and Grenfell 1975). Red wavelengths are quickly absorbed in the surface layers of the ice, so that the amount of energy reaching the water is negligible above 700–800 nm. Once the microalgae develop, the transmission of light is further reduced.

Plamisano et al. (1987b) found that two meters of congelation ice reduced surface photosynthetically available radiation (PAR, light within the waveband available to the microalgae, 400–700 nm) by about 90% with a peak transmission around 500 nm. The depth of snow also greatly influences the availability of light for ice microalgal photosynthesis. Palmisano et al. (1985a) found that the irradiance

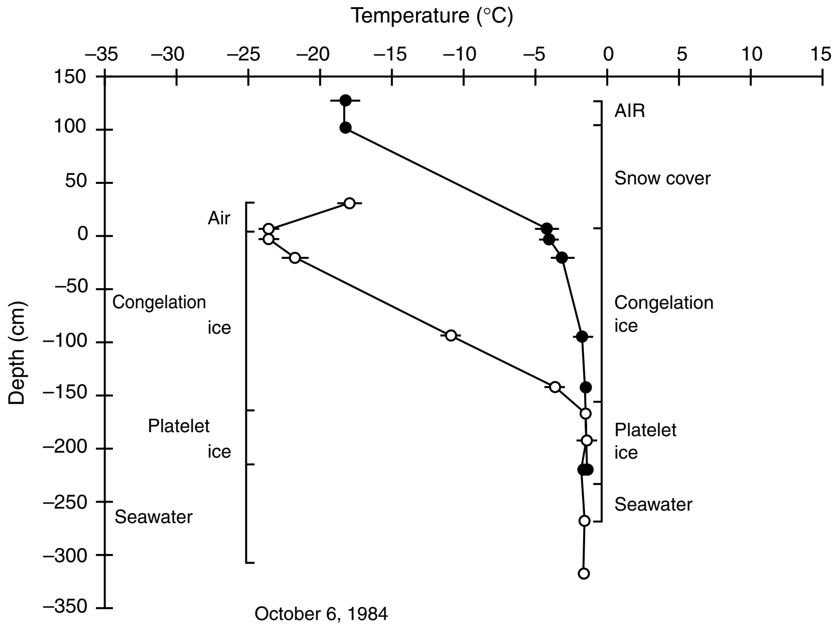


FIGURE 3.2 Temperature gradient in landfast ice at McMurdo sound (o) snow-free ice; (o) ice with 1 m snow cover. (From Palmisano, A.C., Garrison, D.L., *Antarctic Microbiology*, Friedman, I., Ed., Wiley Liss, New York, 173, 1993. With permission.)

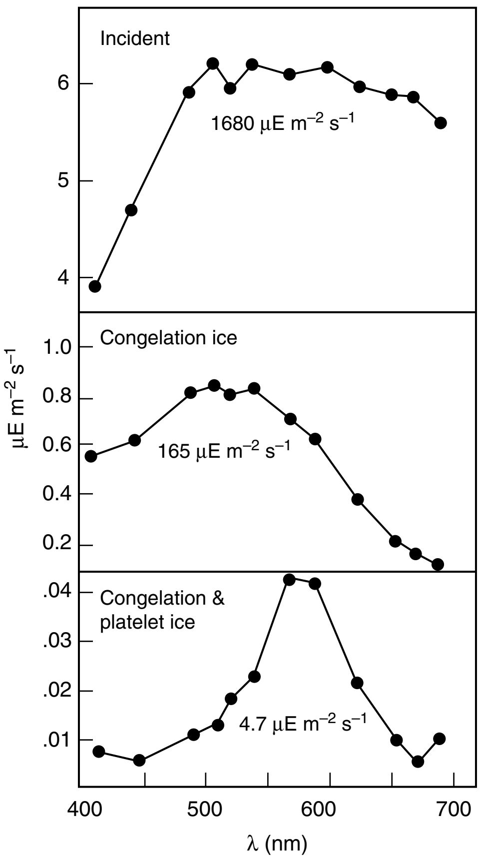


FIGURE 3.3 Changes in spectral composition pf light as it passes through sea ice and sea-ice microbial communities (SIMCO). (From Sullivan, C.W., Palmisano, A.C., Soohoo, J.B., *Int. Soc. Opt. Eng. Proc. Ocean Opt.*, 7, 159, 1984. With permission.)

beneath a quadrant of sea ice artificially shaded with 70 cm of snow was less than 3% of the PAR beneath a control quadrat with 7 cm of natural snow. Sea-ice microalgal assemblages can also strongly attenuate PAR. Palmisano et al. (1987b) found that they could reduce light levels to less than 0.5% of surface levels and shift the transmission peak by selectively absorbing the blue and red wavelengths. The relationship between light and photosynthesis by sea-ice microalgae is discussed further in Section 3.2.7.2.

3.2.3 Dissolved Organic Matter (DOM)

In their synopsis of the biochemical developments of a platelet ice system, Günther et al. (1999a, 1999b) and Grossman et al. (1996) stressed that the significance of dissolved organic matter (DOM) for ice-based productivity and carbon turnover was a major unknown in current concepts of sea-ice functioning. Thomas et al. (1998, 2001a, 2001b), Herborg et al. (2001), and Carlson and Hansell (2002) measured dissolved organic carbon in Antarctic sea ice over various seasons and in different regions of the sea-ice zone including a variety of ice types. The results were variable but concentrations 450-fold greater than that of surface waters were measured (Thomas et al. 2001b; Carlson and Hansell 2002). Such accumulation is clearly indicative of the uncoupling of the DOM resource production and consumption processes (Thomas and Dieckmann 2002). Pomeroy and Wiebe (2004) consider that the reduced substrate affinity of bacteria at low temperatures results in them not being able to utilize the high concentrations of available substrates in the ice.

DOM within sea ice is derived from death, break-up, and lysis of microalgal cells during grazing and from the release of organic matter by the microalgae. Gleitz et al. (1996) and Günther et al. (1999a) have reviewed the changes which occur in the biogeochemistry of sea ice during the development of sea-ice microalgal assemblages. High inorganic carbon, low oxygen, low DOM, and high nutrients are characteristic of newly formed sea ice that, given enough light, will support nitrate-based new primary production. When diffusion and exchange from outside the system is limited, this limitation will lead to reductions in nutrients and the accumulation of DOM and oxygen. Grazing and/or high rates of remineralization will subsequently result in the high concentrations of ammonia and even nitrate and silicate that are often measured with extremely high standing stocks of microalgae. The liberation of nutrients will promote the growth of small algal species.

Arrigo and Thomas (2004) point out that the sea-ice microalgae are responsible for the extensive production of extracellular polymeric substances (EPS) and that this has led to speculation as to the nature of sea-ice brines and the biological–physical interaction at the ice–liquid interface (Deming 2002; Krembs et al. 2002). It is clear that the microbial food web that is dominated by the production and hydrolysis of DOM will be very different from that of the open waters. The close proximity of bacteria and fungi to the primary producers, with high amounts of DOM production, probably indicates that the interactions known from biofilms or interstitial sediment systems are more typical of those processes taking place within the ice (Brierley and Thomas 2002). Additionally, it has been found that ice algae release extracellular macromolecules that are thought to alter recrystallization of ice.

3.2.4 Sea-Ice Biota

Studies of sea-ice biota can be traced back to Hooker's (1847) study of diatoms in pack-ice floes. Most of the early studies focused on taxonomic studies of the sea-ice microalgae (principally diatoms), but more recent studies have involved a wider range of organisms and their ecological relationships as members of complex assemblages living in close association with the ice (Garrison et al. 1986a, 1986b; Garrison and Buck 1989a, 1989b; Garrison 1991a; Horner et al. 1992; Karl 1993; Palmisano and Garrison 1993; Lizotte 2003; Schnack-Schiel 2003). Although the information is extensive, our knowledge of the diversity of the sea-ice communities and the life histories of many of the species is incomplete.

3.2.4.1 Bacteria

Iizuka et al. (1966) first reported that Antarctic sea ice contained a variety of bacteria. In 1985, Sullivan reviewed the data on the occurrence and physiology of the bacteria associated with sea ice. Light and scanning microscopy has revealed that a variety of morphological types of bacteria, including rods, cocci, straight and branching filamentous, fusiform and prosthecate bacteria, have been found in association with sea ice (Sullivan and Palmisano 1984); however, little work has been carried out on their taxonomy.

Sullivan and Palmisano (1984) found that approximately 70% of the bacteria in the sea-ice community at McMurdo Sound were free-living, whereas 30% were attached either to living algal cells or to detritus. In November and December at the same locality, Grossi et al. (1984) found that more than 65% of the epiphytic bacteria were associated with the diatom *Amphiprora*. In contrast, other common ice diatoms such as *Nitzschia stellata* remain virtually uncolonized until the decline of the algal bloom in January, when bacteria colonized the surfaces of senescent diatoms (Grossi et al. 1984). Chaemoautotrophic bacteria are present in sea-ice assemblages in the form of ammonia-oxidizing bacteria (Priscu et al. 1990).

3.2.4.2 Microalgae

Most of the groups of microalgae that are present in the plankton are also found in sea ice (Horner 1986; Garrison 1991). Palmisano and Garrison (1993) list the following algal groups with the number of species recorded in brackets: diatoms (111). Chlorophytes (1), Prasinophytes (3), Pyrmnesiophytes (2), Chrysophytes (6), Archaeomonads (2), Cryptophytes (1), and autotrophic dinoflagellates (2). Amongst the diatoms pennate forms, including several *Nitzschia* spp., *Amphiprora* spp., *Navicula* spp., and *Synedra* spp. are typical of ice-algal assemblages. Additionally, a number of centric diatoms are also found. Some species have physiological survival strategies including spore formation (Garrison 1984) and an increase in heterotrophic potential and an accumulation and breakdown of lipids. Figure 3.6 illustrates some of the typical diatom species of the sea ice microbial community.

A variety of nano- and microflagellates are also found in sea ice. Their abundance and relative importance have probably been underestimated because they are readily destroyed during sampling and preservation (see Garrison and Buck 1986). The prymnesiophyte *Phaeocystis antarctica* (listed as *P. pouchetii* in earlier publications) that often dominates Antarctic phytoplankton assemblages is abundant in the pack ice (Garrison et al. 1987; Garrison and Buck 1989a, 1989b). Both the gelatinous colonial life stage and the solitary, motile stage have been found.

Garrison and Buck (1989a, 1989b) have found that dinoflagellatess are abundant in the sea ice. Most of the dinoflagellates in sea-ice assemblages belong to the so-called athecate genera *Gymnodinium*, *Gyrodinium*, and *Amphidium*.

3.2.4.3 Heterotrophic Protozoa

Heterotrophic protozoa are an important component of the microbial assemblages in sea ice. Palmisano and Garrison (1993) recorded the following with the number of species in brackets: Heterotrophic Flagellates; Choanoflagellates (16), Bodonids (1), Euglenoids (1); Heterotrophic Dinoflagellates (6); Ciliates (30); Sarcodines (5). Heterotrophic (colorless) nanoflagellates are sometimes a significant fraction of the heterotrophic biomass in the ice (Garrison and Buck 1989a, 1989b). Choanoflagellates are widespread. The primary mode of feeding of the heterotrophic flagellates is by phagotrophy of bacteria, although Marchant (1985) has reported that some choanoflagellates may ingest nanoplankton and algal detritus as well as bacteria.

Heterotrophic dinoflagelates are abundant in some sea-ice assemblages (Garrison and Buck 1989a, 1989b). These larger heterotrophic flagellates are capable of consuming a larger range of prey items, including both bacteria and algae (e.g., Lessard and Swift 1985). Ciliates are frequently reported from sea ice (Hoshiai and Kato 1961; Fenchel and Lee 1972; Kottmeier et al. 1987; Spindler et al. 1990). However, their diversity and quantitative importance are poorly documented. The most extensive systematic study is that of Corless and Snyder (1986) who reported 26 taxa in sea ice from the Weddell Sea. Larger protozoans such as the foraminiferan *Neogloboquadrina pachyderma* have been found in sea ice at densities of up to 1,000 cells l^{-1} (Spindler and Dieckmann 1986; Spindler et al. 1990; Dieckmann et al. 1991).

3.2.4.4 Metazoa

The Metazoa associated with Antarctic sea ice include a few species that live within the ice matrix as well as species living on or below the ice. These include a variety of organisms including polychaetes (2 species), amphipods (8 species), copepods (15 species), and fish (principally larval forms). Euphausiids, especially juveniles, are frequently associated with the undersurface of the sea ice.

3.2.5 SEA-ICE ASSEMBLAGES

The sea ice provides a growth substrate and refugium for a complex microbial community (often termed *epontic* or *sea-ice microbial* communities), consisting primarily of microalgae, bacteria protozoa, and small metazoa. Microbial assemblages have been found in several more or less distinct habitats in sea ice, including surface (infiltration and pool assemblages), interior (band and brine channel assemblages), interstitial bottom assemblages, and sub ice (mat strand and platelet layer assemblages) (Figure 3.4) (Horner at al. 1988; Horner 1992; Palmisano and Garrison 1993). The distribution of these community types varies within the sea ice at any one locality, but also in different localities. Figure 3.5 illustrates some of the regional variations that occur in the distribution of the various communities and Figure 3.6

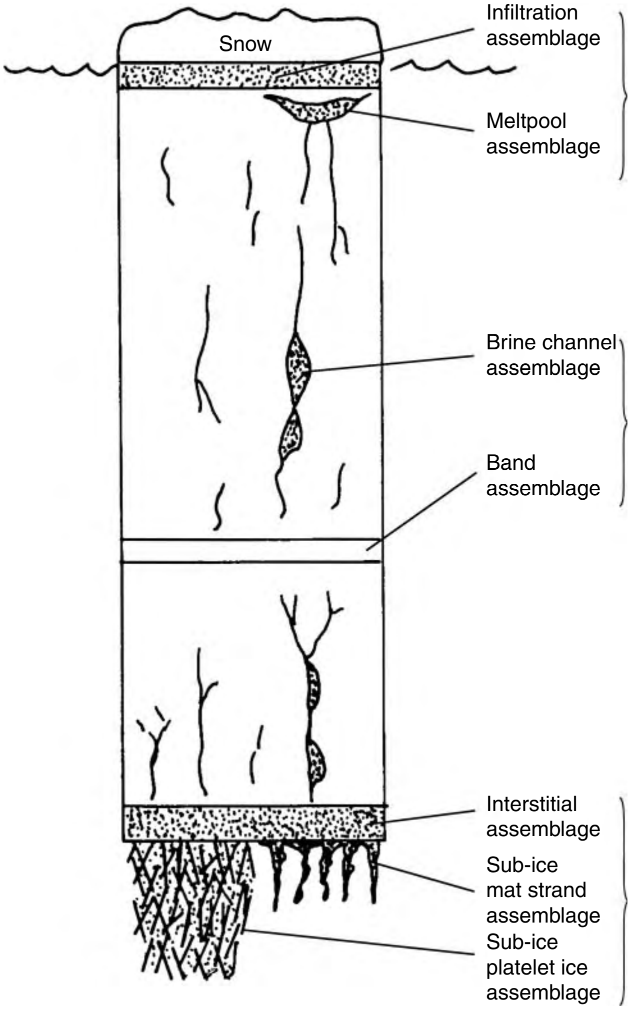


FIGURE 3.4 Schematic representation of the different kinds of microalgal assemblages associated with Antarctic sea ice. (From Horner, R.A., et al., *Polar Biol.*, 8, 249, 1988; Kottmeier, S.T., Sullivan, C.W., *Deep-Sea Res.*, 37, 1311, 1990. With permission.)

depicts some of the typical bacteria and microalgae of the sea-ice microbial community.

3.2.5.1 Community Types

Surface Assemblages. There are three types of surface communities (Figure 3.5 a, b). The first of these is the *infiltration assemblage*, which occurs at the snow–ice interface when seawater floods the ice floes (Meguro 1962; Lange et al. 1990). They often develop as a 20–30 cm layer. The second type of surface assemblage is associated with the ice deformation processes. These *deformation assemblages* include the *pressure ridge infiltration assemblage*, formed during initial pressure ridge formation, and the *surface saline pool assemblage*, formed when the ice surface is deflected below sea level and flooded. The third surface assemblage occurs in *melt pools* formed by thawing of the surface ice (McConville and Wetherbee 1983), or a combination of flooding and thawing.

At Casey Station, McConville and Wetherbee (1983) found that, in mid to late summer, a microalgal community developed in melt a 5–10 cm layer of consolidated snow that was dominated by small diatoms (*Fragilariopsis linearis*, *F. subliquecostata*, *F. ritscheri*), flagellates (*Pyranimonas*, *Gymnodinium*, *Cryptomonas cryphila*, *Mantoniella squamata*), and colonies of *P. antarctica*. The melt pools were initially patchy but spread rapidly, eventually developing a surface crust that was almost completely separated from the ice beneath. In January, the brine channels throughout the ice became interconnected and contained algal species from both the melt pools and bottom interstitial assemblages. At the time of the ice break up in mid-January, the melt pools contaifned large aggregations of cells in densities of up to $2.8\times10^{6}\,\mathrm{l}^{-1}$.

Burkholder and Mandelli (1965) and Whitaker and Richardson (1980) reported biomass accumulations of over 100 (mg chl *a*) $\mathrm{m}-^{2}$ and 200 (mg chl *a*) m^{-2}, respectively, for surface microbial communities found near the Antarctic Peninsula. Additionally, Fritzen et al. (1994) monitored the development of a bloom that reached 30 mg chl *a* in the upper 0.4 m of multiyear sea ice in the western Weddell Sea. The physical environment of surface sea-ice habitats is

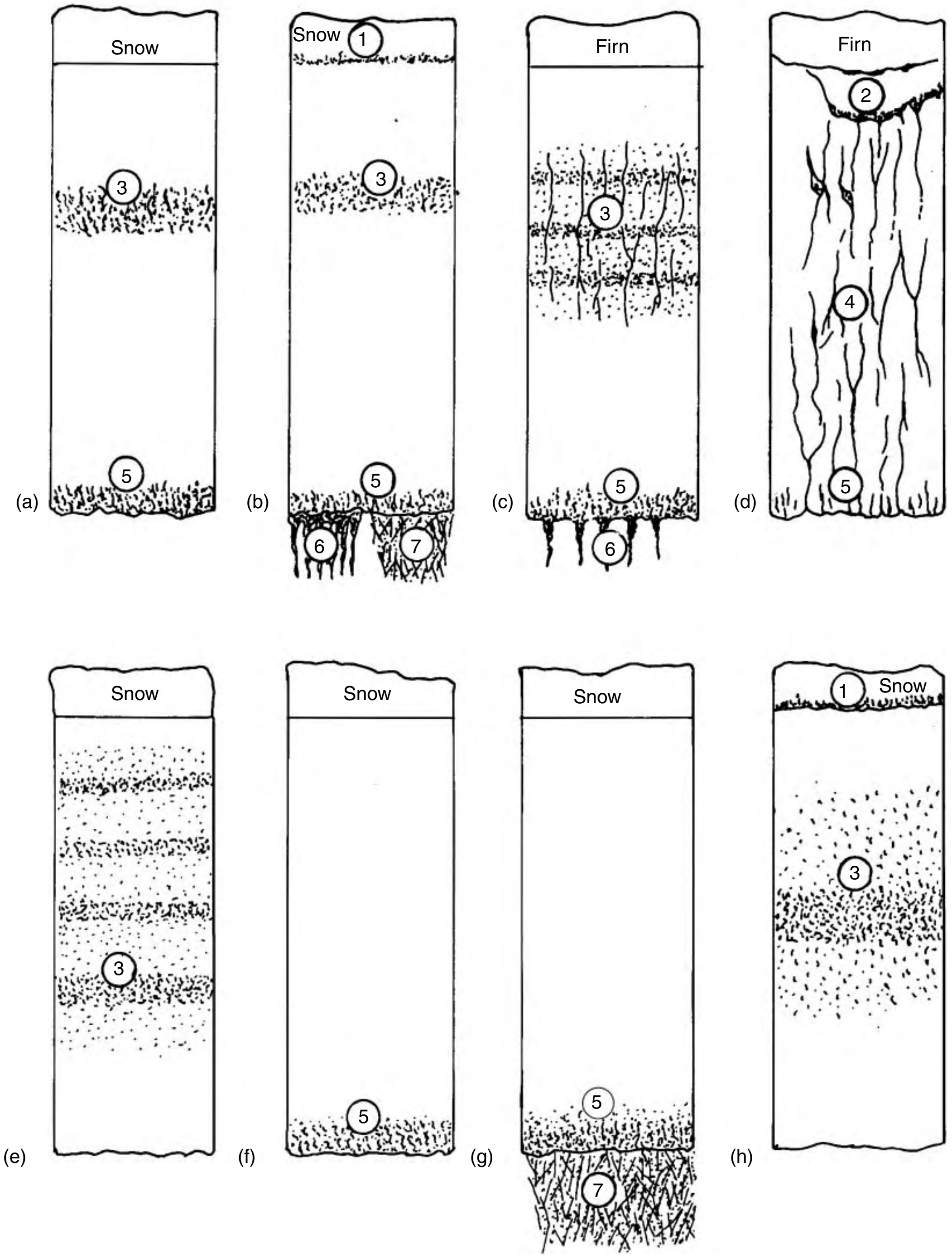


FIGURE 3.5 Typical profiles through sea ice at different localities in Antarctica, showing the occurrence of the different microalgal assemblages. 1, Surface infiltration assemblage; 2, Surface meltpool assemblage; 3, Interior band assemblage; 4, Interior brine channel assemblage; 5, Bottom interstitial assemblage; 6, Bottom sub-ice mat strand assemblage; 7, Sub-ice platelet ice assemblage. (a). Syowa Station, Hoshiai, T., *Polar Oceans*, Dunbar, M.J., Ed., Arctic Institute of North America, Calgary, 85, 1977. With permission; (b). Syowa Station, Watababe, *Jap. J. Phycol.*, 36, 1988 With permission. (c) and (d). Casey Station, McConville, M.J., Wetherbee, R., *J. Phycol.*, 19, 431, 1983. With permission: (e). Antarctic Peninsula, Kottmeier, S.T., Sullivan, C.W., *Mar. Ecol. Prog. Ser.*, 36, 293, 1987. With permission; (f). McMurdo Sound, Soohoo, J.B., et al., *Mar. Ecol. Progr. Ser.*, 39, 175,1987. With permission; (h). Weddell Sea, Ackley, S.F., Buck, K.R., Taguchi, S., *Deep-Sea Res.*, 26, 269, 1979. With permission.

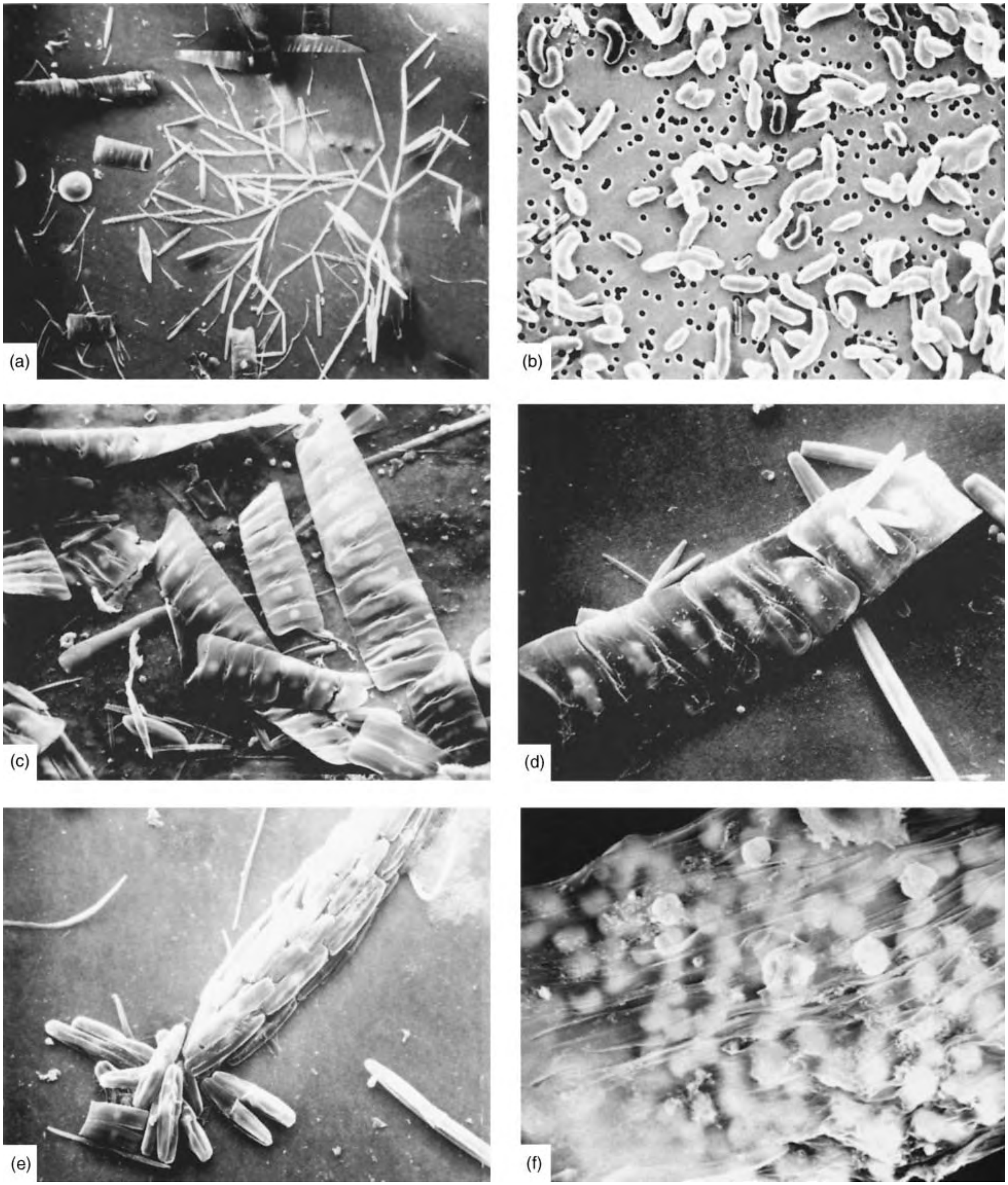


FIGURE 3.6 (a) *Nitschia stellata* colony, (b) bacteria, (c) *Amphiprora* "ribbons" with epibacteria and diatoms, (e) tube-dwelling diatom, (f) *Phaeocyctis* gelatinous colony. (Photographs supplied by Professor C.W. Sullivan. With permission.)

characterized during the austral spring and summer by relatively high irradiance, a long photoperiod, and low temperatures. For example, at the latitude of McMurdo Sound (77° 49″S), the 24-h photoperiod begins in late October and maximum surface irradiance may be greater than 1.400 μmol photons m^{-2} s^{-1} by midsummer (Arrigo et al. 1993). Where snow cover is thin or absent, a large proportion of the irradiance incident at the surface may penetrate into the surface ice habitat. The temperature of liquid water associated with the surface ice habitat is relatively stable at about −0.8°C. Robinson et al. (1997) investigated the microbial assemblage in melt pools on the fast ice in McMurdo Sound. This community was dominated by the diatom *Navicula glaciei*. They found that photosynthesis by the *N. glaciei*-dominated surface ice algal community was super-saturated with respect to incident PAR over most of the 24-h light period. They concluded that the surface ice microalgae successfully inhabit the surface ice habitat by employing a strategy of low-light harvesting, absorbed energy dissipation, and tolerance to photoinhibition damage.

Interior Assemblages. These occur within the ice matrix at various levels and several may occur within a single ice column. One of the closest to the upper surface is the *freeboard* habitat. It apparently occurs when brine drains from the upper layers due to surface warming, algal growth increases, heat is trapped, and the ice melts. The freeboard assemblage occurs 10–30 cm below the surface of the ice where the ice is rotting (Kottmeier and Sullivan 1990). The most common interior habitat occurs between ice crystals throughout the interior of the ice (Ackley et al. 1979; Garrison et al. 1983). The organisms that inhabit it may be scattered between the ice crystals with no definite pattern to their vertical distribution (Garrison and Buck 1989a) or be concentrated in brine channels or bands. *Brine channel assemblages* (Figure 3.4d) occur in brine channels, cavities, and cracks within the ice that are formed in response to temperature changes and internal stresses. They often form long vertical tubes that allow vertical movement of the brine through the ice (Maykut 1985). In the spring the channels may become connected to form a network within the ice (McConville and Wetherbee 1983; Horner et al. 1988). The channels contain microalgae common to both the water column and the bottom ice assemblages. Krill are also found grazing in these brine channels (Bergstrom et al. 1990; Daly 1990).

The *diffuse assemblage* is common in the pack ice where chlorophyll *a* concentrations average less than 10 $\mu g \, l^{-1}$ (Ackley et al. 1979; Clarke and Ackley 1984; Garrison and Buck 1989a). A variety of bacteria, sea-ice microalgae, heterotrophic flagellates, ciliates, foraminiferans, and metazoans, including copepods, are found in this assemblage.

Band assemblages are formed either by the accretion of new ice under a previously formed bottom ice algal layer (Hoshiai 1981a; Ackley et al. 1979; Watanabe and Satoh 1987), or by the incorporation of planktonic algae at the time of first freezing of the surface waters. They were first described from Syowa Station (Hoshiai 1969, 1981a). Diatoms and dinoflagellates are the most abundant organisms in this assemblage.

Although interior communities are not common in McMurdo Sound sea ice, they are a conspicuous feature of pack and fast sea ice in the Weddell Sea and in East Antarctica. Interior band assemblages occur throughout the ice column but are generally characterized by low biomass (Hoshiai 1977; McConville and Wetherbee 1983; Watanabe and Satoh 1987; Watanabe 1988; Watanabe et al. 1990).

Watanabe and Satoh (1987), working at Syowa Station, distinguished three types of microalgal assemblages: surface, interior and bottom. The dominant species of the interior assemblage during its formation in the autumn as a bottom assemblage were *Nitzschia* spp., *Fragilariopsis* spp., and several flagellates (Hoshiai 1977).

Archer et al. (1996) sampled the microbial assemblages in coastal land-fast and sea ice in the vicinity of Davis Station. The ice column was sampled at 5 levels, the first four sampling the interior assemblages, while the fifth sampled the interstitial assemblage in the bottom congelation ice. Twenty-eight autotrophs were recorded (18 species of diatoms, 3 dinoflagellates, 14 species of heterotrophs 2 flagellates, 7 ciliates, 4 dinoflagellates, and 3 euglenoids) The interstitial assemblage differed markedly from the internal band assemblages in taxonomic composition, biomass and the timing and fate of production (Figure 3.7a and Figure 3.7b). It can be seen in Figure 3.7b that the composition of the dominant autotrophic microalgae was more varied in the band assemblages with the interstitial assemblage being dominated by the species of the diatom genus *Entomoneis*. Abundant and diverse assemblages of heterotrophic protozoa inhabited all the horizons (Figure 3.7b). The dominant heterotrophic taxa present in the bottom interstitial assemblage were a species of euglenoid and 2 dinoflagellates. The internal band assemblages were largely composed of heterotrophic flagellates, euglenoids, and dinoflagellates. Bacteria occurred throughout the ice depth. However, biomass varied by several orders of magnitude between the different levels ranging from less than 5 mg $C \, m^{-3}$ in the upper horizon (A) to greater then 1,400 mg $C \, m^{-3}$ in the bottom-ice interstitial assemblage. Total microbial biomass integrated throughout the ice depth declined during the season from a mean of 1150 mg $C \, m^{-2}$ on November 17 to a mean of 628 mg $C \, m^{-2}$ by December 22.

Bottom Assemblages. Bottom-layer assemblages are most characteristic of landfast ice and have been the most extensively studied of the Antarctic ice assemblages. *Interstitial bottom assemblages* occur in the bottom of the ice column and are usually associated with a solid hard layer of bottom congelation ice (McMurdo Sound, Palmisano and Sullivan 1983a; Syowa Station, Watanabe 1988). Pennate diatoms and bacteria are abundant in this assemblage in the fast ice, and centric diatoms may be abundant in some areas (Grossi et al. 1984; Grossi and Sullivan 1985).

Sub-Ice Platelet Assemblages. Sub-ice platelet assemblages are found in loose aggregations of platelets on the under surface of the ice (e.g., McMurdo Sound, Soohoo et al. 1987; Syowa Station, Watanabe 1988). This assemblage may be extensive with layers up to 5 m thick being reported. Platelets accumulate only in close proximity to ice shelves, although in the Weddell Sea they may be formed at depth and harvest cells as they rise through the water column (Dieckmann et al. 1986).

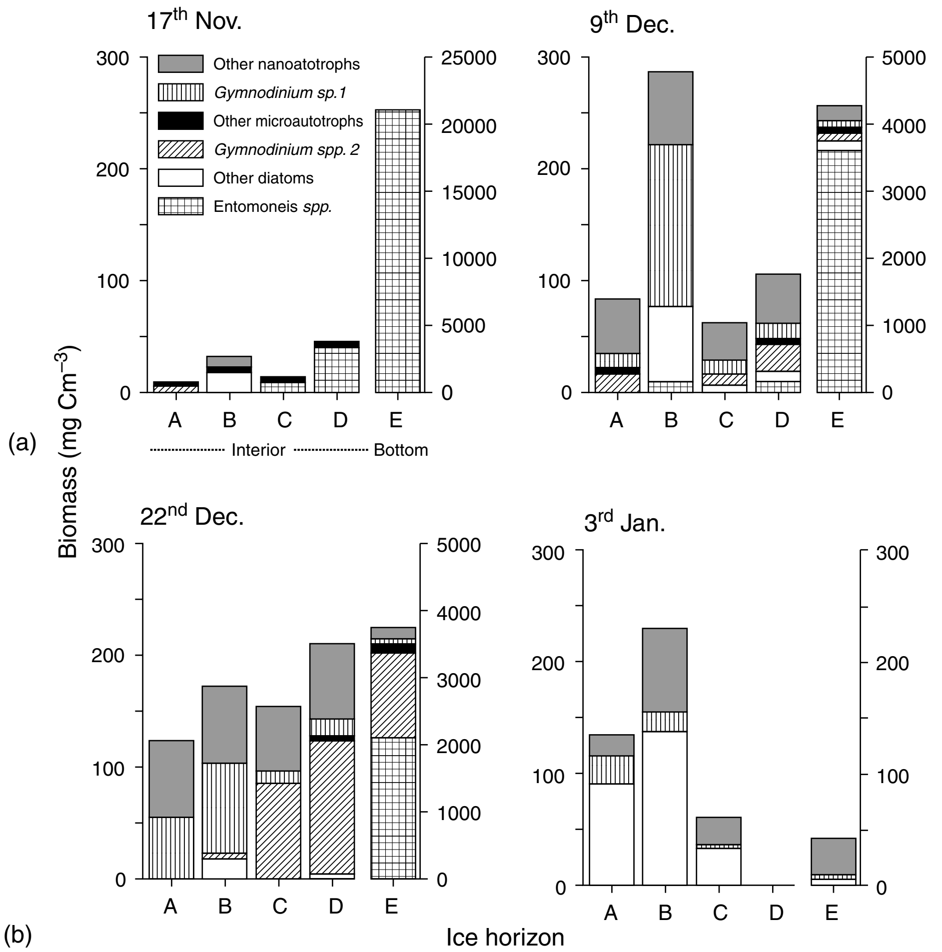


FIGURE 3.7 Mean biomass of 6 major categories of autotrophic taxa recorded from 5 ice horizons in cores sampled on 17 November 1993, 9 and 22 December 1993 and 3 January 1994. Horizon depths: A. B. C. D. E. Note the different scales for Horizon B. (From Archer, S.D., et al., *Mar. Ecol. Prog. Ser.*, 135, 185,1996. With permission.)

Sub-Ice Mat Strand Assemblages. Sub-ice mat strand assemblages are composed of algae floating directly below the ice forming strands that trail into the water column (McConville and Wetherbee 1983). This assemblage has been reported from Casey Station (McConville and Wetherbee 1983), near Syowa Station (Watanabe 1988), and from McMurdo Sound (Grossi et al. 1987) (Figure 3.5b and Figure 3.5c). Watanabe (1988) reports that no strands were seen in mid-July, but strands 10 to 15 cm in length were observed hanging from the sea ice in early November and had reached 50–60 cm in length by early December. The strands were mainly composed of pennate diatoms, especially those that form long colonies.

Most studies on sea-ice microbial communities have focused on diatoms which usually dominate the sea-ice microalgal communities. Pennate species belonging to the *Fragilariopsis* group (*Nitzschia cylindrica* and *N. curta*) often dominate, but several centric species may also be abundant (Watanabe 1982; Horner 1985, 1990; Garrison et al. 1987) (Figure3.6). Although a few diatom species form resting spores, the common species (e.g., *Nitzschia* spp.) do not have a distinctive resting stage (Garrison 1984). A variety of small (nano) and large (micro) autotrophic flagellates occur in the sea-ice assemblages and may sometimes predominate over the diatoms (Garrison and Buck 1985a, 1989a; Garrison 1991a). The relatively small number of flagellate species recorded in some studies is a consequence of the difficulty of species identification, and the fact that nano and microflagellates, as well as other delicate forms may have been missed because they can easily be destroyed during the melting of the ice and are often badly preserved (Garrison and Buck 1986). Both solitary motile cells and the gelatinous colonies of the prymnesiophyte *P. antarctica* are commonly members of the microalgal assemblage. Some nanoflagellates have resting spores. Cyst-like stages that Delfander (Delfander and Delfander-Rigand 1970; Mitchell and Silver 1982) called *archaeomonads* are very abundant in ice floes where they occur in densities of 10^4–10^7 l^{-1}. They are assumed to be the resting stages of chrysophytes and Takahashi (1987) has identified both siliceous and vegetative stages of the chrysophyte *Paraphysomonas* in Antarctic fast ice. Autotrophic dinoflagellates belonging to the so-called

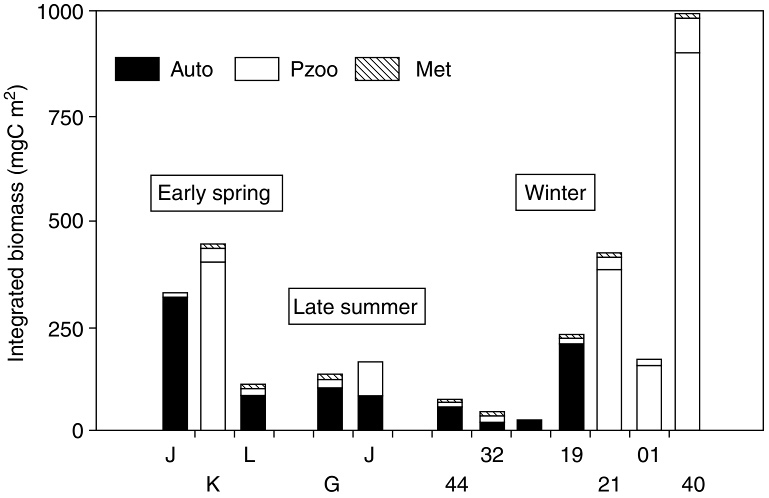


FIGURE 3.8 Early spring (AMERIEZ 83), late summer (AMERIEZ 86), and winter (AMERIEZ 88), comparison of integrated biota in sea-ice floes. Ice floes from AMERIEZ 83 and 86 are all first-year ice. Cores are identified by letter or number at the bottom of the figure. Auto: ice algae; Pzoo: protozoa; Met: metazoa. (From Garrison, D.L., Close, A.R., *Mar. Ecol. Prog. Ser.*, 96, 26, 1993. With permission.)

"unarmoured genera *Gymnodinium*, *Gyrodinium* and *Amphidinium* are sometimes abundant (Garrison 1991a)."

Bottom-Ice Interstitial Assemblages. Interstitial communities have been extensively studied by Sullivan and his coworkers in McMurdo Sound (Palmisano and Sullivan 1983a, 1983b; Sullivan et al. 1984, 1985; Palmisano et al. 1985a, 1985b, 1987a, 1987b). In their pioneer study of sea-ice microbial communities in McMurdo Sound Bunt and Wood (1963) listed two groups of diatoms; species attached to ice crystals, and non-attached species that were living in close association with the ice. Of the 11 dominant species, 5 were centric diatoms, *Biddulphia wessflogii*, *Coccinodiscus subtilis*, *Euchampia balaustium*, *Rhizosolenia alata*, and *R. rostrata*, and 6 were pennate diatoms, *Amphiprora kjellmani*, *A. oestrupii*, *Fragilaria linearis*, *Nitzschia martiana*, *N. serrata*, and *Pleurosigma antarcticum*. More recent investigations in McMurdo Sound have identified the chain-forming *Amphiprora kufferahii*, and a stellate colonial species *N. stellata* as the dominant species (Palmisano and Sullivan 1983a; Grossi and Sullivan 1985) in the interstitial bottom assemblage.

Burkholder and Mandelli (1965) listed the diatom species from ice habitats along the western coast of the Antarctic Peninsula. The ice contained the small diatoms *F. linearis* and *Nitzschia serrata*, plus small numbers of pennate diatoms, centric diatoms, a few dinoflagellates, small green flagellates and *P. antarctica*.

Garrison and Close (1993) investigated the winter ecology of the sea-ice biota in the Weddell Sea pack ice. The biota was concentrated in the surface layer and the internal band assemblages. The ice biota comprised 25 diatom species, 5 autotrophic flagellates, 2 autotrophic dinoflagellates, 6 choanoflagellates, several heterotrophic nanoflagellates, 3 heterotrophic dinoflagellates, several ciliates, foraminiferans and copepod nauplei. Over the season, the diatom biomass, which was dominated by *Nitzschia cylindricus* and *N. lecointei*, increased from 2 to 1,700 µg C l^{-1}. Figure3.8 compares the sea-ice integrated biomass in early spring, late summer and winter. The established ice floes contained significant amounts of frazil ice and its incorporation led to the development of internal band assemblages. These assemblages accumulated algal biomass over the growing season leading to the high winter biomass.

3.2.5.2 Brine Communities

Stoeckner et al. (1987, 1990, 1991, 1992, 1993, 1995) reported dinoflagellate-dominated assemblages in the land-fast ice from McMurdo Sound. This assemblage inhabited brine channels and pockets that extended from about 10 cm below the ice into the congelation ice. Photosynthetic dinoflagellates and their cysts dominated the biomass and comprised over 70% of the total autotrophic biomass in December and over 50% in January. Small ($<$ 5 µm) photosynthetic cells and cysts occurred in most of the samples (including *Montoniella* sp. and small siliceous cyst-like forms). *P. antarctica* was present in about a third of the samples at a density of about 100 ml^{-1}. In some samples photosynthetic ciliates were present, including small and medium-sized *Mesodinium rubrum* and plastidic oligotrichs (*Strombidium* spp.). During the austral summer total autotrophic biomass in the upper ice brine decreased due to dilution by meltwater flushing of the brine into the water column, and grazing. The dominant phagotrophs, *Cryothecomonas* spp., the heterotrophic dinoflagellates and *Strombidium* spp. are all consumers of microalgae and other small eucatyote cells.. These heterotrophic protists can comprise from 1% to 90% of the protist biomass and their grazing can influence algal growth and biomass accumulation (Garrison and Buck 1991).

In their study of sea-ice microalgal assemblages at Casy Station McConville and Wetherbee (1983) describe a bottom-ice interstitial assemblage which colonized the microbrine cells that penetrated up to 5 cm into the congelation ice from the bottom surface (Figure 3.5c). These brine channels were occupied by densely packed cells of the diatoms *Nitzschia frigida* and *Entomoneis* spp. in concentrations of up to 3×10^{8} cells l^{-1}.

3.2.5.3 Bottom Communities

Platelet-Ice Communities. Platelet ice layers that accumulate under the congelation ice provide a favorable environment for the development of microbial communities. They have been investigated in McMurdo Sound (Bunt 1963; Bunt and Lee 1970; Palmisano and Sullivan 1985b; Palmisano et al. 1987a; Arrigo et al. 1993, 1995, 2000; Ackley and Sullivan 1994), the Weddell Sea (Smetacek 1992; Grossman et al. 1996; Günther et al. 1999a, 1999b; Günther and Dieckman 2001), the Ross Sea (Grossi et al. 1987; Kottmeier et al. 1987; Arrigo et al. 1993b), and off Syowa Station in East Antarctica (Watanabe et al. 1990), and Adélie Land (Riaux-Gobin et al. 2000, 2003). The platelet layer is composed of approximately 20% ice and 80% water (Bunt 1964a). Due to its stability, in conjunction with the available space, opportunity for colonization, and capacity for nutrient exchange it can support dense microbial assemblages. The component organisms are suspended within the interstitial water between the platelets or grow attached to the platelets (Smetacek 1992).

Riaux-Gobin et al. (2003) sampled the platelet-ice layer (PLI) and the underlying phytoplankton community in Adélie Land. The dense microphytic PLI community, as well as the phytoplankton, was diatom dominated. The sea-ice communities (PLI and solid bottom ice) were moderately diverse (36 species). Mostly composed of pennate diatoms, of which many were chain forming or tube dwelling. Dominant taxa were *Navicula glacei*, *Berkleya adeliensis*, *N. stellata*, *Amphiprora kufferathii*, and *Nitzschia leconintei*. Under-ice water species composition was mixed. Maximum cell numbers were mostly found in the PLI, reaching up to 10^{10} cells l^{-1} and very high chlorophyll *a* concentrations exceptionally up to 9.8 (mg chl *a*) l^{-1} or 1.9 (g chl *a*) m^{-2}, from a 10 to 20-cm thick PLI layer. Nitrate in very high concentrations was found in the PLI layer apparently related to the high algal biomass. It seemed to have been actively regenerated in this layer.

Grossman et al. (1996) investigated algal and bacterial processes in platelet ice in the late austral summer in the Weddell Sea. Algae and bacteria accumulated within the platelet environment attaining concentrations of up to 500 μg chl *a* l^{-1} and 2 mg bacterial biomass l^{-1}. Pennate diatoms of the genus *Fragilariopsis* were the most common in the platelet layer, while the ice-free water was dominated by autotrophic nanoflagellates. Protozoa contributed only 5% or less to the total microalgae plus protozoan cell concentrations, compared to about 10% in the open water, thus suggesting a low grazing pressure within the platelet habitat. There is a lack of information on the bacterial processes in platelet ice assemblages. Before a microalgal platelet ice bloom Rivkin et al. (1989) found that bacterial production exceeded rates of primary production. In contrast during a summer bloom (Kottmeier et al. 1987) the secondary production in this habitat was only 0.01% of the algal primary production. In the Weddel Sea in the late summer, Grossman et al. (1996) recorded maximum bacterial cell concentrations and biomass of 1.5×10^{10} cells l^{-1} and 1.2 mg C l^{-1}. Grossman et al. also investigated the distribution of nutrients and salinity in open water, a crack in the ice and through a platelet layer (Figure 3.9). At the first two sites the these variable were uniformly distributed with depth, while in the platelet layer nitrate levels were low, but increased in the water column below. On the other hand, phosphate levels were high in the platelet layer. Lower salinity in the platelet layer is indicative of ice melting reducing the salinity.

In an investigation of the congelation and platelet ice layers in McMurdo Sound Arrigo et al. (1993, 1995) found that between 89% and 99% of the algal biomass was located within the 0.68-m thick platelet layer where the standing crop, measured as chl *a*, increased from 280 to 1090 mg m^{-2}. Algal biomass was highly stratified within the platelet ice layer. An increasing fraction, 39–90% of the integrated chl *a* was collected from the upper 0.125 m of the platelet layer near the base of the congelation ice. The peak algal standing crop was greater than 3-fold higher than the previous maximum standing crop of 310 (mg chl *a*) m^{-2} reported from McMurdo Sound (Palmisano and Sullivan 1983a, 1983b).

Sub-Ice Mat Strand Assemblage. Sub-ice mat strand assemblages have been described in western McMurdo Sound (Palmisano and Sullivan 1983a), off Mawson and Davis and Casey Stations (McConville and Wetherbee 1983), and off Syowa Station (Watanabe 1988). In McMurdo Sound the algal dominants were a chain-formimg *Amphiprora* and a stellate colonial species, *N. stellata*. In the New Harbour region in West McMurdo Sound a tube-dwelling pennate diatom was common. This species produced mucilage-encased tubes up to 10 cm long, extending through the brine channels and hanging from the bottom of the congelation ice. McConville and Wetherbee (1983) reported a sub-ice community which developed in September and was largely suspended from the bottom surface of the annual sea ice, often extending into the underlying water as conspicuous strands up to 15 cm long. It was dominated by an unidentified tube-dwelling diatom belonging to the *Amphipleura*/*Berkeleya* group and chain-forming species of *Entomoneis* (=*Amphiprora*). Associated with these colonial species were a number of epiphytic diatoms, particularly *Synedra* spp. During December, several centric diatoms (e.g., *Stephanopyxis*) and phytoflagellates (*Chamydomonas*) became common. At Syowa Station, Watanabe and Satoh (1987) did not observe sub-ice microalgal strands in mid-July but by early November strands 10–15 cm in length were hanging from the ice and by early December they had grown up to lengths of 50–60 cm. The strands were composed mainly of pennate diatoms,

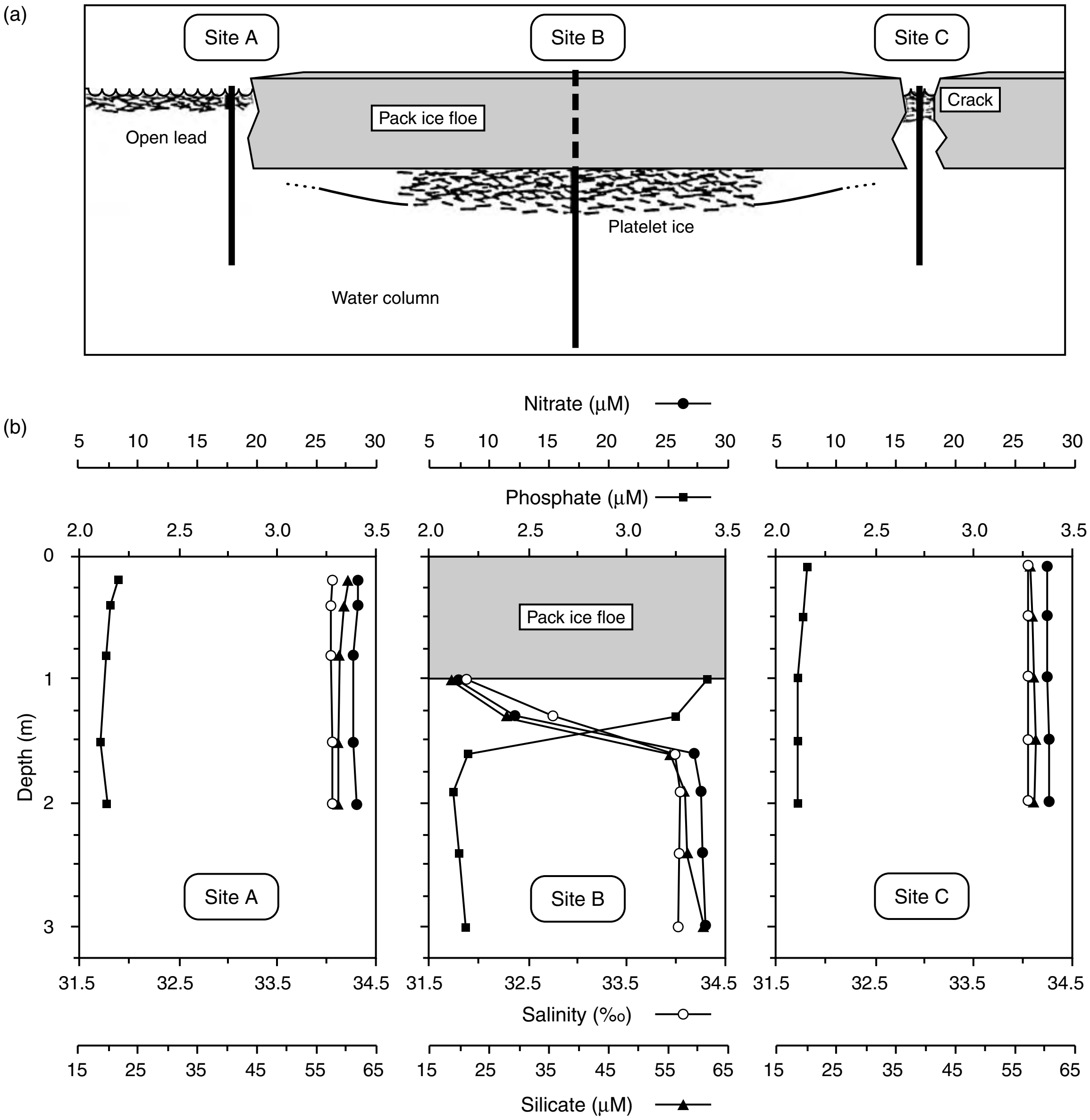


FIGURE 3.9 (a) Schematic depiction of a detailed study of the platelet ice habitat in the Weddell sea. The ice platelets were collected at three sites of an undeformed pack ice floe of ca. 1 m thickness, 1–20 and 39 cm snow and ca. 100×50 m in horizontal extension. Site A. at the sea surface in an open lead at the periphery of the floe, site B underneath the floe, and site C within a crack of approximately 0.8 m in diameter. The distances A, B, and C amounted to 20–25 m each way. Vertical bars indicate locations and maximum depths (2 m at sites A and C; 3 m at site B). (b) Salinity and concentration of inorganic nutrients in the platelet layer and the underlying water column at the three sites. (From Grossman, S., Lochte, K., Scharek, R., *Polar Biol.*, 16, 626, 1993. With permission.)

especially those forming long colonies, including *A. kufferathii*, *Berkeleya mitilans*, *Nitzschia lecointei*, *N. stellata*, *N. turgiduloides*, and several species of *Nitzschia* in the section *Fragilariopsis*, with smaller numbers of the single-celled species *N. glacei*.

Species composition in the sea-ice assemblages in the Weddell Sea were compared with the phytoplankton in the water column by Garrison and Buck (1985b). The ice algal populations comprised species usually characteristic of Antarctic phytoplankton assemblages. Of the species found in the ice, only a few species were considered to be benthic or tycopelagic (e.g., *Nitzschia vanheurchii* and *N. sublineata;* Hasle 1965), or generally have been reported to have distributions restricted to the ice edge (e.g., *N. subcarinata*, *N. obliquecostata*, and *N. castracanei*; Hasle 1964, 1965). The most abundant species found in the ice (e.g., *N. cylindrus* and *N. curta*) were planktonic species with wide distributions (Hasle 1965, 1969; Steyeart 1973; Guillard and Kilham 1977). In addition to the pennate diatoms, which dominated the ice assemblages, they also found *P. antarctica* in densities of up to 10^6 cells l^{-1} and centric diatoms such as *Coscinodiscus* and *Rhizosolenia*.

Tide cracks may also provide a habitat for rich microalgal assemblages. Whitaker (1977a) described abundant, uni-algal populations of *N. glacei* from the slush ice in coastal tide cracks at Signy Island. *Nitzschia curta*, *N. lineate*, and *Thalassiosira tumida* were found on the vertical walls of the tide cracks. At White Island, on the McMurdo Ice Shelf, McMurdo Sound, Rawlence et al. (1987) described the standing crop and succession of microalgae in the surface water of the tide cracks. The tide cracks contained dense aggregations of platelet ice. The dominant species during late November was *Pyranimonas* sp. (Chlorophyta). Diatoms were dominant from early December until the end of the study in late January. The five most abundant species were *Nitzschia cylindrus*, *N. curta*, *N. obliquecostata*, *Fragiaria* sp. and *Synedra tabulata* (see Figure 3.14).

The vertical distribution patterns of the species in the various assemblages have been described from Lutzow–Holm Bay (Hoshiai and Kato 1961), and McMurdo Sound (Grossi and Sullivan 1985; Knox 1986). At McMurdo Sound algal abundances in the ice decreased with increasing distance from the ice–seawater interface and with the depth of snow cover (Grossi and Sullivan 1985). Grossi and Sullivan hypothesized that microalgae, once incorporated into the sea-ice matrix, exhibit differential growth along physicochemical gradients within the ice column. Figure 3.10 depicts the theoretical gradients for light, salinity and temperature over the depth of a snow-free, 2-m ice column. After ice accretion has ceased competition amongst the algae for light, nutrients and space leads to a vertical zonation along these gradients. Diatoms may achieve this zonation either by active migration of motile species, or by differential growth rates dependent upon the physicochemical milieu. *N. stellata*, the dominant diatom species "showed peak abundance in the bottom 5 cm of the ice." A second colonial diatom, *Amphiporora kufferathii*, and an epiphytic diatom, *Fragilaria islandica* var. *adeliae*, had peak abundance in the bottom 5–10 cm. Other algal species showed distribution patterns different from those of the dominants, e.g., two motile species, an *Auricula* Castracane sp. and *N. glacei*, reached highest concentrations at depths of 10–20 cm above the ice–water interface.

In central McMurdo Sound Knox (1986) found a total of 30 species in sea-ice cores in the fast ice. Figure 3.11 shows the vertical distribution of the diatom species and the total number of cells in a standardized subsample of melted 2 cm sections of the bottom 24 cm of an ice core. Cell numbers peaked at 6–8 cm from the ice–seawater interface and then declined rapidly up the ice column, with only small numbers being present at 12 cm. Species numbers peaked at 2–4 cm (20 species) and remained high through 8–10 cm, thereafter declining to a low of 5 species at 20–24 cm.

3.2.5.4 Annual Cycle

Only a limited number of studies (e.g., Bunt and Lee 1970; Hoshiai 1977; McConville and Wetherbee 1983; Watanabe and Satoh 1987) have followed the development over the full period from the initial ice formation to ice breakout and decline. At McMurdo Sound, Bunt and Lee (1970) found increased numbers of algae in the ice from mid-July to early December. They counted cells in both interstitial water and melted frazil crystals. Cell numbers increased

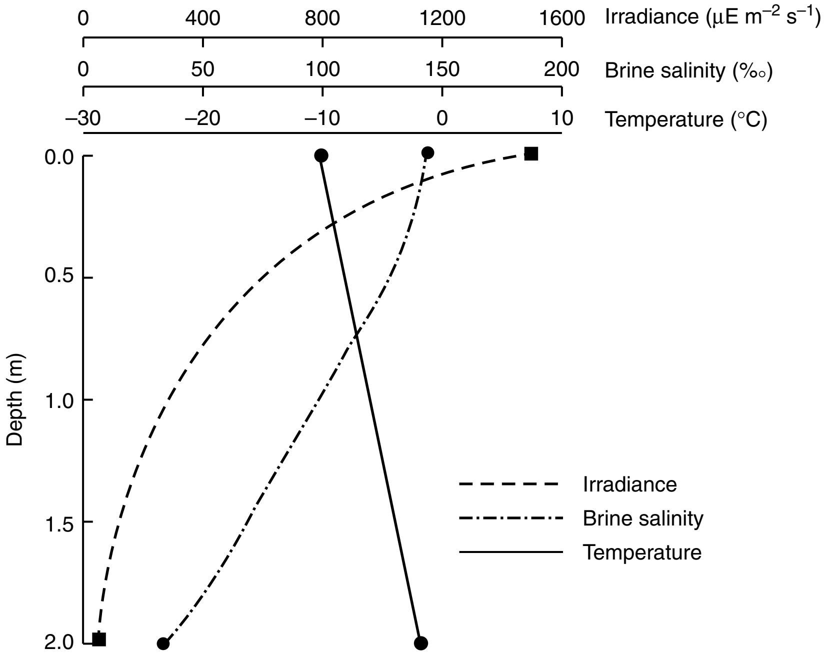


FIGURE 3.10 Theoretical gradients for irradiance, temperature, and salinity for a 2 m ice column at McMurdo sound, Antarctica in November. (From Grossi, S.McG., Sullivan, C.W., *J. Phycol.*, 21, 401,1985. With permission.)

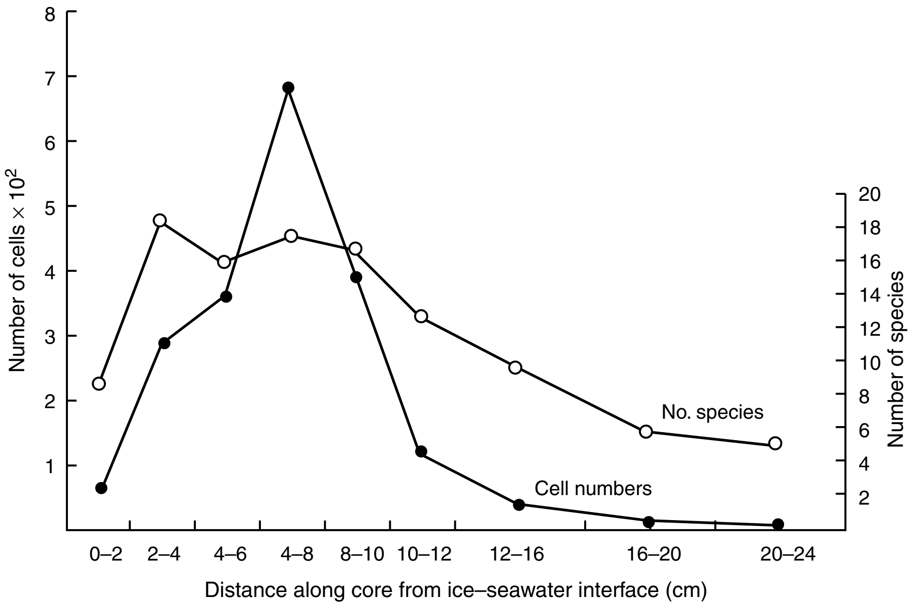


FIGURE 3.11 Distribution of microalgal species and total cell numbers in the bottom 24 cm of a core through the sea ice in McMurdo sound. (The cell numbers are based on standard microscope counts of a small subsample from a 2 cm melted section.) (From Knox, G.A., *Mem. Nat. Inst. Polar Res., Special Issue*, 40, 345, 1986. With permission.)

even during the winter dark period, remained relatively constant from late August through October, and then increased sharply by early December. Chlorophyll *a* concentrations followed the same pattern. Bunt (1964) reported peak development of the ice microalgae in December or early January. The ice algae disappeared when the bottom layer of the ice was lost.

Figure 3.12 depicts the seasonal succession of the ice microalgal assemblages near Syowa Station (Hoshiai 1977). Freezing of the seawater began in the middle of February and a brown algal layer had formed in the brine pockets in the bottom of the ice by the end of March, when the ice was about 30 cm thick. During the winter, the sea ice grew downwards by the formation of congelation ice to form a hard ice column below the brown layer which now formed an interior assemblage. A second brown layer appeared at the bottom of the sea ice in the spring (bottom infiltration assemblage). There was also a seasonal change

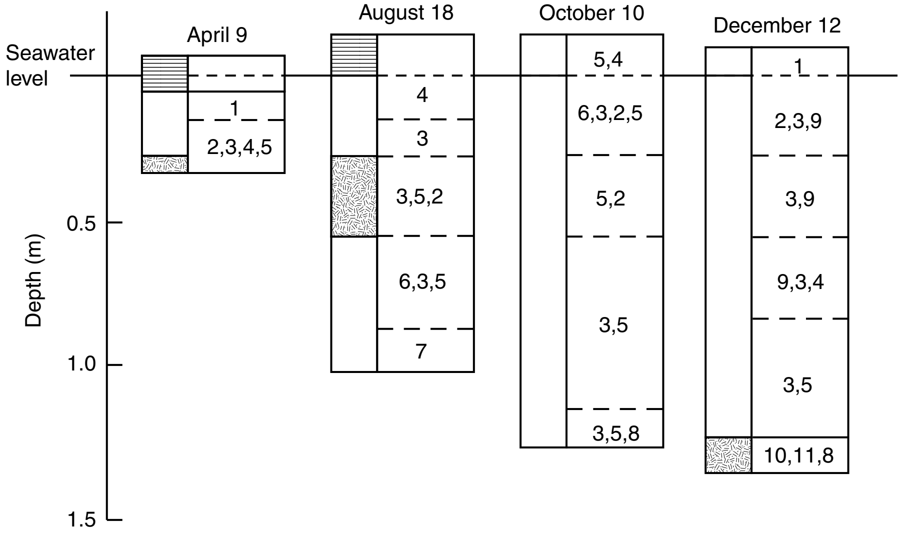


FIGURE 3.12 Seasonal succession of microalgae in various strata of sea ice off Syowa station. The left side of each ice profile (lined section), and light brown stained ice (light shading), or dark stained brown ice (dark shading). 1, *Biddulphia*; 2, *Nitzschia*, a; 3. *Nitzschia* b; 4, Dinoflagellate a; 5, *Fragilariopsis* b; 6, *Nitzschia frigida*; 7, *Peridinium*; 8, *Amphiporora*; 9, Dinofagellate b; 10, *Navicula*; 11 *Stephanopyxis*. (From Hoshiai, T., *Polar Oceans*, Dunbar, M.J., Ed., Arctic Institute of North America, Calgary, 307, 1977. With permission.)

in the species composition of the two ice communities, with *Nitzschia* spp., a dinoflagellate, and *Fragilariopsis* sp. being present in the bottom layer in April. These species, plus *N. frigida*, were still present in the layer in mid-August when the layer was in the middle part of the total ice thickness. A *Peridium* sp. was present in the bottom of the ice. In October when no brown layer was visible, *Nitzschia* spp. and *Fragilariopsis* sp. were present throughout the ice and *Amphiprora* sp. was also present in the bottom of the ice. By mid-December when the spring-summer bottom ice community was present, *Navicula* sp., *Stephanopyxis* sp., and *Amphiprora* sp. were present in the bottom layer; *Nitzschia* spp., *Fragilariopsis* sp., and a different dinoflagellate were present throughout the rest of the ice except at the surface where *Biddulphia* sp. was present. Watanabe and Satoh (1987) have described the seasonal succession of the ice microalgal assemblages in the same area at four stations from March 1983 to January 1984. They confirmed the observations of Hoshiai (1970b) on the initial development of what later became the interior assemblage.

Whitaker (1977a) has followed the seasonal growth cycle of a diatom population (*N. glaciei*) in a tide crack at Signey Island (Figure 3.13). Growth was slow until early September, then as irradiance increased the population grew rapidly to a peak in early November and then declined continuously until the breakup of the fast ice in the first week of December. In a tide crack at White Island on the McMurdo Ice Shelf the peak diatom biomass occurred in early December, but was preceded in early December by the development of a very large population of the flagellate *Pyranimonas* sp. (Rawlence et al. 1987) (see Figure 3.14).

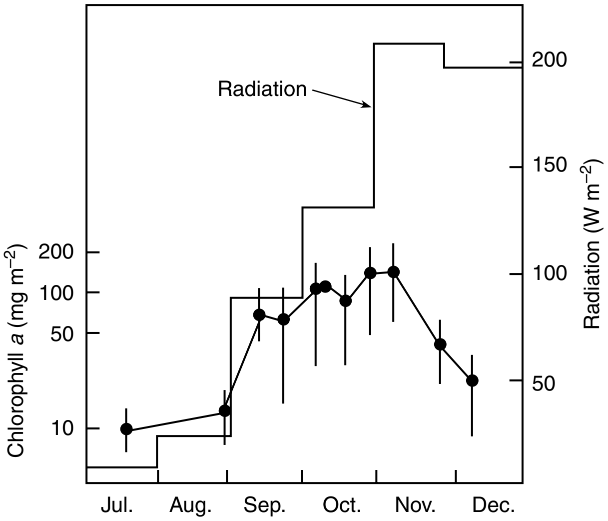


FIGURE 3.13 The seasonal growth of a diatom population (as measured by chlorophyll *a*) in a tide crack at Signy Island. (From Vincent, W.F., *Microbial Ecosystems of Antarctica*, Cambridge University Press, Cambridge 1988; redrawn from Whitaker, T.M., *Adaptations Within Antarctic Ecosystems*, Llano, G., Ed., Smithsonian Institute, Washington, DC, 75, 1977; the radiation data are from Walton, D.W.H., *Br. Ant. Sur. Data.*, 1, 1, 1977. With permission.)

The *Pyranimonas* population declined rapidly and by mid-December very low numbers were present. The *Pyranimonas* and the five dominant diatom species showed an interesting pattern of succession (Figure 3.14) with *N. cylindrus* dominant in the early phase of the diatom bloom and *N. curta* in the declining phase.

3.2.6 SEA-ICE MICROALGAE

3.2.6.1 Biomass Structure

In any given locality the sea-ice microbial biomass is dependent on a number of factors; the season, the relative development of surface, interior, bottom and sub-ice assemblages, downwelling irradiance (dependent on latitude, ice depth, the nature of the ice and the amount of snow cover), availability of nutrients, salinity, temperature and grazing intensity.

In McMurdo Sound where the microalgal biomass was concentrated in the bottom interstitial assemblage the standing crop averaged 131 (±121) (mg chl *a*) m^{-2} (Palmisano and Sullivan 1983a). Chlorophyll *a* levels rose by more than four orders of magnitude from the top to the bottom of the ice column with a sharp maximum in the bottom 20 cm where concentrations averaged 656 mg m^{-3}, with similarly high phaeophytin (369 mg m^{-3}). These concentrations were more than two orders of magnitude higher than those in the underlying seawater. Particulate organic carbon (POC) also increased with depth to a lesser extent than chlorophyll *a* and a similar trend was also observed in bacterial carbon (Sullivan and Palmisano 1984) (Figure 3.15).

The seasonal variation in sea-ice microalgal standing crop near Syowa Station has been studied by Hoshiai (1977) and Watanabe and Satoh (1987) (Figure 3.16). Hoshiai (1977a) found that the bottom infiltration assemblage demonstrated two biomass maxima over the year. Chlorophyll *a* concentrations were high in the autumn (up to 829 mg m^{-3}), decreased in the winter and then increased again in the spring when high concentrations (greater than 1,000 mg m^{-3}) were recorded. Although peak chlorophyll *a* concentrations occurred in the bottom interstitial assemblage during the early spring, the biomass maximum was in the interior assemblage higher in the ice column. Watanabe and Satoh (1987) found that the chlorophyll *a* standing crop had peaks in April–June and October–November. The largest standing crop was recorded in mid-November under moderate snow cover with 95.1% of the chlorophyll *a* concentrated in the bottom 4-cm layer of the ice, where the chlorophyll *a* concentration was 2,980 mg m^{-2}. In contrast to these high standing crops those measured by Ackley et al. (1979) in the Weddell Sea pack ice were very much lower with a maximum of 4.5 mg m^{-3}.

Table 3.1 gives data for the maximum standing crop (mg chl *a*) m^{-3}, or (mg chl *a*) m^{-2} for a variety of sea-ice microalgal assemblages from around the Southern Ocean. It can be seen that there are wide variations in the values from

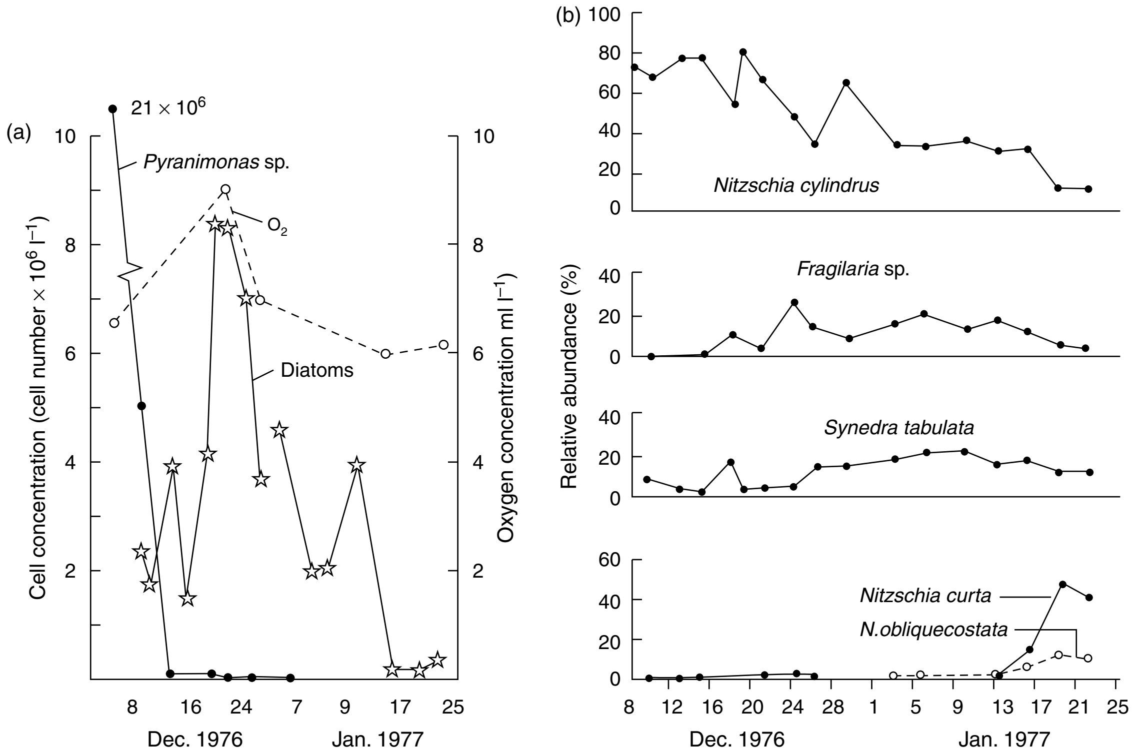


FIGURE 3.14 (a) Dissolved oxygen concentration and concentration of diatoms and *Pyramimonas* sp. in a tide crack at White Island, McMurdo sound, December 1976 to January 1977. (b) The relative abundance of diatoms in the tide crack. (From Rawlenced, D.J., Ensor, P.H., Knox, G.A., *N.Z. J. Mar. Freshwat. Res.*, 21, 91, 1987. With permission.)

the different localities and assemblages, reflecting local environmental conditions and the season in which the sampling took place. Standing crops in the vicinity of 300 (mg chl *a*) m^{-2} as found in McMurdo Sound (Sullivan et al. 1982; Palmisano and Sullivan 1983a) approach the theoretical maximum diatom standing crop of 400 (mg chl *a*) estimated by Steeman-Nielsen (1952) for natural waters.

Dieckmann et al. (1998) analysed the standing crop of chlorophyll *a* in sea ice from 448 cores collected during 13 U.S. and German research cruises between 1983 and 1994 (Figure 3.17). While the data had high variability there was a clear seasonal trend in the standing stock. The highest mean values were recorded in February and then they declined to the lowest values in July, after which they increased slowly.

Arrigo and Thomas (2004) lists chlorophyll *a* concentrations from some 54 investigations. Chl *a* in terms of mg m^{-3} range from 3.8 (late winter in the Weddell Sea) to greater than 6000 (spring platelet ice in McMurdo Sound). In terms of mg m^{-2}, the concentrations ranged from 0.6 (winter in the Weddell Sea) to 1075 (platelet ice in McMurdo Sound). Photosynthetic rates (mg C mg chl *a* h^{-1}) ranged from 0.11 to 8.8. Production rates in the pack ice are as much as four-fold higher than in the land-fast ice, but the former accumulates only half the biomass indicating that a large fraction was being consumed by the higher trophic levels.

3.2.6.2 Primary Production

Hoshiai (1981a) assumed a C:chl *a* ration of 50:1 to calculate carbon biomass in the vicinity of Syowa Sration. From chlorophyll *a* maxima of 30 and 35 (mg chl *a*) m^{-2} in the autumn and spring blooms, respectively, he estimated production rates of 1.5 and 3.2 g C m^{-2} (an annual primary production of at least 4.7 g C m^{-2}). Watanabe and Satoh (1987) estimated a similar level of primary production (0.5–3.4 g C m^{-2} yr^{-1}) at the same location. Using a similar approach, but an experimentally derived C:Chl *a* ratio of 31, Palmisano and Sullivan (1983a) estimated a seasonal production of 4.1 g C m^{-2} for the fast ice community of McMurdo Sound.

A number of investigators have used the ^{14}C technique to measure primary production in sea ice (e.g., Burkholder and Mandelli 1965; Bunt and Lee 1970; McConville and Wetherbee 1983; Palmisano and Sullivan 1983a; Grossi et al. 1987; Kottmeier and Sullivan 1987, 1990; Garrison and Buck 1991). While the primary production rates that they reported are variable, chlorophyll *a* specific rates range from 0.1 to more than 4.0 mg C (mg chl $a)^{-1}h^{-1}$ (Burkholder and Mamdelli 1965; Grossi et al. 1987; Lizotte and Sullivan 1991a, 1991b). On an aerial basis, maximum production rates greater than 1.0 g C m^{-2} day^{-1} in surface layer assemblages in the pack ice (Burkholder and Mandelli 1965; Kottmeier and Sullivan 1990; Garrison et al. 1993) and as high as 2.1 g C m^{-2} in bottom layer

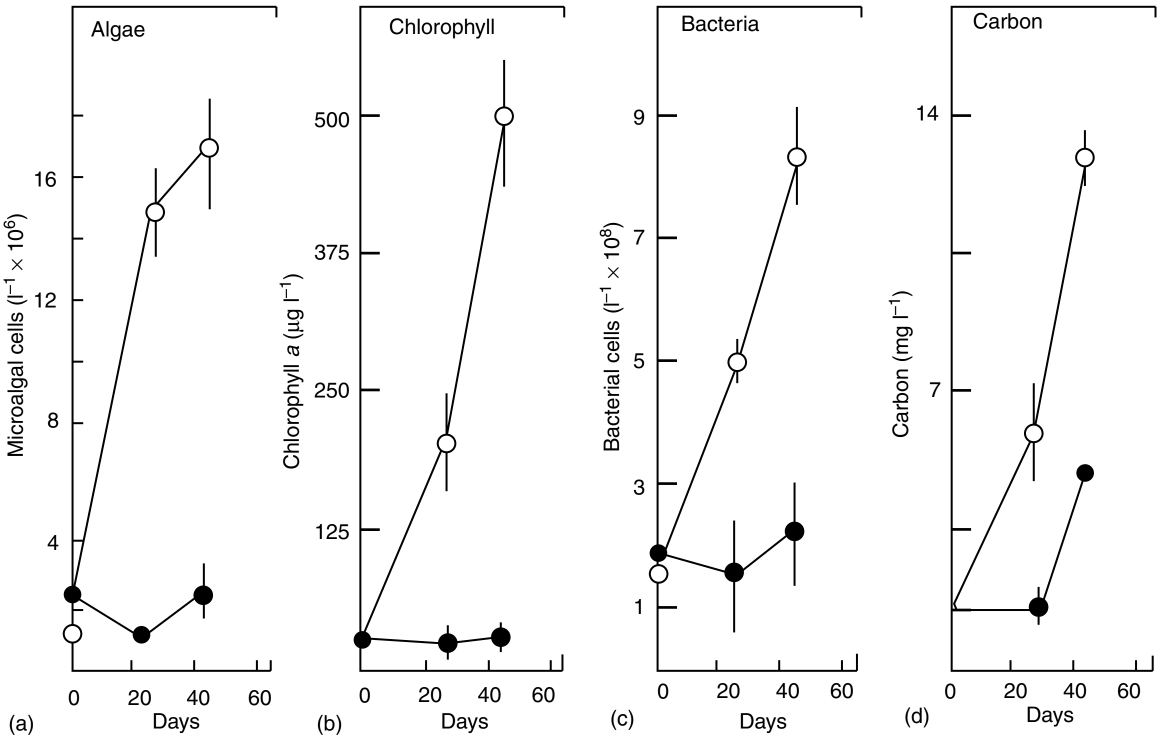


FIGURE 3.15 Accumulation of (a) microalgal cell numbers; (b) chlorophyll *a*, (c) bacterial cell numbers; and (d) organic carbon in the bottom 20 cm of the annual sea ice in a light perturbation experiment conducted in McMurdo sound. Open circles, data from control quadrat covered with 70–15 mm natural snow. Closed circles, data from an experimental quadrat covered with 70 cm snow. (From Sullivan, C.W., Palmisano, A.C., Kotmeier, S., Grossi, S.McG., Moe, R., *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer-Verlag, Berlin, 78, 1985. With permission.)

assemblages in landfast ice (Grossi et al. 1987) have been estimated. Table 3.2 lists productivity estimates for sea-ice microbial assemblages.

For the entire Pack-Ice Zone Horner (1985a) cited an estimate of 19 g C m^{-2} yr^{-1} in surface assemblages based on Burkholder and Mandelli's (1965) measurements. Garrison and Buck (1991) measured production rates of 0.1 mg C m^{-2} day^{-1}. Kottmeier and Sullivan (1987) estimated that production in the bottom layer of pack ice during the winter (June to September) was about 1 g C m^{-2} month^{-1}.

Arrigo et al. (1998) developed a numerical model of the Antarctic pack ice ecosystem for the purpose of investigating the spatial and temporal patterns of primary production. The annual rate of production within the Antarctic pack ice was calculated to be ~35.7 Tg C yr^{-1}, consistent with other estimates of 30–70 Tg C yr^{-1} (Legendre et al. 1992; Mathot et al. 1992, 1995). First-year ice accounted for nearly 75% of annual primary production within the pack. Nearly 60% of the annual production took place between November (11.5 Tg C) when the sea ice was near its maximum extent and December (9.80 Tg) when the rate of production per unit area was near its peak. The Weddell Sea accounted for ~50% of the annual production (15.8 Tg C) because of its extensive ice coverage and high rate of carbon fixation. The most productive region of the Weddell Sea was located within first-year ice near the eastern margin of the multiyear ice, along 45°W. Together, the Weddell Sea, the Ross Sea (7.7 Tg C), and the southern Indian Ocean (6.6 Tg C) accounted for 85% of the annual production in the Antarctic sea ice.

Estimates of annual primary production in the Southern Ocean over the past 30 years have varied widely as new information became available. Early estimates of annual phytoplankton production made by Ryther (1969) and Bunt (1968a) ranged from 6 to 130 g C m^{-2} yr^{-1}, and total production in the Southern Ocean was estimated to be 3000 Tg C yr^{-1}. However, estimates dropped 80% to 600 Tg C yr^{-1} as the number of measurements in pelagic waters under non-bloom conditions increased (Holm-Hansen et al. 1977; El-Sayed 1978). Recognition of phytoplankton blooms in the marginal ice zone led to adding 140–400 Tg C yr^{-1} (Smith and Nelson 1986; Legendre et al. 1992), bringing estimates of Southern Ocean phytoplankton production to 740–1000 Tg C yr^{-1}. Table 3.3 gives estimates of microalgal production and sea-ice extent for various regions of the Southern Ocean.

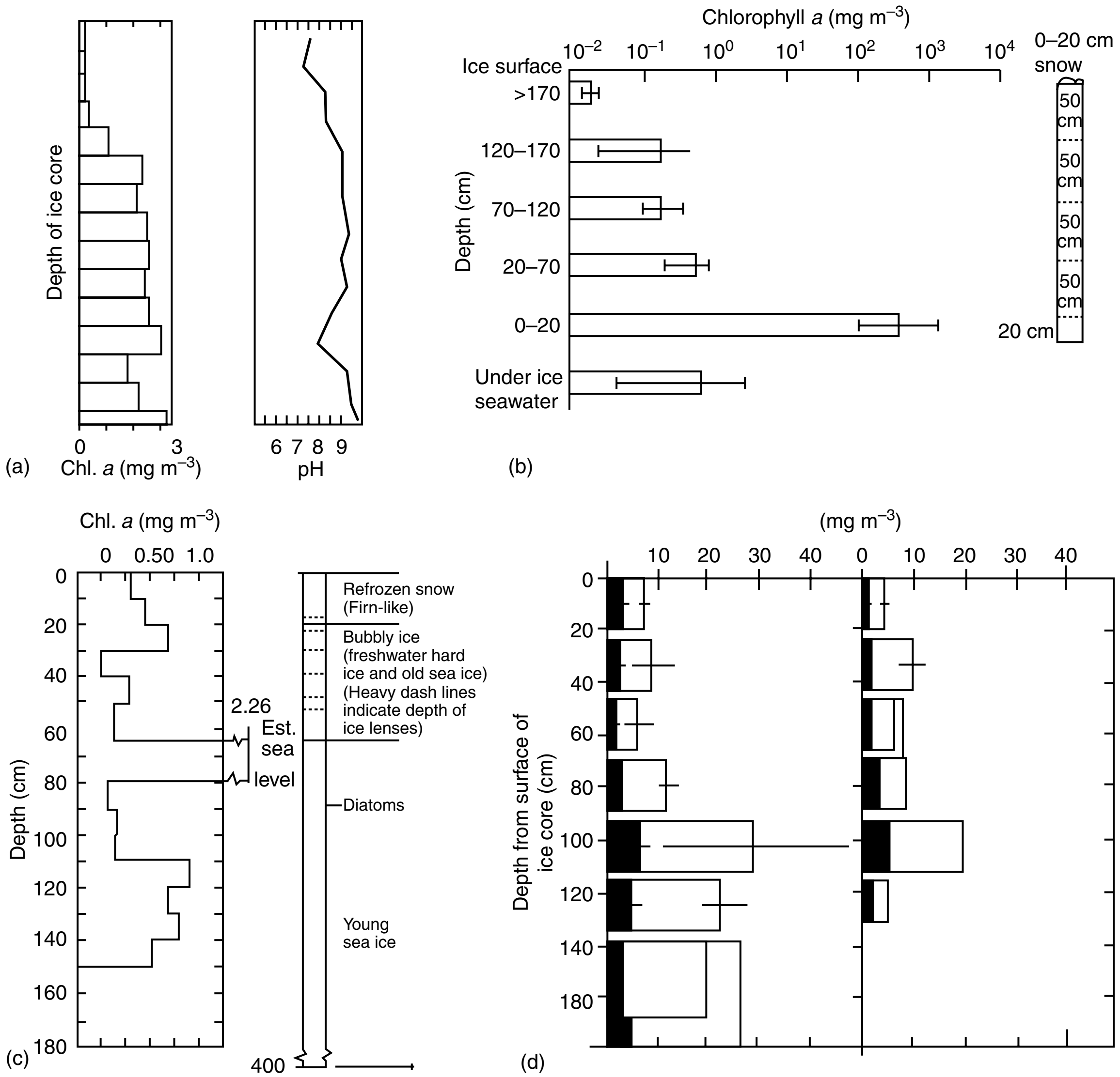


FIGURE 3.16 Vertical distribution of chl *a*: (a) In the sea ice off Syowa station, East Antarctica (left-hand diagram). The right-hand diagram is a vertical profile of the pH. (From Hoshiai, T., *Polar Oceans*, Dunbar, M.J., Ed., Arctic Institute of North America, Calgary, 307, 1977. With permission.) (b) Mean and range for the vertical sections of 15 sea-ice cores and for the under-ice seawater from McMurdo Sound. (From Palmisano, A.C., Sullivan, C.W., *Polar Biol.*, 2, 171, 1983a. With permission.) (c) In the sea ice of the Weddell Sea pack ice (left-hand diagram). At the 60–80 cm level the chl *a* concentration was 2.26 mg m^{-3}. (d) The right-hand diagram is a profile of the sea-ice characteristics. (From Ackley, S.F., Buck, K.R., Taguchi, S., *Deep-Sea Res.*, 26, 269,1979. With permission.) In sea-ice cores off the Antarctic Peninsula. Phaeopigment concentration (black areas) are shown in addition to chl *a* concentrations (white areas). The bars represent the ranges from duplicate cores. (From Kottmeier, S.T., Sullivan, C.W., *Polar Biol.*, 8, 293, 1977. With permission.)

The estimate of 35.7 Tg C yr^{-1} given by Arrigo et al. (1998) for the Antarctic pack ice algal productivity is about 1–4% of the annual biogenic carbon production in the Southern Ocean. However, the estimate of sea-ice primary production is 9–25% of the total production in the ice-covered region of the Southern Ocean. Although sea ice represents a small part of the Southern Ocean production, it is important as a highly concentrated food source for zooplankton, especially larval krill (Stretch et al. 1988).

3.2.6.3 Origin and Fate of the Sea-Ice Microbial Community

The origin of the sea-ice microbial community has been the subject of much speculation (Horner 1985a). The number of species common to both ice and water (Garrison and Buck 1985b) suggests that the two populations constitute a closely coupled system. Garrison and Buck (1985a) consider that "the striking similarity, both in species and relative abundance, may be maintained by a seasonal cycle where algal

TABLE 3.1
Maximum Standing Crop of Microalgae Measured as Chlorophyll *a* from Different Ice Microalgal Assemblages in the Antarctic

Community and Location	Chlorophyll *a*		Source
	mg m^{-2}	mg m^{-2}	
Surface melt pool			
Lutzow-Holm bay	97	670	Meguro (1962)
Lutzow-Holm bay	3.82	—	Watanabe and Satoh (1987)
Antarctic Peninsula	~122	407	Burkholder and Mandelli (1965)
South Orkneys	244		Whitaker (1977a)
Weddell sea pack ice			
Late winter	—	43	D.B Clarke and Ackley (1984)
Spring	—	54	Garrison et al. (1986)
Interior-band			
Lutzow-Holm bay	16.4	—	Watanabe and Satoh (1987)
Weddell sea pack ice			
Late summer	1.4	4.5	Ackley et al. (1979)
Late summer	9.6	9.8	Garrison and Buck (1982)
Spring	51.0	77.0	Garrison et al. (1986)
Late winter	0.6	3.8	D.B. Clarke and Ackley (1984)
Young ice			
Weddell sea late summer	3.9	26.8	Garrison et al. (1983)
Bottom infiltration			
McMurdo Sound	309	>656	Palmisano and Sullivan (1983a)
McMurdo Sound	294	—	Sultivan et al. (1982)
Syowa station, autumn	—	829	Hoshiai (1977)
Syowa station, spring	—	>1000	Hoshiai (1977)
Syowa station, autumn	30	944	Hoshiai (1981a)
Syowa station, spring	35	5320	Hoshiai (1981a)
Davis station	15	—	McConville et al. (1985)
Sub-ice			
Mat strand	1.58–32.92 h^{-1}		McConville and Wetherbee (1983)
Davis station			
Platlet layer	~164	132	Bunt and Lee (1970)
McMurdo Sound	~125	250	Bunt (1963, 1968b)
Tide crack			
Signy Island	236	—	Whitaker (1977a)
White Island		30µg l^{-1}	Rawlence et al. (1987)

~ integrated values not given but could be estimated from ice thickness date.

Source: Modified from Garrison et al. (1986).

populations are regularity harvested from the water column and trapped in the ice, where cells persist in the ice, and where ice populations are again released into the water during melting."

A number of studies have reported that organisms ranging from microalgae to foraminifera may be harvested from the water and concentrated in newly forming sea ice (e.g., Bunt 1968a; Bunt and Lee 1970; Garrison et al. 1983; Spindler and Dieckmann 1986; Ackley et al. 1987; Watanabe and Satoh 1987; Dieckmann et al. 1988). Phytoplankton cells in the surface waters may become incorporated in the ice when grease ice is formed by frazil crystal accumulations. This incorporation has been observed both by Hoshiai (1977) and Watanabe and Satoh (1987) near Syowa Station. Cells are accumulated in the ice by a combination of scavenging and nucleation (Ackley 1982). Scavenging occurs when ice crystals moving up the water column collide with and collect algal cells from the water. Nucleation occurs when a frazil ice crystal nucleates on an algal cell in seawater at its freezing point. In a series of experiments Garrison et al. (1989) demonstrated that frazil ice can concentrate organisms up to four times the levels in natural water. The bottom ice assemblage may be formed when phytoplankton cells are scavenged by frazil platelets that attach and freeze to the underside of the ice (Ackley et al. 1979). The sub-ice mat strand assemblages probably originate from the growth of cells originally incorporated in the bottom ice. Where platelets form an unconsolidated layer below the

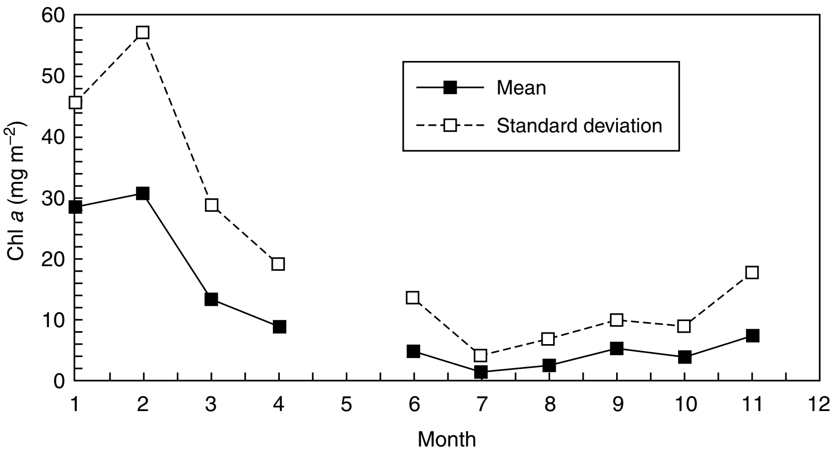


FIGURE 3.17 Monthly mean integrated chl *a* derived from all cores, irrespective of geographic location or year. Data from ANT III/3 have been excluded because the high biomasses recorded on this cruise were predominantly from fast ice cores which have a unique and localised ice assemblage, with extremely high biomass. Data from May and December have been omitted because of low numbers. (From Dieckmann, G.S., et al., *Ant. Res. Ser.*, 73, 90, 1998. With permission.)

undersurface of the ice, their associated microalgal assemblages may have originated from cells scavenged as the platelets floated up the water column, or from cells trapped within the platelet layer as currents moved through the loose platelet aggregations.

In their examination of young ice, Garrison and Buck (1985b) found that the assemblages in the water and the ice were essentially identical, except that the cells were more concentrated in the ice, indicating that the initial algal populations were nonselectively incorporated from the water column. However, the generally fewer species in ice cores, as compared with the water, may indicate that there is selective survival of some species from the more diverse assemblages initially trapped by the ice.

There have been a number of conflicting views concerning the fate of the ice microalgae. During the seasonal melting and recession of the ice edge, ice-bound algae and other members of the microbial community are released into the waters of the ice edge zone. Krebs et al. (1987), in a study of neretic diatoms in Arthur Harbour, Anvers Island, considered that the diatoms of the sea ice were an important inoculum for the subsequent phytoplankton bloom. However, the direct input of algae from the melting ice is a relatively small contribution. Sullivan et al. (1988) calculated that the release of algae into the water column in the Weddell Sea ice edge zone would result in an increase into the water column on the Weddell/Scotia Sea ice edge would result in an increase of chlorophyll *a* in the upper 50 m of 0.2 μg Chl *a* l^{-1}. The sea-ice microbial community is made up of many species that are also common in the plankton, so that the sea-ice assemblage could be a source of "seed" populations to developing plankton blooms. Kuosa et al. (1992) studied the potential seeding impact of sea ice microbial communities in the Weddell Sea in a series of experiments in seawater aquaria. The results showed the potential seeding effect of algae, protozoa, bacteria, nutrients and DOC. They found that the seeding of seawater by ice rich in algae, flagellates and/or POC leads to the development of communities dominated either by diatoms or flagellates.

TABLE 3.2
Comparison of Sea-Ice Extent and Productivity within the Antarctic Pack-Ice Zone

Area	Sea-Ice Extent October–April(10^4 kg^2)	Productivity (g C m^{-2} mth^{-1})	Productivity (Tg C mth^{-1})	Annual Production (Tg C)
Weddell Sea	1.16–5.85	0.26–1.90	0.37–4.60	15.97
Bellingshausen-Amundsen Seas	0.44–1.85	0.09–0.99	0.17–1.06	3.57
Ross Sea	0.37–3.94	0.71–1.24	0.23–2.68	7.73
Western South Pacific Ocean	0.22–1.01	0.11–0.95	0.13–2.76	1.92
South Indian Ocean	0.23–3.70	0.19–1.93	0.13–2.76	6.66
Southern Ocean total	2.43–13.6	0.17–1.52	1.06–9.80	35.7

TABLE 3.3
Growth Rate Estimates for the Bottom Microalgal Assemblage in McMurdo Sound during a Light Perturbation Experiment

	Control Quadrant (Snow depth 15–72 mm)		Perturbed Quadrant (Snow depth 670–700 mm)	
Basis for Growth Rate Estimates	**Specific Growth Rate (μg day^{-1})**	**Generation Time (days)**	**Specific Growth Rate (μg day^{-1})**	**Generation Time (days)**
Algal cell numbers	0.099	7	0	No net growth
Chlorophyll *a*	0.097	7	0	No net growth
Bacterial cell numbers	0.050	14	—	—
$H^{14}CO_3$primary production	0.014–0.086	8–50	0–0.27	26

Source: From Sullivan, C.W., Palmisano, A.C., Kottmeier, S., Grossi, S., McG., Moe, R., *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer-Verlag, Berlin, 78–83, 1985.

The release of high concentrations of biological matter contained within the ice is an important event in the seasonal sea-ice cycle (Leventer 2003). The fate of this material has consequences for biogeochemical cycling, bentho-pelagic coupling and ultimately for the sequestration of organic carbon into the sediments. Biological material released from the sea ice can be in the form of dissolved or particulate organic matter, living cells or aggregations of dead and living cells and the fecal pellets of the grazers (reviewed by Brierley and Thomas 2002; Leventer 2003).

3.2.7 ENVIRONMENTAL FACTORS AND THE SEA-ICE MICROBIAL COMMUNITY

Microalgae living in sea ice are unique in their ability to photosynthesize under a set of extreme environmental conditions. Surface water temperatures in the Pack-Ice Zone are continually low (e.g., in McMurdo Sound they range from −1.81°C to 0.08°C (Littlepage 1965)), and the bottom ice assemblage will be exposed to these temperatures. Algae trapped in the hypersaline brine pockets within the ice column may experience temperatures several degrees lower (Kottmeier et al. 1986). The microalgae at the bottom of the congelation ice are subject to considerable salinity fluctuations. As the ice forms excluded salts are concentrated in microscopic ($<$ 1 mm) brine pockets. However, as snow and surface ice melts in the early summer, meltwater percolates through porous sea ice, flushing the sea-ice microalgae with low salinity water. The light regime to which the microalgae are subjected is highly variable and light is considered to be the most important environmental factor. Thus the environment in which the microalgae grow is an extreme one and their success reflects their metabolic adaptation to these extremes.

3.2.7.1 Growth

Relatively few estimates have been made of the growth rates of natural populations or laboratory cultures of sea-ice microalgae. Estimates of annual production have usually been based upon the standing crop of chlorophyll *a* prior to the summer melt (Bunt 1963; Sullivan et al. 1985a). Such estimates are based on the assumption that losses from the sea-ice habitat (e.g., by grazing or sinking) are negligible due to the physical confinement of the cells within the ice (Bunt and Lee 1970). In situ estimates of growth rates have been made by determining algal cell numbers in the ice at two different point in time during the spring bloom. However, increases in algal numbers may in large part be the result of algal accumulation rather than cell division (Palmisano and Sullivan 1985b). Growth of the sea ice itself can lead to the entrapment of algae from the water column (Ackley 1982; Garrison et al. 1983) and thus overestimation of algal growth. On the other hand, loss of algae due to ice ablation could lead to underestimation of growth rates.

In a study of the microalgae of the platelet ice and interstitial water in McMurdo Sound Bunt (1963) found that they increased from 2.3×10^6 to 40.6×10^6 cells l^{-1} over an 18-day period. Assuming that this increase was solely due to cell division this represents a specific growth rate of 0.12 day^{-1}, or a doubling time of 6 days. From the data given in Bunt and Lee (1970) Palmisano and Sullivan (1985b) calculated a range of specific growth rates of 0.80–0.21 day^{-1} (doubling times 3–9 days) for the spring bloom. This compares with the maximum growth rate found for Antarctic phytoplankton by Holm-Hansen et al. (1977) of 0.33 day^{-1}; in most samples the maximum growth rates were closer to 0.1 day^{-1}.

In culture experiments Palmisano and Sullivan (1982) found an average doubling time of 2.5 days ($\mu = 0.28$ day^{-1}) for three sea-ice diatoms, including two clones of *N. cylindrus* grown at 46 μE m^{-2} s^{-1}, 0°C, and 20% in modified f/2 medium to mimic summer conditions under annual sea ice. Palmisano and Sullivan (1985b) point out that these growth rates should not be considered maximal as the growth rate was light limited at the irradiance used. By growing a culture of *Fragilaria sublinearis* at 7°C after adaptation to higher light intensities (about 220 μE m^{-2} s^{-1}) Bunt (1968) obtained growth rates equivalent to 1.16 day^{-1}.

3.2.7.2 Light and Photosynthesis

Several studies in different areas of the Southern Ocean have proposed that light is the major factor limiting the growth of sea-ice microalgae (Bunt 1964b; Horner and Schrader 1982; Palmisano and Sullivan 1982; Sullivan et al. 1984, 1985; Grossi et al. 1987; Soohoo et al. 1987; Arrigo et al. 1993, 1995; Garrison and Close 1993; Robinson et al. 1997; Terenrry et al. 2002).

Downwelling irradiance is attenuated by snow cover, the sea ice itself, and the development of various microalgal assemblages, so that the under-ice irradiance is typically less than 1% of that of the surface downwelling irradiance (Sullivan et al. 1982, 1984; Palmisano et al. 1987a, 1987b). Sullivan and Palmisano (1981) reported under-ice irradiances between 0.3 and 13.0 $\mu E\ m^{-2}\ s^{-1}$ during the 1980 phytoplankton bloom in McMurdo Sound. In a light perturbation experiment in which 15–70 mm of snow was maintained on one quadrat and 700 mm on another Sullivan et al. (1985) found that the under-ice irradiance under the former quadrat ranged from 0.0 to 0.11 $\mu E\ m^{-2}$ and 0.7 to 2.9 $\mu E\ m^{-2}\ s^{-1}$ under the latter, while Palmisano and Sullivan (1985c) found that during the spring bloom the irradiance under annual sea ice with 50 mm of snow cover was low with a mean of 6 $\mu E\ m^{-2}\ s^{-1}$, representing only 0.4% of the surface downwelling irradiance.

Profiles of spectral irradiance through the ice column in McMurdo Sound (Soohoo et al. 1987) have demonstrated that the irradiance environment of the sea ice is both vertically and horizontally heterogeneous (Figure 3.18), changing from being blue dominated to green dominated with depth in the ice column, and varying from site to site depending on the snow and ice microalgal patchiness. Changes in both total PAR and spectral irradiance that occur over tens of meters in an open water column are compressed within a vertical distance of only 2 or 3 m within the sea-ice column.

In spite of the reduced irradiance available to the bottom ice and platelet microalgal assemblages substantial standing stocks of microalgae are found and their productivity may be high (Palmisano and Sullivan 1983a; Sullivan et al. 1985). Bunt and Lee (1970) were the first to establish that the size of the standing crop of the sea-ice microalgae was a function of snow cover. In 1967 a site in McMurdo Sound with surface snow yielded 520 mg C m^{-2}, whereas a snow-free site yielded 1076 mg C m^{-2} (Bunt and Lee 1970). Palmisano and Sullivan (1985) and Sullivan et al. (1982) conducted a light perturbation experiment in which snow cover over 1.5 m of congelation ice was manipulated to reduce the irradiance reaching the sea-ice microalgae (Figure 3.19). At the end of the growing season in 1981 a standing crop of 100 (mg chl *a*) m^{-2} was found under 1.5 cm of natural snow cover, while only 5.5 (mg chl *a*) was found under 100 cm of snow on a quadrat with an artificially increased amount of snow.

Subsequent studies have confirmed these results (Grossi et al. 1987). Five quadrants were established in early October with 0.5, 10, and 100 cm of snow cover. Under ice irradiances ranged from less than 0.02 to 100 $\mu E\ m^{-2}\ s^{-1}$. Standing crop, growth rate and photosynthetic "rate were greatest under the snow-free quadrat where the chlorophyll *a* concentration increased from 0.1 to 76 mg m^{-2} in the platelet ice layer ($\mu = 0.41\ day^{-1}$) and from 0.05 to 9.0 mg m^{-2} in the congelation layer ($\mu = 0.29\ day^{-1}$) over a 5-week period." Blooms occurred later in the snow-covered quadrat and growth rates were less than half of those in the snow-free quadrat (Table 3.4, Figure 3.19).

Photosynthesis–irradiance (P–I) (Table 3.5) relationships are used to describe the photoadaptive states of microalgae. The initial slope of the P–I curve indicates the photosynthetic efficiency under light-limited conditions. The maximum rate of photosynthesis under light-saturated conditions is designated P_m. I_m, the so-called "index of photoadaptation." The irradiance of maximum photosynthetic rate (I_m) and an index of photoinhibition (P_m/I_m) can be calculated from the model of Platt et al. 1980).

Ice algal assemblages are generally considered to be "shade adapted." Bunt (1967) found that photosynthesis by natural populations of sea-ice microalgae in McMurdo Sound was light saturated at 100 fc (about 22 $\mu E\ m^{-2}\ s^{-1}$) and photoinhibited at 1100 fc (about 240 $\mu E\ m^{-2}\ s^{-1}$. Assimilation numbers were found to be less than 1.5 mg C (mg chl *a*)$^{-1}$h^{-1}. Bunt (1968b) later confirmed these observations in laboratory studies with the sea-ice diatom *F. sublinearis* in which cells grown at −2.0°C and 13 fc in an assimilation number of only 0.37. Growing the cultures at 5.0°C and 1000 fc increased the assimilation number to 1.2.

Preliminary studies by Palmisano and Sullivan (1983b) indicated that the photosynthetic capacity (P_{MAX}) for natural populations of sea-ice microalgae in McMurdo Sound was only 0.5 mg C (mg chl *a*)$^{-1}$h^{-1}, a value less than one fourth that of temperate phytoplankton. The microalgae had a *I* (irradiance at which the photosynthesis is light saturated) of only 19 $\mu E\ m^{-2}\ s^{-1}$, a value that compares with the lowest *I*s reported for microalgae (Figure 3.20). Palmisano and Sullivan, in short-term experiments in McMurdo Sound in 1983, found that the bottom congelation ice microalgae were photoinhibited at irradiances above 25 $\mu E\ m^{-2}\ s^{-1}$, a value about the same as that obtained by Palmisano et al. (1985b). However, Grossi et al. (1987) in the snow perturbation experiment discussed above found that the microalgae grew fastest, reached the highest standing crop, and demonstrated maximum assimilation numbers in the snow-free quadrat, where ambient irradiance was close to 100 $\mu E\ m^{-2}\ s^{-1}$. They concluded that several factors may have contributed to their divergent results. First, unlike previous investigators, they sampled the quadrants repetitively over a three month period, including the early phase of bloom development. Second, because snow manipulation was effected early in the season when algal biomass was low, the light gradient apparently selected for different species assemblages under the snow-cleared and snow-covered quadrants. Finally, extensive underwater observations allowed interpretation of disparities in production estimates derived from biomass and in situ photosynthetic rates in the light of physical changes.

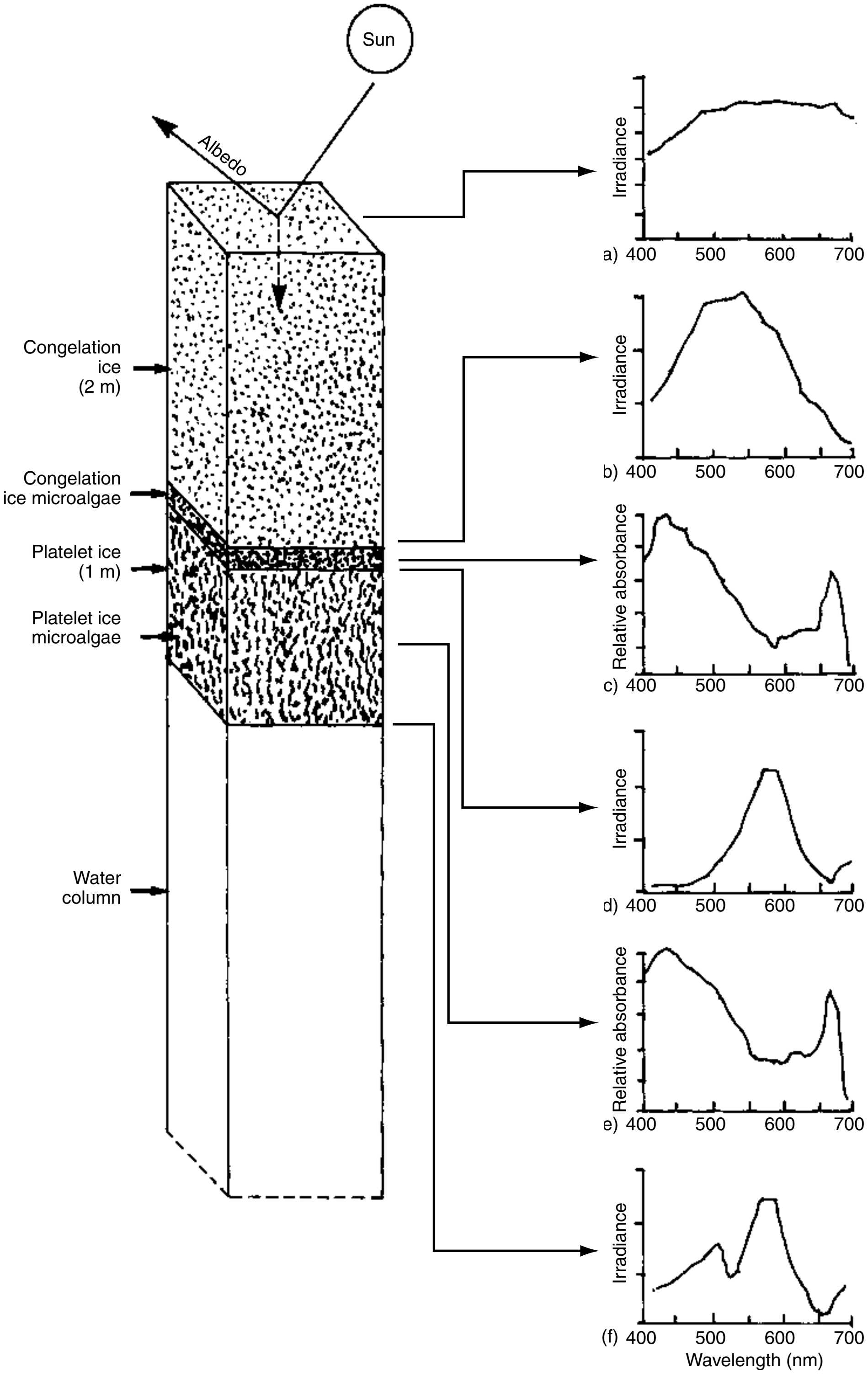


FIGURE 3.18 Diagram showing the spectral characteristics of irradiance (μE m^{-2} s^{-1}) at different depths within the ice structure in McMurdo Sound and the in vivo spectral absorption characteristics of the microalgal assemblages. (a) Spectral irradiance incident on the surface of the ice. PAR = 1364 μE m^{-2} s^{-1}. (b) Resulting irradiance spectrum after a 65% loss to albedo, and after passing through 1.8 m of firstyear congelation sea ice. PAR = 46 μE m^{-2} s^{-1}. (c) In vivo absorption spectrum for the bottom infiltration microalgal assemblage from the bottom 0.2 m of the ice column. (d) Spectral irradiance measured just underneath the congelation ice. PAR = 1.379 μE m^{-2} s^{-1}. (e) In vivo absorption spectrum of the microalgae of the sub-ice platelet ice layer. (f) Spectral irradiance measured beneath the platelet ice layer. PAR = 0.656 μE m^{-2} s^{-1}. (From Soohoo, J.B., et al., *Mar. Ecol. Prog. Ser.*, 39, 175, 1987. With permission.)

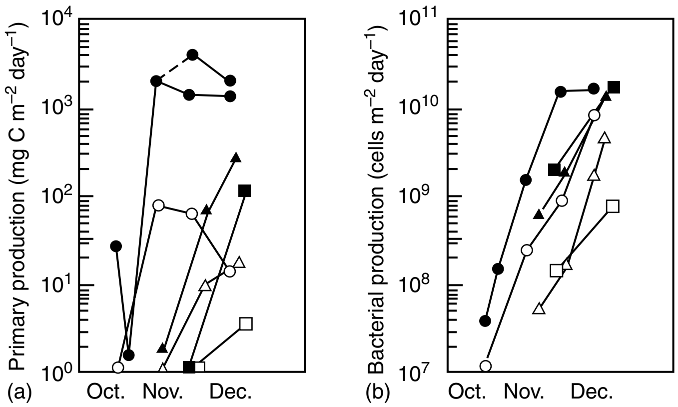


FIGURE 3.19 (a) Microalgal primary production, and (b) bacterial cell production in sea-ice cores from experimental quadrats with variable snow cover (0, 5, 25 cm), for bottom congelation ice (open symbols) and sub-ice platelet ice (closed symbols). Circles: 0-cm snow cover; triangles: 5-cm snow cover; squares: 25-cm snow cover. (From Kottmeier, S.T., Grossi, S.McG., Sullivan, C.W., *Mar. Ecol. Prog. Ser.*, 35, 175, 1987. With permission.)

Sea-ice microalgae from bottom ice communities in McMurdo Sound showed classic shade adaptation; that is, light-saturated photosynthesis was achieved at very low irradiance (Palmisano et al. 1984, 1985b; Figure 3.20). The I_k of 7 μE m^{-1} s^{-1} ranks amongst the lowest reported for microalgae in natural environments. Photosynthesis was inhibited above 25 μE m^{-1} s^{-1}. Photosynthetic efficiency (a^b) 0.019 ± 0.005 mg C (mg chl *a*) h^{-1} (μE m^{-2} s^{-1}). In sea-ice microalgae, in general, P_m*s* ranked lower ($<$ 2 mg C (mg chl *a*)$^{-1}$ h^{-1}) whereas s were within the range of values reported for temperate phytoplankton. Using a species-specific technique Rivkin and Putt (1987) determined I_k*s* for Antarctic sea-ice diatoms *Amphiprpra kufferathii* and *Pleurosigma* sp. of 25 and 13 μE m^{-2} s^{-1}, respectively.

Trenerry et al. (2002) used oxygen electrode measurements of bottom ice microalgal production in McMurdo Sound to investigated irradiance relationships. Figure 3.21 illustrates the relationship between irradiance and production over a 24-h period, while Table 3.6 lists photosynthetic parameters for fast ice bottom microalgae recorded in a series of investigations. PARs (mid-day surface irradiance) ranged from 1500–2050 μmol photons m^{-2} s^{-1}, while PAR$_{UI}$ (under-ice irradiance) (ice thickness 1.75 m) ranged from 0.2 to 17.7 mol photons m^{-2} s^{-1}. P_{MAX} (maximum photosynthetic rate) ranged from 0.05 to 2.10 mg C (mg Chl *a*)$^{-1}$ h^{-1}, while E_k (the minimum irradiance required to saturate photosynthesis) ranged from 3.149 to 9.724 μmol photons m^{-2} s^{-1}.

Two other important aspects of light affecting primary production in bottom and sub ice microalgal assemblages are photoperiod and the spectral composition of the light. Sullivan et al. (1982) found a pronounced diel change in under ice irradiance during the spring bloom in McMurdo Sound, ranging from 2.9 μE m^{-2} s^{-1} at 1200 h to 0.5 μE m^{-2} s^{-1} at 2,300 h on November 14, 1981, despite continuous surface downwelling irradiance of 1500 μE m^{-2} s^{-1}. Palmisano and Sullivan (1985b) suggest that diel rhythms in photosynthesis may exist in sea-ice

TABLE 3.4
Photosynthetic Parameters of Fast-Ice Bottom Algae, McMurdo Sound, Antarctica

Reference	PAR^S	PAR^{UI}	Ice Thickness (m)	P_{MAX}	*x*	E_k
Palmisano et al. (1985a)	1,410–1,543	0.5–2.9	1.5	0.062(0.079–0.13)	0.019(0.02–0.026)	3.5(4.2–5.4)
Palmisano et al. (1985b)		0.5–7.4	2.3	0.35	0.024 ± 0.19	10.3 ± 4.4
Cota and Sullivan (1990)	1,500–1,700	17.7	1.75	0.22–0.10	0.0019	25
McMinn et al. (199b)	2,050	0.2–5.0	1.75	0.05	0.003	14
McMinn et al. (2000)	1,600	3–55	0.9	0.29–2.01	0167–0.275	3.149–9.724
Trenerny et al. (2002)	1,610	8	1.9–2.0	0.01		

PAR^S: midday surface irradiance, in μmol photons m^{-2} s^{-1}: *PAR*^{UI}: under-ice irradiance, in μmol s^{-1}; ice thickness in meters (m); P_{max}: maximum photosynthetic rate, in mg C (mg chl *a*) h^{-1}: E_k: the minimum irradiance required to saturate photosynthesis, in μmol photos m^{-2} s^{-1}; *x*: the light-limited photosynthetic efficiency, in nmol O_2 cm^{-2} μmol photons m^{-2} s^{-1}.

Source: From Trenerny, L.J., McMinn, A., Ryan, K.G., *Polar Biol.*, 25, 72, 2002. With permission.

TABLE 3.5
Productivity Estimates for Sea-Ice Microalgal Assemblages

		Productivity	
Locality	**Assemblage**	**mg C m^{-2} day^{-1}**	**mg C (mg chl *a*)$^{-1}$ h^{-1}**
McMurdo sound[a]	Platelet ice (interstitial water)	3.8[b]	0.4
McMurdo sound[c]	Bottom congelation ice	—	0.6–7.5[d]
McMurdo sound[e]	Platelet ice (snow-free)	1–2106	0.006–1.33
	Bottom congelation ice (snow - free)	0.07–240	0.20–1.95
	Platelet ice (5 cm snow)	1–334	0.04–0.24
	Bottom congelation ice (5 cm snow)	0.5–19	0.03–0.66
Casey station[f]	Sub-ice mat strand	1.58–32.9[g]	—
Antartic Peninsula[h]	Interior band (late winter)	35.0 ± 11.87	—

[a] Bunt and Lee (1970).
[b] mg C m^{-3} day^{-1}.
[c] Palmisano and Sullivan (1983a).
[d] mg C (mg chl *a*)$^{-1}$.
[e] Grossi et al. (1987).
[f] McConville and Wetherbee (1983).
[g] mg C (m^{-2} C m^{-2} h^{-1}).
[h] Kottmeier and Sullivan (1987).

Source: Adapted from Palmisano, A.C., SooHoo, J.B., Sullivan, C.W., *Mar. Biol.*, 94, 299, 1987a. With permission.

diatoms similar to those reported for temperate phytoplankters (Prézelin and Ley 1980).

Soohoo et al. (1987) have measured the spectral irradiance and in vivo absorption spectra for both the congelation ice and sub ice platelet layer assemblages in McMurdo Sound, as well as the spectral irradiance throughout the ice column and below the ice (Figure 3.18 and Figure 3.22). The bottom congelation microalgae have available a spectrum with the quanta concentrated between 450 and 580 nm (Figure 3.18b). A significant proportion of the quanta are available in the blue and blue–green regions of the spectrum where they can be absorbed by the photosynthetic pigments. Total PAR at this level of the ice column is about 46 μE m^{-2} s^{-1}, or 3% of the value of PAR incident upon the surface. The absorption spectrum for the bottom congelation ice microalgae is shown in Figure 3.18c. Blue and green light are selectively absorbed by the algal photosynthetic pigments further reducing the spectrum of available light (Figure 3.18d). Photosynthetically usable radiation (PUR) for the bottom congelation ice microalgae was calculated at 57 ± 7% of their PAR. After passing through the 20 cm of this bottom

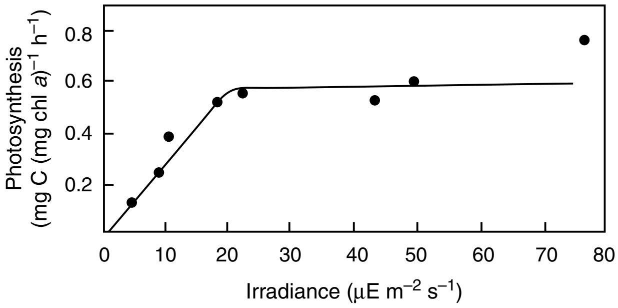


FIGURE 3.20 Photosynthesis irradiance curve relationships of the microalgae of the subice platelet ice assemblage in McMurdo Sound. (From Palmisano, A.C., Sullivan, C.W., *Sea Ice Algae*, Horner, R.A., Ed., CRC Press, Boca Raton, Florida, 131, 1985. With permission.)

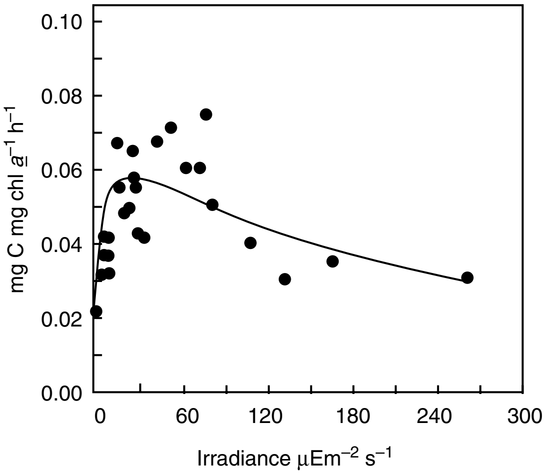


FIGURE 3.21 Change in production (mg C m^{-2} h^{-1}) with irradiance (μmol photons m^{-2}s^{-1}). (From Trenerry, L.J., McMinn, A., Ryan, K.G., *Polar Biol.*, 25, 76, 2002. With permission.)

TABLE 3.6
Photosynthetic Parameters for Antarctic Sea Ice Microalgae

a^h	Photosynthetic efficiency, the intial slope of the P–I curve	mg C (mg chl a)$^{-1}$h^{-1}(μE m^{-2} s^{-1})$^{-1}$
P^b_m	Photosynthetic rate at optimal irradiance	mg C (mg chl *a*)$^{-1}$ h^{-1}
P^b_k	P^b_m/P^b_a an index of photoadaptation	μE m^{-2} s^{-1}
P^b_m	Irradiance at which photosynthesis is maximal	μE m^{-2} s^{-1}

Source: Adapted from Palmisano, A.C., Soohoo, J.B., Sullivan C.W., *Mol. Biol.*, 94, 299, 1987a. With permission.

assemblage, available quanta were reduced to less than 1.5 μE m^{-2} s^{-1}, or about 0.1% of the incident surface radiation, and were concentrated in a band from 540 to 620 nm (Figure 3.18d), wavelengths where algal absorption is minimal. The microalgae of the platelet layer showed enhanced absorption in the blue–green region of the spectrum between 500 and 550 nm (Figure 3.18e). This corresponds to the absorption region of the major carotenoid accessory pigment in the diatoms, the xanthophyll fucoxanthin. Consequently, the spectrum of irradiance available to the platelet ice microalgae was 31 ± 2% of PAR as PUR. Platelet ice microalgae have consistently been found to show enhanced blue–green absorption relative to the bottom congelation ice microalgae (Sullivan et al. 1984; Soohoo et al. 1987). After passing through the platelet layer less than 1 μE m^{-1} s^{-1} (PAR = 10.05% incident PAR) is available at the top of the underlying water column for phytoplankton photosynthesis (Figure 3.18f), and most of this is in the green spectrum where microalgae do not absorb light effectively. As a consequence PUR is only 25 ± 2% of PAR. Absorption in the blue–green region of the spectrum (480–550 nm) for the platelet ice microalgae is enhanced relative to that for the congelation ice microalgae. Thus the rate and extent of development of the sea-ice microalgal assemblages can have a dramatic effect on the downwelling irradiance. Palmisano et al. (1987b) found that the changes in the under-ice spectrum occurred in time scales as short as 10 days (Figure 3.22).

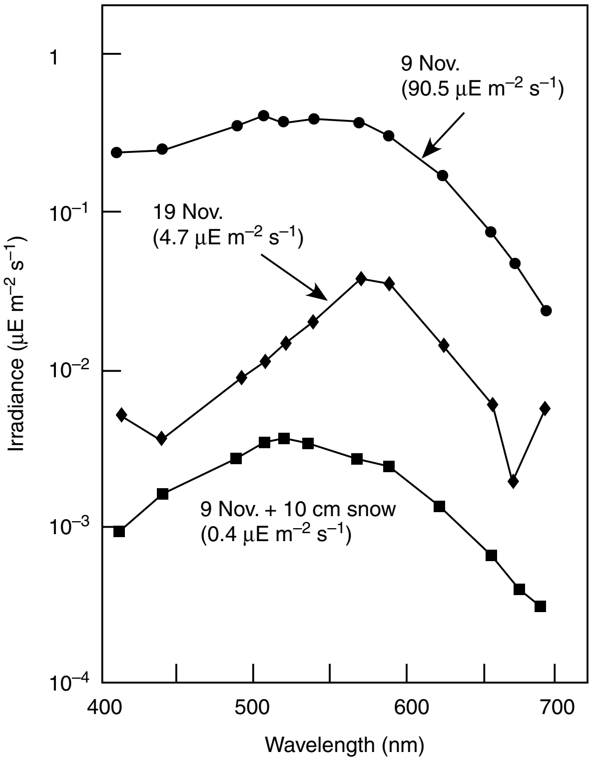


FIGURE 3.22 Spectral distribution of irradiance beneath sea ice in McMurdo sound. Snow reduces PAR penetration at all wave lengths. The bottom sea-ice infiltration microalgal bloom is responsible for the reduced irradiance on 19 November and it strongly attenuates light at the blue and red ends of the spectrum. (From Palmisano, A.C., Soohoo, J.B., Moe, R.L., Sullivan, C.W., *Mar. Ecol. Prog. Ser.*, 35, 165, 1987b. With permission.)

While the interior, bottom and sub-ice assemblages are considered to be "shade adapted." Burkholder and Mandelli (1965) found that surface microalgal assemblages had a maximum photosynthetic rate of 18 klx (about 400 μE m^{-2} s^{-1}) with an assimilation number of 2.6 mg C (mg chl *a*)$^{-1}$ h^{-1}. Microlagae dominating the brash ice in blooms at the ice edge also appear to be sun adapted (Plamisano and Sullivan 1985b).

Most of the work on photosynthesis by sea-ice microalgae in the Antarctic has been carried out on fast ice communities near land-based stations (see Horner 1985a; Palmisano and Sullivan 1985b; and Garrison et al. 1986 for reviews). Pack ice on the other hand at its maximum extent covers eight to nine times the area of the fast ice, and includes a greater variety of microenvironments with different physicochemical conditions (Ackley et al. 1979; Clarke and Ackley 1984), different microlagal species composition (Horner 1985b; Garrison et al. 1986, 1987), and different photosynthetic characteristics (Burkholder and Mandelli 1965; Irwin 1990; Lizotte and Sullivan 1991a, 1991b). Lizotte and Sullivan (1991a) in the western Weddell Sea found that the sea-ice microalgae from the pack ice had higher photosynthetic capacities (higher P^b_m (g C (g Chl *a*)$^{-1}$ h^{-1}); higher light saturation volume, I_k (μE m^{-2} s^{-1})) relative to fast ice microalgae. The pack ice microalgae had photosynthetic capabilities that were indistinguishable from Antarctic phytoplankton. They inhabit microenvironments with higher irradiances than those of fast ice microalgae suggesting that they could have higher rates of primary production than previously estimated on the basis of evidence from fast ice regions. These findings have been confirmed by Gleitz and Kirst (1991) in studies of ice algal assemblages in the north-western part of the Weddell Sea. During the winter the ice cover, low sun angle (higher reflective), short photoperiod, low incident radiation, and little stratification of the water column inhibits primary production by the phytoplankton. Thus, in the pack ice region the sea-ice microalgae may be the most important primary producers in the winter and early spring and their contribution to the overall primary production has been underestimated.

3.2.7.3 Nutrient Concentrations

Early research concluded that in general nutrients probably do not limit the growth of sea-ice microalgal assemblages (e.g., Meguro et al. 1967; Bunt and Lee 1970; Holm-Hansen et al. 1977; Sullivan and Palmisano 1981; Clarke and Ackley 1984). However, this view has been challenged by Thomas and Dieckman (2002) in their review of the biochemistry of Antarctic sea ice. In their Table 1, they list the ranges (maximum–minimum) recorded from a variety of sea-ice habitats. They found that of the four main nutrients—nitrate, silicate, ammonium, and phosphate—there were documented cases of compete exhaustion and concluded that nutrient limitation could have significant effects on the biochemical composition of sea-ice assemblages (Lizotte and Sullivan 1992; Gleitz and Thomas 1993; Gleitz et al. 1996; McMinn et al. 1999; Thomas et al. 2001b). Five processes are usually advanced to explain observed nutrient abundances in the sea-ice habitat: (1) the replenishment of nutrients in the platelet layer by water currents; (2) replenishment of nutrients by exchange between the lower part of the ice and the underlying water; (3) the replenishment of the nutrients in surface assemblages by seawater flooding; (4) desalination; and (5) in situ bacterial regeneration (Sullivan and Palmisano 1981).

In the platelet-ice layers where water exchange can be extensive (Dieckman et al. 1992; Arrigo et al. 1995), nutrient exhaustion has been recorded on only a few occasions Similarly in porous summer sea ice and surface layers such as infiltration, melt pond and freeboard layers (Ackley and Sullivan 1994) the high stocks of algae that have frequently been recorded are supported to a large degree by replenishment and exchange of nutrients from the surrounding sea water (Garrison and Buck 1991; Fritzen et al. 1994; Thomas et al. 1998). The rate of replacement at the lower ice–water boundary depends on the downward flux by salt rejection, brine cell drainage from the ice and upward flux from the underlying water (Demers et al. 1985). According to Legendre et al. (1992) active upward transport of nutrients from the water column is required for the growth of the bottom microalgal assemblages. Nutrient enrichment of the ice–water interface can be caused by tidal mixing. The upward flux of nutrients depends on the stability of the boundary layer beneath the ice. Stability varies from connectively unstable during brine rejection to very stable when meltwater forms a thin layer beneath the ice (Demers et al. 1985). Thus the rate of nutrient input to the sub-ice and bottom microalgal assemblages depends on the degree of destabilization of the boundary layer by factors such as brine rejection, tidal movement and current variability. Thus, under conditions where boundary layer is unstable upward nutrient exchange is reduced and the biomass of the microalgae may decline to nutrient depletion.

Thomas and Dieckman (2002) list numerous instances of extraordinarily high concentrations of nutrient species: values of silicate up to 316 μM, nitrate 300 μM, ammonium 150 μM, and phosphate 42 μM. As an approximate guide, typical of surface waters in the Southern Ocean are of the order of 70 μM silicate, 30 μM nitrate, less than 1 μM ammonium, and less than 2 μM phosphate. The possibility for the accumulation of these nutrients, especially the high ammonium and phosphate levels has frequently been related to high rates of herotrophic activity within the ice leading to the production of these products with the microalgal assemblages. Arrigo et al. (1995) consider that such high regeneration rates (phosphate 35 $\mu\mathrm{mol\,l^{-1}\,day^{-1}}$ and ammonium greater than 31 $\mu\mathrm{mol\,l^{-1}\,day^{-1}}$) are due to bacterial or protozoan metabolism, a view shared by Grossman et al. (1996), and explain the high phosphate levels in platelet ice assemblages. Arrigo et al. (1995) consider that the high ammonium values up to 178 μM in the platelet ice assemblage are related to the grazing and excretion of metazoans, the numbers of which can reach high values. Günther et al. (1999a) consider that algal mortality and cell lysis, amplified by inefficient grazing within assemblages of high algal standing stocks result in the liberation of dissolved matter, including nutrients.

Kristiansen et al. (1992, 1998) have shown that nitrate was the main nitrogen source for infiltration algae accounting for over 90% of the nitrogen source in spring. During the summer, ammonium became a much more important nitrogen source and accounted for up to 21% of nitrogen assimilation. The uptake of nitrate was highly dependent on irradiance and was inhibited at irradiances frequently encountered by such assemblages near the surface of ice floes. Nitrogen uptake models developed by Priscu et al. (1991) predicted that bottom ice assemblages were always irradiance-limited, whereas the nitrogen uptake of surface assemblages was saturated at low irradiances and frequently photoinhibited. Ammonium oxidizing bacteria were found in sea-ice assemblages by Priscu et al. (1990) and these may compete with algae for ammonium. Although silicate is often depleted compared with surface water concentrations it is rarely exhausted. Many of the high silicate concentrations in ice algal assemblages are also associated with high standing stocks of diatoms.

3.2.7.4 Salinity

The salinity environment of the sea-ice microalgae is highly variable. Salinities within the brine chambers have been observed to range from greater than 150 to

34. During the summer melt salinities at the ice–water interface may drop to 0, as the result of snow and ice melting, and a freshwater lens may form beneath the ice (Bunt 1968b; Grossi et al. 1984, 1987; Palmisano and Sullivan 1985b).

Kottmeier and Sullivan (1988) have measured the rates of carbon fixation versus salinity. For congelation ice from Granite Harbour, McMurdo Sound maximum carbon fixation occurred at a salinity of 30, with a secondary peak at 10–20. A marked decline in carbon fixation occurred at salinities above 30. In a second sample from Hutt Point, maximum carbon fixation occurred at a salinity of 50 with a secondary peak at 40. There was a marked decline in carbon fixation in salinities above 50, with no net carbon fixation from 70 to 90. Thus, the sea-ice microalgae are capable of substantial metabolism at the salinities which are characteristic of those encountered in situ. Before the onset of melting the congelation ice in McMurdo Sound (from as early as mid-November through to December) the maximum rate of carbon fixation occurred close to a salinity of 34, the average salinity of surface seawater in McMurdo Sound (Littlepage 1965). Following the onset of the melting of the congelation ice, maximum rates of carbon fixation occurred at lower salinities, close to those found by Bunt (1964) for platelet ice microalgae collected in McMurdo Sound in late December (7.5–10).

Palmisano et al. (1987a) found that the sea-ice microalgae were actively photosynthetic at salinities ranging from 20 to 23 and that $P_{\mathrm{m}}^{\mathrm{b}}$ (photosynthetic rate at optimumal irradiance) was slightly higher at the lower salinities. They were not able to detect photosynthetic activity at a salinity of 60. Thus, high brine salinities may be a factor limiting the vertical distribution of microalgae in the ice column. Dilution of the high-salinity brine with seawater in the lower portion of the ice column (Reeburg 1984) may be essential for algal growth, and this may be a partial explanation for why microalgae is primarily confined to the bottom 5–25 cm of the congelation ice in McMurdo Sound.

Gleitz and Kirtz (1991) in their studies of the physiological ecology of ice microalgal assemblages collected from the Weddell Sea pack ice found that while light-saturated production rates of three infiltration assemblages under hypersaline conditions (salinities approximately 50 and 110) decreased by 15–55%, while rates under hyposaline conditions (salinity approximately 20) decreased only slightly (−9%), or were even stimulated (14–22%). The tolerance to reduced salinity coupled with high photosynthetic activity enables the pack ice microalgae to survive seasonal ice melt and to contribute to the open water phytoplankton.

3.2.7.5 Temperature

Metabolism and growth of microalgae are hypothesized to be limited in part by the low temperatures of the Southern Ocean (Holm-Hansen et al. 1977; Neori and Holm-Hansen 1982; Jacques 1983; El-Sayed 1984; Tilzer at al. 1985, 1986). Sea-ice microalgae in McMurdo Sound may be exposed to temperatures at the upper ice surface that may range from −42°C in the winter to about 4° in the summer (Littlepage 1965; Palmisano and Sullivan 1982; Kottmeier et al. 1987). The microalgae of the brine chambers at the bottom of the ice column and those in the sub-ice assemblages may experience temperatures close to that of the underlying seawater (approaching −2.0° in the winter).

Palmisano et al. (1987a) in a series of experiments on short-term physiological responses of photosynthesis parameters to temperature (Table 3.7) found that the maximum photosynthetic rates ($P_{\mathrm{m}}^{\mathrm{b}}$) increased more than two-fold in bottom congelation ice microalgae, and three- to four-fold in sub-ice platelet ice microalgae between −2°C and +6°C. $P_{\mathrm{m}}^{\mathrm{b}}$ decreased when both types of microalgae were incubated at +10°C, indicating that the optimum temperature for light-saturated photosynthesis was around +6°C. This falls at the low end of such estimates for sea-ice microalgae and Antarctic phytoplankton; e.g., 10−15°C for platelet ice microalgae (Bunt 1964), near 12°C for Antarctic phytoplankton (Jacques 1983), and 7°C as the optimum temperature for phytoplankton (Holm-Hansen et al. 1982). While the temperature optima were low they were about 8°C higher than the ambient surface water temperatures. The $P_{\mathrm{k}}^{\mathrm{b}}(P_{\mathrm{m}}^{\mathrm{b}}/P_{\mathrm{a}}^{\mathrm{b}})$ (photosynthetic efficiency) which is an index of photoadaptation, increased steadily with temperature from 7.4 (at −2°C) to 14.8 $\mu\mathrm{E\,m^{-2}\,s^{-1}}$ in congelation ice microalgae, and from 11.7 to 54.3 $\mu\mathrm{E\,m^{-2}\,s^{-°1}}$ in platelet ice microalgae. Even greater increases were found in $P_{\mathrm{m}}^{\mathrm{b}}$ (irradiance at which photosynthesis is maximal) which changed from 31.4 to 88.4 $\mu\mathrm{E\,m^{-2}\,s^{-1}}$ in congelation ice microalgae and from 11.7 to 238 $\mathrm{E\,m^{-2}\,s^{-1}}$ in platelet ice microalgae. Palmisano et al. (1987a) concluded that in the low-temperature-adapted sea-ice microalgae, even relatively small changes in temperature could have a significant effect on photosynthesis-irradiance relationships.

Kottmeier and Sullivan (1988) in another series of experiments measured the rates of sea-ice microalgal carbon fixation over a range of temperatures. Carbon fixation increased several-fold from −1.9°C up to a maximum temperature ranging from 8°C to 14°C (Figure 3.23). This maximum was followed by a marked decline in carbon fixation from 14°C to 30°C, with rates from 20°C to 30°C less than those at 1.9°C. Thus, while substantial carbon fixation can occur at temperatures close to the −1.9°C found in situ at the ice–seawater interface, maximum metabolic rates occur at temperatures considerably above −1.9°C, but below 15°C. The enhanced metabolic activity by sea-ice microalgae up to a maximum temperature of 15°C is probably due to the energetic cost of enzyme production and the thermodynamics of enzyme catalysed reactions. The microalgae appear to be well adapted for growth at low temperatures, although they are not maximally active at the temperatures found in the sea ice.

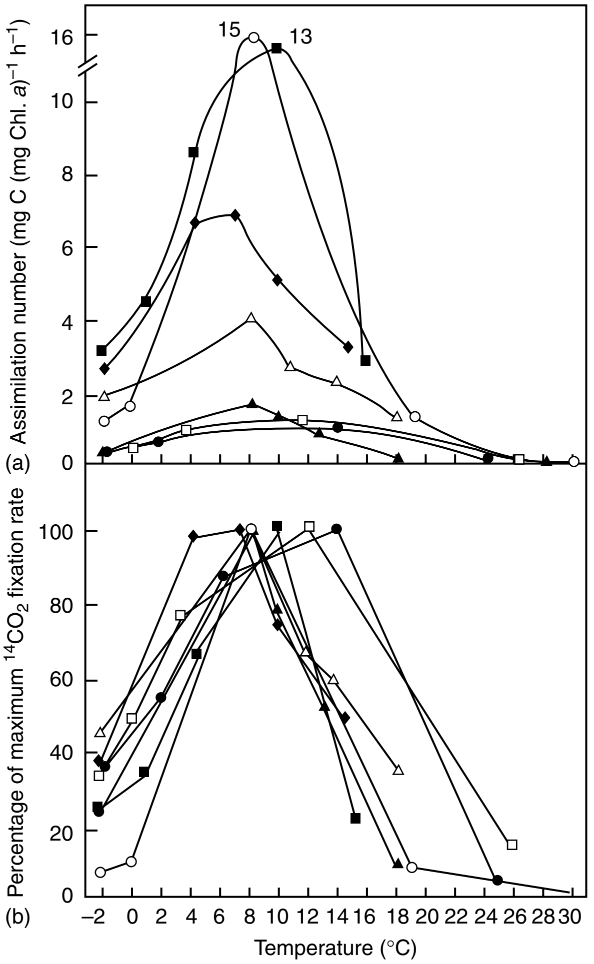


FIGURE 3.23 Effect of temperature on carbon fixation by sea-ice microalgae from a series of stations in McMurdo Sound from November to January expressed as (a) assimilation numbers, and (b) percent of maximum carbon fixed. (○) Hut Point, Nov. 16, 1983; (●) edge of fast ice, Nov. 18, 1983; (□) Hut Point, Nov. 30, 1983; (■) edge of fast ice, Dec. 9, 1983; (△) Cape Armitage, Dec. 27, 1083; (▲) Dunlop Island, Dec. 29, 1983; and (♦) Dunlop Island, Jan. 5, 1984. (From Kottmeier, S.T., Sullivan, C.W., *Polar Biol.*, 8, 293, 1988. With permission.)

TABLE 3.7
Range of Temperatures Where Maximal Activities Occurred in Rates of Nitrate Uptake, Ammonium Uptake, and Nitrate Reductase Activity, and Q_{10} Values for Each Process Measured

Acitivity	Temperature of Maximum Activity (°C)	$Q_{10} \pm$ SD
Nitrate uptake	0.5–2.1	11.7 ± 5.7
Ammonium uptake	2.1–3.8	15.4 ± 0.1
Carbon uptake	2.1–3.8	16.3 ± 0.1
Nitrate reductase activity	8.0–9.0	1.4 ± 0.02

Source: From Priscu, J.C., et al., *Ant. J. U.S.*, 20, 196, 1987. With permission.

Table 3.7 summarizes the results of a series of experiments designed to examine the influence of temperature on nitrate and ammonium uptake, and the activity of the enzyme nitrate reductase on natural assemblages of sea-ice microalgae from McMurdo Sound (Priscu et al. 1987). Nitrate, ammonium and carbon dioxide uptake had temperature maxima ranging from about 0.5°C to 3.8°C. These results clearly show that the metabolic pathways involved in these reactions characterize the microalgal assemblages as being psychophilic. This is supported by the similarities in the Q_{10} values (Q_{10} represents the increase in metabolic rate for each 10°C increase in temperature). Nitrate reductase showed a distinctly different activity versus temperature relationship. These results provide further evidence that low environmental temperatures have imposed selection pressures on sea-ice microalgae resulting in physiological characteristics closely fitting habitat conditions.

3.2.7.6 Heterotrophy

Diatoms are nutritionally diverse; they may be obligate autotrophs, faculative heterotrophs (mixotrophs), or obligate heterotrophs. Faculative heterotrophy is not uncommon in pennate diatoms species and the substances taken up include sugars, amino acids and organic acids (Hellebust and Lewin 1977; Palmisano and Sullivan 1985b). Sea-ice microalgae may use heterotrophic nutrition to supplement photosynthesis during the low light conditions of the spring bloom, or to support maintenance metabolism during the continuous darkness of the polar winter.

Palmisano and Sullivan (1982) found that the uptake of ^{14}C glucose by three sea-ice diatoms was enhanced by as much as 60% when incubated in the dark. However, the dark uptake of glucose provided less than 1% of the carbon needed for cell division, although it could be sufficient for maintenance metabolism. In another study Palmisano and Sullivan (1983b) demonstrated the dark incorporation and respiration of ^{14}C-serine by natural populations of sea-ice microalgae. This was confirmed in a subsequent study (Palmisano and Sullivan 1985b) in which natural populations of platelet ice microalgae were found to take up ^{3}H-serine at natural substratum conditions under both dark and low-light conditions (15–48 $\mu E\ m^{-2}\ s^{-1}$), but they found no significant differences in serine uptake among three different light treatments. Palmisano and Sullivan (1985a) concluded that some sea-ice microalgae may use heterotrophic nutrition not only during the dark polar winter, but also during the spring bloom itself. Although microalgal heterotrophy does not provide new C for the microalgal assemblages, it could provide a means for more efficient utilization of the total carbon fixed. It is probable that some portion of the fixed carbon that is lost by extracellular release may be re-assimilated by certain species and used as a source of carbon and energy.

3.2.7.7 Dark Survival

With the onset of the polar winter, sea-ice microalgae are subject to a prolonged period of total darkness. There is ample evidence to demonstrate that the sea-ice microalgae can survive this period. Both Hoshiai (1981a, 1985) and Watanabe and Satoh (1987) have followed the development of the ice microalgal assemblages in the sea ice near Syowa Station over a full year. From the results of these investigations it is clear that the microalgae survive the winter darkness as the chlorophyll *a* standing crops had peaks in both April–June and October–November.

In 1982 a pigmented band of microlagae was found 80 cm from the ice–seawater interface in two-year sea ice at New Harbour, McMurdo Sound (Palmisano and Sullivan 1985b). This apparently was a remnant of the 1981 bottom congelation ice bloom to which an extra season's ice growth had been added. Samples stained with acridine orange and DAPI weakly flouresced under epifluorescence microscopy, and a pennate diatom was cultured from the cells in the band thus confirming that some cells could maintain their viability over the winter.

Little is known of the physiological mechanisms of dark survival in sea-ice diatoms. Bunt and Lee (1970) found that three of four sea-ice microalgae remained viable after three months in the absence of organic supplements. Palmisano and Sulivan (1982) found that 1–100% of the populations of three sea-ice diatom cultures were able to grow autotrophically after dark incubation for 5 months at −2.0°C. Subsequently Palmisano and Sullivan (1983b) subjected three anexic diatom cultures to a 30-day simulated summer–winter transition (gradually decreasing light and temperature, and increasing salinity). The diatoms responded to these changes by (1) a decline in growth rate and photosynthetic rate; (2) a decrease in cellular ATP; and (3) the storage and subsequent use of endogenous carbon reserves. In addition, the heterotrophic potential of the three clones increased as much as 60-fold. Palmisano and Sullivan (1983b) proposed three survival strategies to cope with the polar winter: faculative heterotrophy; storage and utilization of carbohydrates at a reduced rate; and resting spore formation. Ample evidence exists for the first two of these mechanisms but the formation of resting spores has yet to be established for Antarctic diatoms (Fryxell et al. 1979).

3.2.8 SEA-ICE BACTERIA

Up until the late 1980s, most of our knowledge concerning these bacteria comes from studies by Sullivan and Palmisano (1981, 1984) and their coworkers (Grossi et al. 1984; Sullivan et al. 1984; Kottmeier et al. 1987; Kottmeier and Sullivan 1988) in the McMurdo Sound region. Data on studies up to 1985 were reviewed by Sullivan (1985). More recently investigations have been carried out in the "Terre Adélie" area (Delille and Rosiers (1995b), in the vicinity of Davis Station, East Antarctica (Archer et al. 1996), in the Weddell Sea (Delille 1995, 1995b; Gleitz et al. 1996; Grossman et al. 1996), and in the coastal area of the Vestfold Hills, East Antarctica (Bowman et al. 1997).

(Sullivan and Palmisano 1984). Sullivan (1985) lists the following areas in which ice bacteria play an important role in the sea-ice ecosystem:

1. Secondary microbial production mediated through the microbial loop
2. Remineralization and recycling of ice-associated organic matter
3. Maintenance of a balance in the ice microenvironment with regard to detoxification and oxygen consumption
4. Ice nucleation and early stage of ice formation

Bacteria contribute significantly to the carbon and energy transfers within sea-ice assemblages (Sullivan and Palmisano 1984). More than 50% of primary production in the Southern Ocean can be attributed to microbial regeneration of nutrients (Koike et al. 1986).

3.2.8.1 Distribution and Abundance

Sullivan and Palmisano (1984) found an abundant and diverse bacterial community in the brine channels of the annual sea ice and at the ice–seawater interface in McMurdo Sound. The mean bacterial standing crop was 1.4×10^{14} cells m^{-2} (9.8 g C m^{-2}) with bacterial concentrations as high as 1.02×10^{12} cells m^{-2} being found in the ice core meltwater. A study of the vertical distribution of the bacteria in sea-ice cores 1.3–2.5 m in length showed that 47% of the bacterial numbers and 93% of the biomass was located in the bottom 20 cm of the ice column. The bacterial cells were much larger (average 80 fentograms (fg) C $cell^{-1}$) in the bottom section than those higher in the ice column (5 (fg) C $cell^{-1}$). Concentrations of bacterial carbon in the sea ice was more than ten times higher than that of the bacteriolankton in the water column below.

Scanning electron microscopy (Sullivan and Plamisano 1984) identified 155 bacterial strains (Kottmeier et al. 1987) of which 21% were psychophylic (Morita 1975), i.e., those capable of growth at 0°, but not above 18°C (Kobori et al. 1984). Free-living bacteria comprised 70% of the total numbers, with the remaining 30% being attached to either living microalgal cells or detritus. Epibacteria were primarily living in close physical association with healthy intact cells of one of the dominant diatoms, *Amphiprora* spp., suggesting a symbiotic association. Sullivan and Palmisano (1984) have advanced two hypotheses to account for this association. *Amphiprora* spp. may leak or excrete a large proportion of their photosynthesis to the extracellular environment where it is taken up and utilized by the epibacteria, or *Amphiprora* spp. may fail to produce antibacterial substances by which other ice diatoms inhibit growth or attachment of the bacteria (Siebruth 1967).

Epibacteria were also found to be abundant in the sub-ice mat strand assemblage off Casey Station (McConville and Wetherbee 1983). They were mostly Gram-negative rods, although Gram-negative cocci were also present, and they were attached to the mucilage sheaths of *Amphipleura* sp. (=*Berkeleya*) and the fustules of *Entomoneis*. Many other diatom species (e.g., *N. frigida*) were largely devoid of epibacteria. Bacterial densities ranged from 4×10^{11} to 2×10^{13} cells m^{-2}, up to ten times higher than those recorded in McMurdo Sound.

In sea-ice cores taken in the Weddell Sea (Miller et al. 1984) the bacteria, unlike those in McMurdo Sound which were concentrated in the bottom 20 cm of the ice column, were distributed throughout the depth of the ice. The range of bacterial biomass present in 1–2 m of sea ice was from 6.15 to 99.6 mg C m^{-2}, while that in the 100 m of the water column below the ice was from 24 to 97.5 mg C m^{-2}.

Delille and Rosiers (1995, 1995b) investigated the distribution of bacterial populations in the sea ice and underlying water in the "Terre Adélie" area over a full year. In the seawater, the total bacterial abundance ranged from 0.5×10^{5} cells ml^{-1} in July to 6.0×10^{5} cells ml^{-1} after the ice break. Values reaching 2.5×10^{6} cells ml^{-1} were recorded in the overlying ice cover.. Mean cell volumes were twice as high in brine as in seawater. Within the ice column bacterial abundance decreased from the top to the bottom (Figure 3.24). The enrichment in bacterial abundance observed in the surface layer assemblages could be related to infiltration ice that was formed when seawater flooded the ice sheet (Meguro 1962; Lange et al. 1990). Observations on the percentages of attached and free living bacteria and the larger size of the ice bacteria found in previous studies were confirmed.

Archer et al. (1996) investigated the microbial ecology of sea ice in the vicinity of Davis Station. They found that bacteria occurred throughout the ice depth (Figure 3.25). However, biomass varied by several orders of magnitude between horizons within the ice column ranging from less than 5 mg C m^{-3} in horizon A to greater than 1400 mg C m^{-3} in the bottom ice (horizon E). The much higher bacterial biomass found in the bottom ice was attributable to epiphytic bacteria attached to both living and dead *Entomoneis* spp. cells. Like *Entomoneis* spp. these bacteria were most abundant in the bottom ice contributing up to 93% of bacterial and 33% of total biomass. Unattached bacteria were considerably smaller than epiphytic forms having a mean cell volume of 0.13 μm^{-3} compared to 0.42 μm^{-3}. The maximum biomass of unattached bacteria of 193 mg C m^{-3} recorded in the bottom ice was also considerably lower than that of epiphytic forms.

3.2.8.2 Growth and Production

Bacterial cells are likely to accumulate in the ice, especially where frazil ice formation dominates, by the same mechanism as are operative for the microalgae (see Section 1.3.4 above). Sullivan and Palmisano (1984) and Sullivan et al. (1985) found that the ice bacteria were robust compared to the bacterioplankton of the underlying waters. A high frequency of dividing cells were found and one morpholgically distinct type was found to have a division frequency of 10%, a frequency indicative of high growth rates. Microautoradiographic evidence of ^{14}C-L-serine uptake by sea-ice

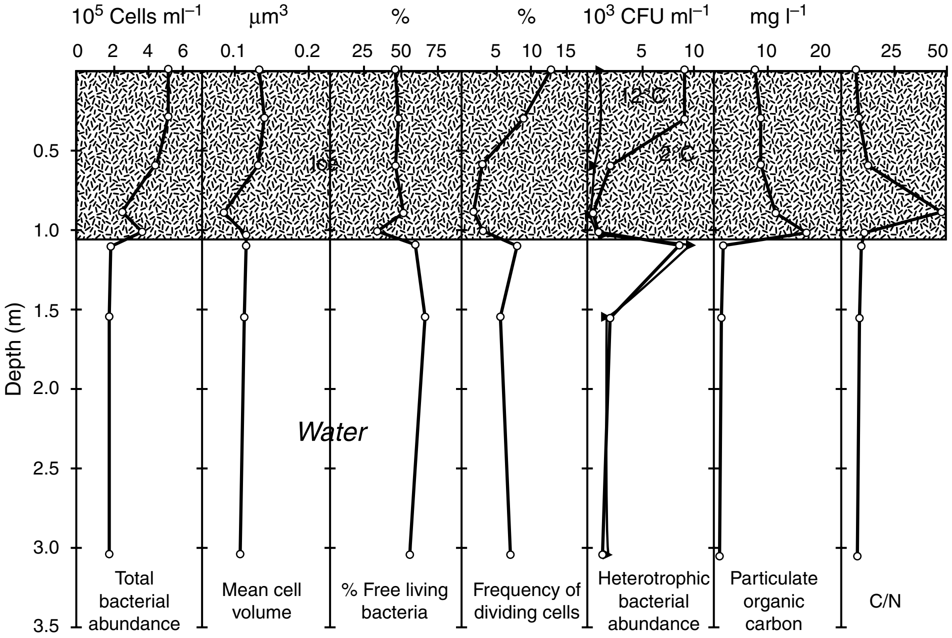


FIGURE 3.24 Vertical profiles of annual mean values of total bacterial abundance, mean cell volume, percentage of free living bacteria, frequency of dividing cells (FDC), psychrophylic and psychrotrophic saprophytic bacterial abundance, particulate organic carbon (POC) and C/N ratio recorded in sea ice (brine not included) and underlying seawater. (From Delille, D., Rosiers, C., *Polar Biol.*, 16, 31, 1995. With permission.)

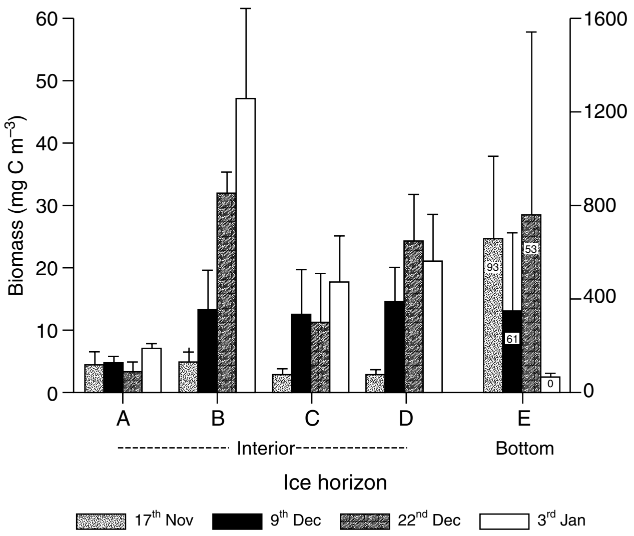


FIGURE 3.25 Mean ($n = 3$) and standard deviation of bacterial biomass recorded from 5 ice horizons in cores collected on 4 dates during the sampling period. Values in the bars are the mean percentage of total bacterial biomass contributed by epiphytic bacteria in the bottom ice on each sampling date. Note the different scale for Horizon E. (From Archer, S.D., et al., *Mar. Ecol. Prog. Ser.*, 135, 18, 1996. With permission.)

bacteria under simulated in situ conditions provided additional evidence that the bacterial populations were capable of active metabolism at -1.8°C. It is likely that selection takes place for those bacterioplankton whose growth is permitted or even favored by the unique ice environment, i.e., high salinities, low temperatures, surfaces (ice crystals, organic detritus, and microbial cells) and high concentrations of micronutrients and dissolved and particulate organic matter.

Seasonal changes in the sea-ice bacterial assemblage was followed by Grossi et al. (1984) and Sullivan et al. (1985), during a light perturbation experiment in McMurdo Sound in which a control quadrat with 7 cm of snow was left undisturbed while a second quadrat had the snow cover artificially increased to 70 cm. The bacteria in the control quadrat grew at a rate of 0.05 day^{-1}, whereas in the snow covered quadrat no growth occurred (Figure 3.15c). Sullivan et al. (1985) determined a doubling time of 14 days. While this generation time is long it is within the range of values reported for other low-temperature systems. Over the six-week study period bacterial numbers increased six-fold to 1.8×10^{11} cells m^{-2}, whereas biomass increased ten-fold to 2.0 g C m^{-2}. This disparity was due to the fact that epiphytic bacteria grew at a rate twice that of the non-attached bacteria. In further support of the idea that bacteria undergo active growth in the sea-ice microenvironment, Sullivan et al. (1985) showed that the attached bacteria took up ^{3}H-serine, ^{3}H-glucose, and ^{3}H-thymidine, demonstrating that net DNA synthesis occurred by the incorporation of ^{3}H-thymidine. Net DNA synthesis is a prerequisite for growth.

In the late winter in the Weddell Sea, Kottmeier and Sullivan (1987) found that bacterial production in the sea ice averaged 20.5 ± 11.0 (SE) $\times 10^{10}$ cells m^{-2} day^{-1}, whereas the carbon production averaged 5.2 ± 2.8 (SE) mg C m^{-2} day^{-1}. The bacterial cell and carbon production in the seawater 3 m below the ice were much lower than in the sea ice, averaging 4.5 ± 3.5 (SE) $\times 10^{10}$ cells m^{-2} day^{-1}, and 1.0 ± 0.7 (SE) mg C m^{-2} day^{-1}.

The most comprehensive study of the growth and carbon production by sea-ice bacteria is that of Kottmeier et al. (1987) during the 1982 austral spring and summer bloom in McMurdo Sound (Figure 3.26). Bacterial cell numbers and biomass increased logarithmically during the prolonged microalgal bloom to less than 10-fold the initial values, reaching concentrations in the bottom congelation ice and sub–ice platelet layers ranging from 0.2 to 1.4×10^{12} cells m^{3} of ice meltwater. On the other hand, bacterial carbon production rate increased by three orders of magnitude. The final bacterial biomass was less than 1% of the microbial biomass. This is much lower than the 8–75% reported for the bacterioplankton of the world's oceans (Ducklow 1983). Bacterial carbon production was only 9% of that of the microalgal carbon production. Maximal growth rates ($\mu = -0.02$ to 0.2 day^{-1}) were comparable to those reported for bacterioplankton in the Southern Ocean. Significant correlations were found between bacterial production (cell, biomass, and thymidine incorporation per cell) and growth, and microalgal biomass, production and growth suggesting a potential coupling between bacterial growth and microalgal photosynthetic metabolism in the sea-ice microbial community. The significance of this will be discussed below.

Archer et al. (1996) has summarized data on growth rates of sea-ice bacteria. Studies of bacterial growth in bottom ice indicate a faster rate of growth for epiphytic than unattached forms (Grossi et al. 1984; Kottmeier et al. 1987). However these measurements were carried out during the bloom in bottom ice autotrophic production. Archer et al. (1996) carried out their investigation off Davis Station during a period of decline in the bottom ice autotrophic production. They found that the bottom ice bacterial biomass was highly variable. The growth rates (μ) of unattached bacteria integrated throughout the ice depth (0.040–0.046 day^{-1}) were comparable to those measured in the bottom of congelation ice in McMurdo Sound from the accumulation of biomass (0.03–0.09 day^{-1}; Grossi et al. 1984) and thymidine incororation (0.007–0.200 day^{-1}; Kottmeier et al. 1987).

Table 3.8 compares bacterial biomass, production and generation time in samples of platelet water and the meltwater of thawed platelets from Grossman et al. (1996) investigation in the Weddell Sea. Estimates of bacterial carbon production ranged from approximately 0.3,12 μg C l^{-1} h^{-1}, while generation times ranged from 1.9 to 3.0 day^{-1}. The patterns of bacterial characteristics in the platelet ice indicated that substantial heterotrophic potential could be established within this habitat leading to the accumulation of considerable bacterial biomass.

3.2.8.3 Environmental Factors

The principal environmental factors influencing the growth and development of the bacterial assemblages in the sea ice are salinity, temperature, the available DOM and nutrient pools. Kottmeier and Sullivan (1988) investigated the effects of salinity and temperature on the metabolic rates and growth of sea-ice bacteria. They found that autotrophs and heterotrophs exhibited two quite different patterns of metabolic rates in response to variations in salinity. Maximum rates of carbon fixation by microalgae occurred at salinities which characterized the ice from which they were collected (see Section 3.2.7). In contrast, bacteria exhibited a more stenohaline response to variable salinity, with maximum incorporation of thymidine and uridine from salinities of 20 to 30. In addition the bacteria may be better adapted for growth at higher salinities than the microalgae as significant incorporation of thymidine and uridine was found at salinities from 50 to 70.

The rate of incorporation of thymidine by sea-ice bacteria, like that of carbon fixation by the microalgae, increased several-fold at temperatures above the ambient −1.9°C (Kottmeier and Sullivan 1988). Maximum incorporation of thymidine, however, occurred at lower temperatures (4–7°C) than those found for carbon fixation (see Section 3.2.7.5). Pomeroy and Deibel (1986) have recently suggested that the rate of phytoplankton photosynthesis declines more slowly at lower temperatures than does bacterial metabolism, leading to an uncoupling of primary production and bacterial production in cold waters. Kottmeier and Sullivan (1988) tested this hypothesis in relation to sea-ice microalgae and bacteria. Their experiments can be defined by the envelopes in Figure 3.26. These envelopes show similar responses of the microalgae and bacteria to low temperatures with their maximum growth overlapping from 4°C to 7°C. This suggests that sea-ice microalgae and bacteria from the same environment exhibit similar growth responses at low temperatures. Primary production and bacterial production are not uncoupled due to differential growth of microalgae and bacteria at low temperatures.

Kottmeier et al. (1987) have proposed that the timing and amount of bacterial production in sea ice are dependent on the phase and growth of the microalgae, the quality and quantity of the compounds in the DOM pool available for bacterial growth, and the rates of bactivory and herbivory. Grossi et al. (1984) considered that the sea-ice microalgae may provide the bacteria with DOM, either dissolved photosynthate and/or EPS, while the bacteria in turn may provide the microalgae with vitamins and/or recycled inorganic nutrients. The nature of the extracellular material produced by the microalgae is diverse, and includes actively secreted high molecular weight polysaccharides, as well as a number of low molecular weight metabolites (amino-acids, monosaccharides and frequently glycolate) (McConville and Wetherbee 1985). Recent studies of the release of extracellular organic carbon (EOC) have given varied results; 1% (Grossi et al. 1984); 4% for the microalgaeof the platelet ice layer (Palmisano and Sullivan 1985a); 4% to 10% (Palmisano pers. commun., quoted in Kottmeier et al. 1987). These amounts may not be sufficient to support more substantial bacterial production in the sea ice. Assuming a 50% efficiency of bacterial utilization of DOM (Fuhrman and

TABLE 3.8
Bacterial Biomass, Growth and Production in Sample Fractions Gained from Platelet Ice

Sample Fraction	Bacterial Biomass (μg C l^{-1})	Bacterial Production (μg C l^{-1} h^{-1})	Generation Time (day)
Platelet water	800.7 ± 90.6	12.1 ± 3.4	1.9
Meltwater	934.9 ± 107.1	9.1 ± 3.1	3.0
Platelet water	24.6 ± 2.9	0.35 ± 0.60	2.1
Meltwater	20.5 ± 2.1	0.29 ± 0.31	2.0
Platelet water	15.4 ± 1.7	0.34 ± 0.32	1.9

Platelet water and corresponding meltwater of the thawed ice platelets were separated by sieving the samples prior to melting. Errors denote standard error of means ($n = 30$ microscopic grids counted. Sixty bacterial cells sized. Three replicates radio assayed each).

Source: From Grossman, S., Lochie, K. and Scharek, R., *Polar Biol.*, 16, 626, 1996. With permission.

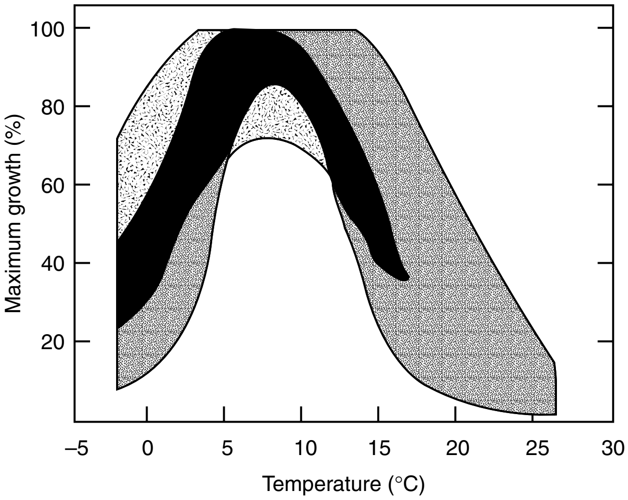


FIGURE 3.26 Comparison of the relative growth rates of sea-ice microalgae (autotrophs) and bacteria (heterotrophs) as a function of temperature. *Stipled areas* represent "envelopes" which describe the relative growth rate versus temperature relationships for autotrophs (*dark stipling*) and heterotrophs (*light stipling*). *Darkened areas* represent region of overlap. Growth rate data is based on rates of fixation of CO (autotrophs) and incorporation of H-thymidine (heterotrophs). (From Kottmeier, S.T., Sullivan, C.W., *Polar Biol.* 8, 1311, 1311, 1988. With permission.)

Azam 1982; Ducklow 1983), and a maximum bacterial carbon production of 9% primary production, bacteria would consume a maximum of 18% of the total fixed carbon in the sea ice, which is more than the estimated DOC provided by the microalgae. However, bactivory and herbivory by protozoans, death and lysis of diatom cells, and excretion and secretion by the meiofauna can also contribute to the DOM and mineral pool.

Grossman et al. (1996) consider that the platelet ice layers constitute a favorable environment for the development of the ice biota including bacteria. Due to its stability in combination with available space, opportunity for colonization, and capacity for nutrient exchange, this habitat can support dense microbial assemblages. A number of studies (e.g., Dieckmann et al. 1992; Grossman et al. 1996) found higher concentrations of phosphate and ammonium within the platelet layers than in the underlying water column during summer, indicating active heterotrophic remineralization exceeding algal uptake. Regeneration rates of phosphate calculated by Arrigo et al. (1993) for platelet ice communities in McMurdo Sound were as high as 35 μmol l^{-1} day^{-1}.

3.3 SEA-ICE MICRO- AND MEIOFAUNA

Early research on sea-ice microbial communities concentrated on the microalgae and bacteria. However, in recent years this community has been shown to be diverse with an abundant micro- and meiofauna (Garrison and Mathot 1996; Palmisano and Garrison 1993; Schnack-Schiel et al. 2001). Protozoans and metazoans associated with sea ice include heterotrophic flagellates, ciliates, foraminifers, turbellarians and copepods (Spindler et al. 1990; Gradinger 1999). Nematodes have been found in Antarctic pack ice sample (Blome and Rieman 1999). Many of these organisms, especially some copepod species, appear to spend their entire life cycle, or at least a major part of it, within the sea ice (Dahms et al. 1990a, 1990b; Schnack-Schiel et al. 1995; Tanimura et al. 1996). The sea-ice peripheries or ice/water interfaces, which include nooks and crannies, larger gaps and enclosures, as well as floe edges, provide a tremendous surface area for algal growth. These zones are frequented by larger grazers, particularly krill and amphipods, which feed directly on the ice algae (Richardson and Whitaker 1979; Marschall 1988; Stretch et al. 1988; Daly 1990). The sea ice is an important nursery ground for the juveniles of many species providing an abundance of food as well as shelter from predators. It therefore plays a significant role in the survival of overwintering zooplankton.

The heterotrophic flagellates found in the pack ice include bodonids, choanoflagellates, euglenoids, and dinoflagellates (Garrison 1991a). These heterotrophic nanoflagellates are phagotrophs that feed primarily on bacteria, while Marchant (1985) had reported that choanoflagellates may ingest small autotrophs and detritus. The largest heterotrophs in the sea ice are dinoflagellates. Species such as *Gyrodinium* and *Amphidinium* closely resemble the autotrophic forms. One large unidentified species usually contained large vacuoles filled with large diatoms (Buck et al. 1990). Dinoflagellate cysts are also commonly found (Buck et al. 1990). In studies of the sea-ice brine communities in McMurdo Sound Stoeckner et al. (1993) found that heterotrophic dinoflagellates (primarily a small *Gymnodinium* sp. and *Polykritos* sp. increased in abundance over time. The average microalgal biomass in the brine tended to decrease as the heterotrophic biomass increased.

Ciliates are also abundant in sea-ice communities, and at times they comprise a major fraction of the heterotrophic biomass (Kottmeier et al. 1987; Garrison and Buck 1989a; Spindler et al. 1990). Their concentrations in the ice are generally higher than in the underlying seawater and they may compose up to 70% of the total heterotrophic biomass (Garrison et al. 1986; Garrison and Gowing 1992; Garrison and Mathot 1996). Corless and Snyder (1986) found 26 taxa, including 9 new species, in sea ice from the Weddell Sea. The most abundant ciliates are the non-sheathed oligotrichs (e.g., *Strombidium* spp.). Several species, such as *M. rubrum* and *Strombiidium* spp., are common in the plankton, whereas others, such as *Euplotes*, are only abundant in the sea ice. In their study of sea-ice brine communities in McMurdo Sound, Stoeckner at al. (1993) found that the most common ciliates in the brine were oligotrichs comprising about 70% of the ciliate biomass. Six *Strombidium* spp. dominated the oligotrich assemblage and they occurred at average individual species densities of greater than 100 l^{-1} of brine. One *Strombidium* sp. which occurred at average densities of ca. 10^3 cells l^{-1} and in 76% of the samples taken near the ice edge it accounted for about 45% of the total ciliate biomass. Grazing by ciliates can have a considerable impact on the microalgal community (Scott et al. 2001). Reported clearance rates vary enormously ranging over 5 orders of magnitude from tens of nanolitres to hundred of microlitres per cell per hour (Sherr and Sherr 1984; Sherr et al. 1989; Hall et al. 1993; Christaki et al. 1998).

Larger protozoans such as the formaniferan *Neogloboquadrinia pachydera* have been found in sea ice at densities of up to 1000 cells l^{-1} (Lipps and Krebs 1974; Spindler and Dieckmann 1986; Spindler et al. 1990; Dieckmann et al. 1991). Spindler and Dieckmann (1986) suggested that Foraminifera are harvested from the plankton and concentrated in newly formed sea ice by processes similar to those reported for microalgae.

Archer et al. (1996) investigated the microbial ecology of the sea ice off Davis Stations. They found an abundant and diverse heterotrophic protozoan community that inhabited all horizons of the land fast ice (Figure 3.27). The dominant heterotrophic taxa occurring in the bottom few centimeters of ice were a species of euglenoid and 2 dinoflagellates The carbon biomass of the euglenoid reached a maximum on 22 December, accounting for 7% of the total microbial biomass

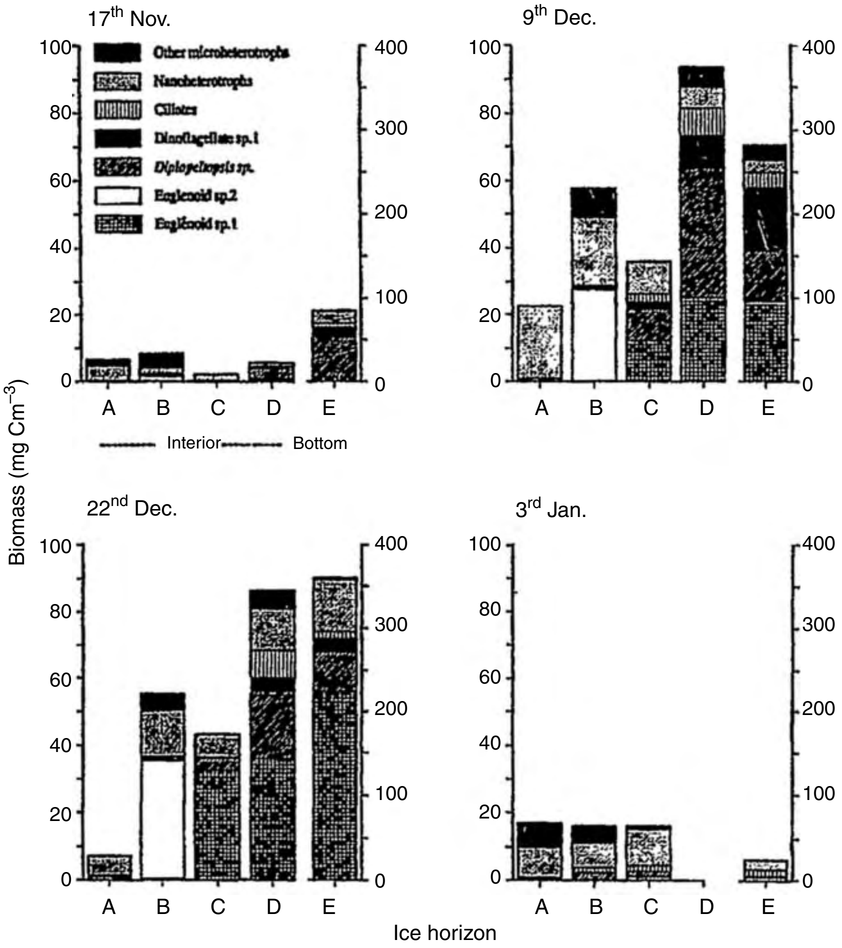


FIGURE 3.27 Mean ($n = 3$) biomass of the 7 major categories of heterotrophic protozoan taxa recorded form 5 ice horizons, in cores sampled on 17 November 1993, 9 and 22 December 1993 and 3 January 1994. Note the different scale for horizon E. (From Archer, S.D., et al., *Mar. Ecol. Prog. Ser.*, 135, 185, 1996. With permission.)

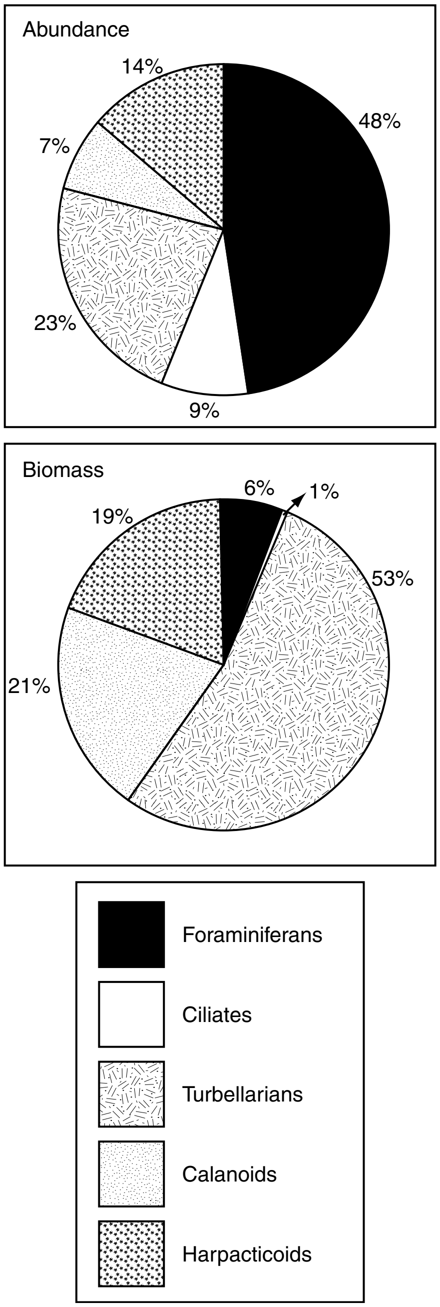


FIGURE 3.28 Relative contribution of sea-ice meiofauna taxa in the Weddell Sea to mean abundance and biomass. (From Schnack-Schiel, S.B., et al., *Polar Biol.*, 24, 724, 2001. With permission.)

in one sample and almost 70% of the microbial biomass on that date. Two dinoflagellates each made up 25% of the mean heterotrophic protozoan biomass on occasions. Internal assemblages were made up of heterotrophic flagellates, including nanoflagellates, euglenoids, and dinoflagellates. The biomass of heterotrophic protozoa increased throughout the ice depth during summer and taxon-specific net growth rates ranged between 0.168 day^{-1} for a heterotrophic euglenoid and 0.05 day^{-1} for the heterotrophic nanoflagellate population over a 23-day period.

Metazoa associated with Antarctic sea ice include a few species living within the ice as well as others living on or below the ice. These include a variety of organisms such as the larvae of benthic invertebrates, amphipods, nauplii and other development stages, as well as adults, of copepods, mites, and euphausiids. As discussed in Chapter 12, larval and adult copepods may be present in large numbers.

Schnack-Schiel et al. (2001) investigated the meiofauna of sea ice in the Weddell Sea. Figure 3.28 depicts the relative contribution of the sea-ice meiofauna to mean abundance and biomass. Foraminifers dominated the sea-ice meiofauna by numbers (48%), ciliates, turbellarians, harpacticoid and calanoid copepods making up between 7% and 23%. However, in terms of biomass, turbullarians were dominant (53%), followed by harpacticoids (21%), calanoids (19%), foraminiferans (6%) and ciliates (1%). In contrast to Arctic ice, rotifers have not been recorded in the Antarctic and nematodes are extremely rare.

3.4 DYNAMICS OF SEA-ICE MICROBIAL COMMUNITIES

The lowermost circle in Figure 3.29 depicts the food web of the sea-ice microbial community involving diatoms, autotrophic flagellates and dinoflagellates, heterotrophic flagellates and dinoflagellates, protozoa and small metazoans, POM, DOM and bacteria. Figure 3.29 is a conceptual model of the feeding relationships of the sea ice microbial food web. Feeding relationships are complicated by the fact that some species feed at more than one trophic level. For example, a heterotrophic dinoflagellate would be a primary consumer (level 2) when feeding on a diatom, a secondary consumer (level 3) when feeding on a small ciliate that had grazed on diatoms, or a tertiary consumer (level 4) when feeding on a small ciliate that had consumed a small flagellate that had consumed a diatom. Following Whitaker (1977a) and Carey (1985) this constitutes the sea-ice *sympagic* community.

On the basis of various estimates for DOM production, cell death to form detritus, and consumption by the various consumers, it is estimated that somewhere between 74% and 80% of the annual production of the microalgae is released into the water column upon the melting of the ice.

Associated with the bottom ice and platelet ice is the *cryopelagic* community (Andriashev 1968; Bradford 1978) composed of the adult and larval stages of invertebrates, especially euphausiids and copepods, and some fish species. Some of these species feed directly on the ice microalgae, others feed on them and other species associated with the underside of the ice. Prominent among the algal grazers are the amphipods, *Paramoira walkeri*, *Orchomene plebs* and *Eusirus antarcticus*, adult and larval euphausiids, especially *Euphausia superba* (see Chapter 12) and *E. crystallorophias*, and copepods. Secondary consumers are dominated by larval fish, mainly *Pleurogramma antarcticum* (DeWitt and Hopkins 1977), which feed mainly on the nauplii and adult copepods.

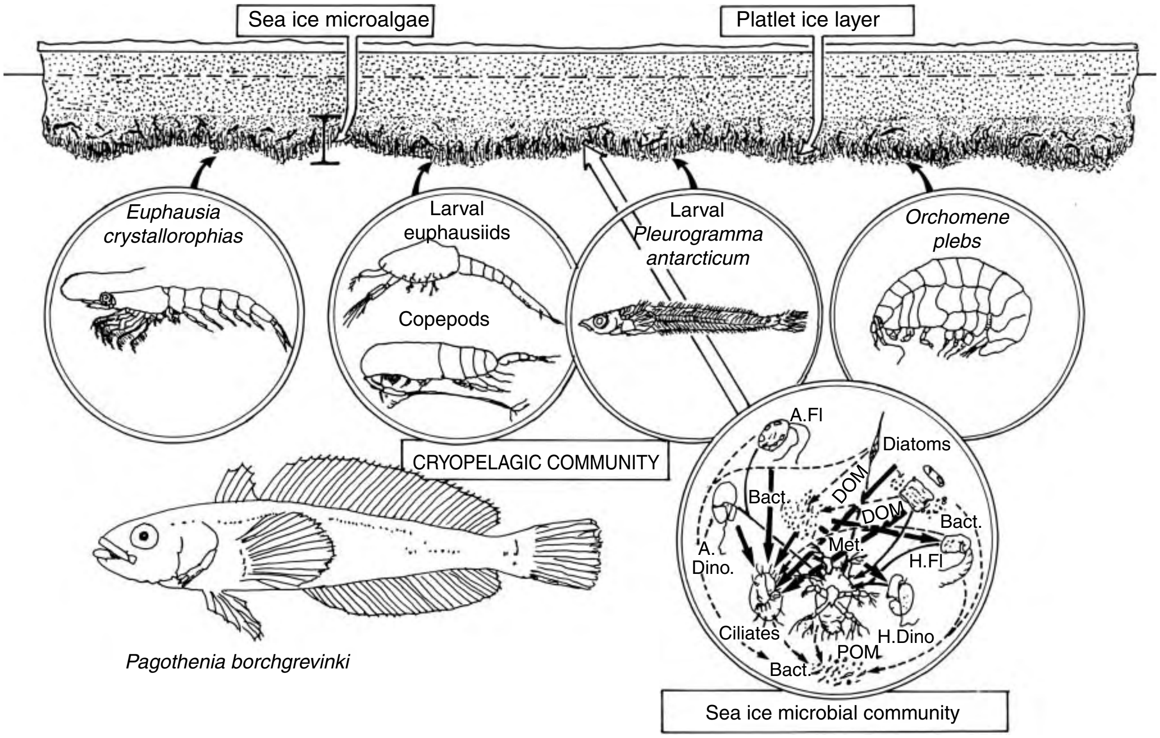


FIGURE 3.29 Diagrammatic representation of the feeding relationships of the sea-ice microbial community and the cryopelagic community associated with the sea ice. A.Fl., Autotrophic flagellate; H.Fl., Heterotrophic flagellate; Dino., Dinoflagellate; H.Dino., Heterotrophic dinoflagellate; Bact., Bacteria; DOM, Dissolved organic matter; POM, Particulate organic matter.

A common species which is abundant in schools of varying size in the top few meters of the water beneath the ice is the small pelagic fish *Pagothenia borchgrevinki*. The feeding of this species has been studied by Bradfield (1980), Eastman and De Vries (1985) and Forster et al. (1987). The prey taken varied according to the season and locality and included species prominent in the cryopelagic community such as the polychaete *Harmothoe* sp., the amphipods *O. plebs* and *E. antarcticus*, and larval *P. antarcticum*. Other zooplankton species eaten included copepods (*Calanoides acutus*, *Metridia gerlachi*, *Calanus propinquus* and *Euchaeta antarctica*), hyperiid amphipods (*Hyperiella dilata* and *Epimerella macronyx*) euphausiids and chaetognaths. The role of *P. borchgrevinki* in inshore ecosystems will be discussed further in 12.

4 Zooplankton

CONTENTS

4.1 INTRODUCTION

Investigations of Antarctic zooplankton date back to the *Challanger* expeditions of 1982–1876. However, it was not until the beginning of the twenty-first century that intensive studies commenced with the program of research undertaken by the research vessel *Discovery* in 1926–1929, followed by the *Scoresby* in 1950–1951. The extensive collections of these expeditions have contributed valuable information on distributional patterns as well as the life cycles of many of the major zooplankters (e.g., Ommaney 1936; Bargman 1945; Marr 1962; Andrews 1966; Foxton 1966; Mackintosh 1972). Mackintosh (1934) distinguished different zones and defined boundaries of distribution based on the association of zooplankton species with certain water masses and identified four groups: warm-water species, cold-water species, neretic species, and widespread species.

In the mid-1960s research into Antarctic zooplankton increased, stimulated by the possibility of the exploitation of Antarctic krill, *Euphausia superba*. Since that date, a number of major coordinated research activities have been carried out by national Antarctic programs coordinated by SCAR, such as the BIOMASS Programme (El-Sayed 1996).

As a result of the studies of the *Discovery* expeditions (e.g., Hardy and Gunther 1936; David 1958, 1965) and more recent Soviet studies, we had a relatively thorough knowledge of the taxonomy, general distribution, and life cycles of the dominant zooplankton species. However, literature on the Southern Ocean zooplankton is dominated by studies on *Euphausia superba* because of its large biomass, ecological

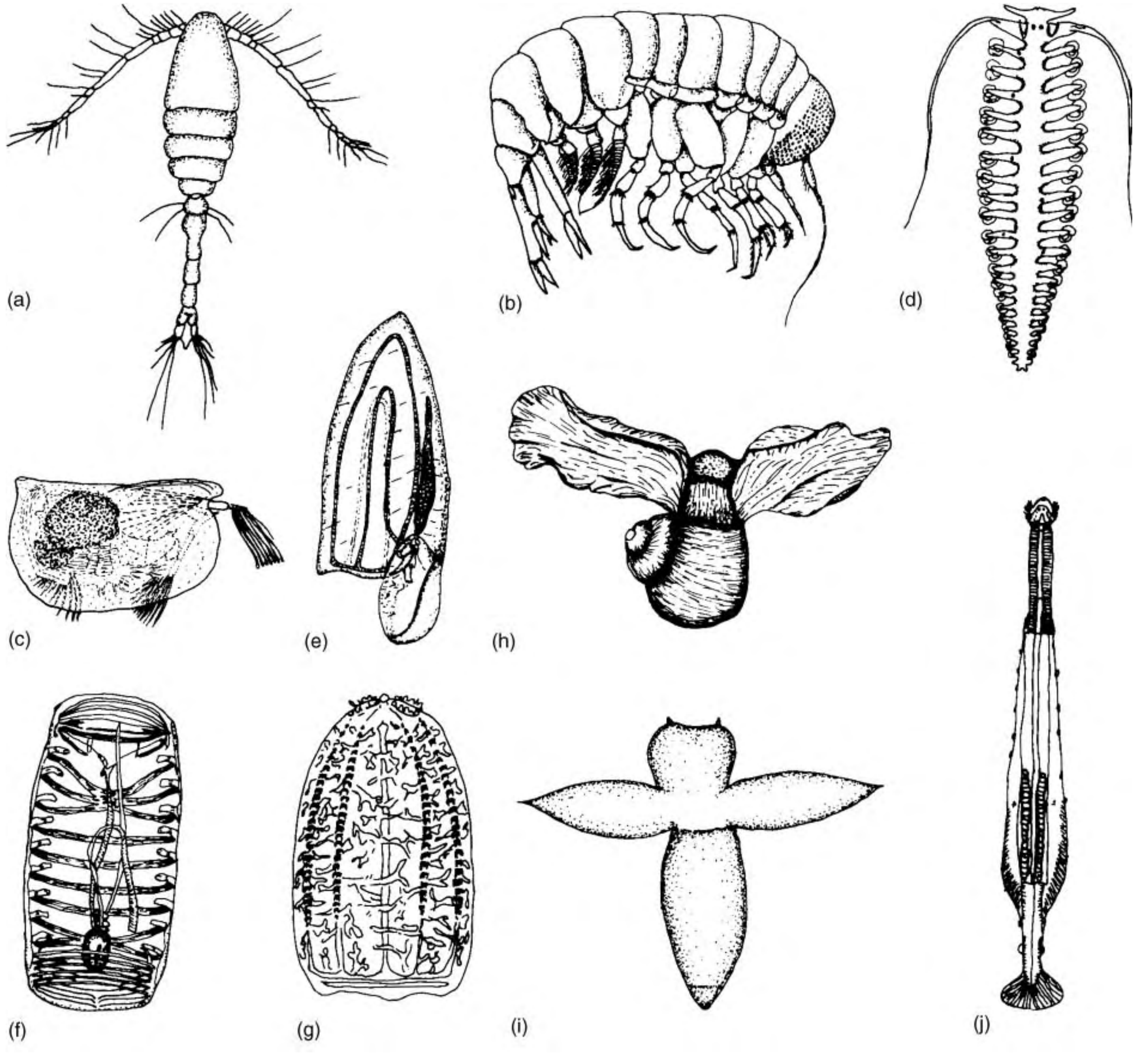


FIGURE 4.1 Some common Southern Ocean zooplankton species. (a) *Calanoides acutus* (copepod);(b) *Epimeriella macronyx* (amphipod); (c) *Euphausia crystallorophias* (euphausiid); (d) *Pelagobia longicirrata* (polychaete); (e) *Limacina helicina* (pteropod); (f) *Salpa thompsoni* (salp); (g) *Sagitta gazallae* (chaetognath).

importance, and resource potential. While the term *krill* is generally taken as referring to *E. superba*, it is also used in a sense including all the other Southern Ocean euphausiids. Euphausiids are generally considered to comprise at least 50% of the standing crop of zooplankton (El-Sayed 1971c, 1977; Knox 1983). However, there is evidence that other groups, especially the copepods, are significant in the pelagic ecosystem in terms of biomass and production. In this chapter, we shall concentrate on the zooplankton groups other than euphausiids, which will be dealt with in the next Chapter.

There are a number of characteristics that distinguish the Antarctic zooplankton (Figure 4.1). These are:

- The comparative rarity of the larval forms of bottom-living invertebrates, which seasonally form an important component of the zooplankton in temperate and tropical areas. They do, however, occur in some neretic areas.
- The surface layers tend to be poor in species but rich in individuals, with the number of species increasing with depth. This relationship is illustrated in Figure 4.2, which shows the increase in copepod species with depth off South Georgia.
- In addition to diurnal vertical migration patterns exhibited by some species, the dominant zooplankton species perform an annual vertical migration (see Section 4.4) (Mackintosh 1970, 1972, 1973).
- Reproduction in most species is timed to coincide with the extremely seasonal pulse of primary production that occurs over a very restricted time period.

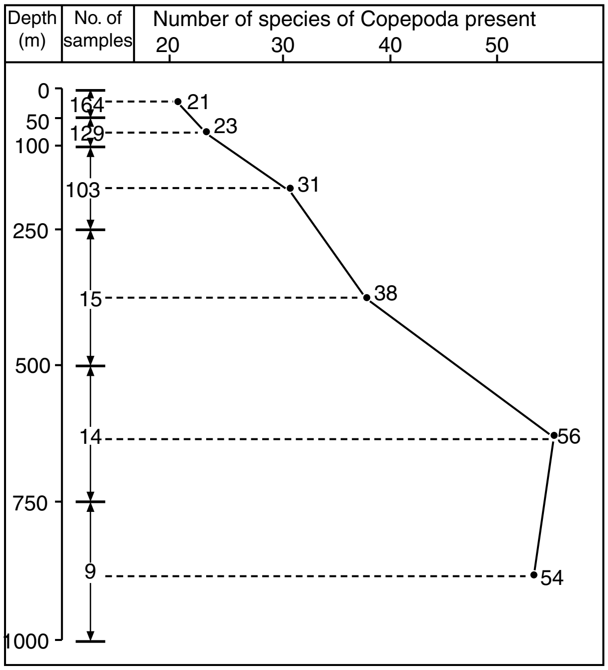


FIGURE 4.2 Graph showing the number of species of Copepoda with increasing depth in Antarctic waters off South Georgia. (From Knox, G.A., Holdgate, M.W., Ed., *Antarctic Ecology*, Academic Press, London, 69, 1970; after Hardy, A.C., *Great Waters*, Collins, London, 1967. With permission.)

In recent years, numerous studies of the systematics, composition, and distribution of zooplankton communities in the Southern Ocean have been published (e.g., Chojnacki and Weglenska 1984; Hopkins 1985a, 1985b; Hubold et al. 1985; Witek et al. 1985; Hopkins and Torres 1986; Piatkowski 1987a, 1987b; Atkinson and Peck 1988; Foster 1989; Lancraft et al. 1989; Tucker and Burton 1990; Boysen-Ennen et al. 1991; Siegel et al. 1992; Hopkins et al. 1993; Quetin et al. 1994; Quetin and Ross 1996). Most of these deal with copepods and euphausiids, the main components of the Antarctic zooplankton.

4.2 SPECIES COMPOSITION AND DISTRIBUTION

By size, the zooplankton can be subdivided into the following categories: protozooplankton (0.02–20 µm), microzooplankton (20–200 µm), mesozooplankton (< 14.5 mm), macrozooplankton (14.5–39.5 mm), and megazooplankton (< 39.5 mm). The protozooplankton category includes the heterotrophic flagellates, dinoflagellates, and ciliates, choanoflagellates, tintinnids, and amoeboid forms, including the Foraminifera and Radiolaria. The microzooplankton category is comprised mainly of the smaller copepod and ostracod species as well as the larval stages of some of the larger zooplankton and fish larvae. Mesozooplankton include the larger crustacea, such as the euphausiids, ostracods, mysids, amphipods (especially the Hyperiidae), chaetognaths, pelagic mollusca (Pteropoda and Heperopoda), and pelagic polychaetes, especially the Tomopteridae. The macrozooplankton and megazooplankton categories are comprised mainly of the gelatinous metazoan, such as the coelentrate medusae, ctenophores, siphonophores, the Scyphozoa (true jellyfish), and the Ascidiacea (appendicularians and thaliaceans or salps).

4.2.1 ZOOPLANKTON SPECIES COMPOSITION AND ABUNDANCE

Although copepods and euphausiids dominate the zooplankton assemblages, in some years they may be outnumbered by salps, mainly *Salpa thompsoni* (Mujica and Asencio 1985; Piatkowski 1985b; Witek et al. 1985; Montu and Oliveira 1986; Nast 1986; Huntly et al. 1989). Data from the Antarctic Peninsula region (Schnack-Schiel and Mujica 1996) confirms that groups other than copepods, euphausiids, and salps such as polchaetes, molluscs, appendicularians, ostracods, amphipods, chaetognaths, and coelenterates contribute only moderately (< 10%) to zooplankton biomass. The literature on Antarctic zooplankton is dominated by studies on a single species, *Euphausia superba*, while other zooplankton species have received less attention. For instance, Hopkins (1985b) estimated the biomass of *E.superba* in the Croker Passage west of the Antarctic Peninsula to be more than fifteen times larger than that of all other zooplankton (i.e., contributing 55–59 g dry mass m^{-2}). However, Brinton and Antezana (1984) for the Scotia Sea estimated that, excluding krill swarms, non-krill zooplankton accounted for 94%. Around Elephant Island and in Bransfield Strait, non-krill zooplankton made up about 26% and 31%, respectively, of the total zooplankton biomass within the krill swarms. In Admiralty Bay, Knig George Island, copepods contributed between 60 and 87% of the total summer biomass of the zooplankton, including euphausiids (Chojnacki and Weglenska 1984). Boysen-Ennen et al. (1991) summarized biomass values of zooplankton from different regions of the Southern Ocean: mesoplankton biomass generally ranged from 0.8 to 3.6 g dry mass m^{-2} and macrozooplankton from 2.0 to 2.4 g dry mass m^{-2}. Thus, mesozooplankton biomass was higher than macrozooplankton biomass and was in the same order of magnitude as krill biomass. Because of the higher production biomass ratio of copepods (4.5) compared with krill (1.0), Boysen-Ennen et al. (1991) concluded that copepods, which constitute the main component of the mesozooplankton biomass, contributed most to zooplankton production in the Southern Ocean.

The distribution of the protozooplankton will be considered later in, Chapter 14. Here, the composition of the other zooplankton groups will be considered.

4.2.1.1 Copepods

Copepods are the most diverse group, accounting for more than 70 species in the upper 1000 m of the water column in the western Weddell Sea (Hopkins and Torres 1989). In the upper 200 m of Bransfield Strait, approximately 30 species were reported (Zmijewska 1985). The copepod assembages are often dominated by cyclopoid copepods: *Oithona* spp. and *Oncaea* spp. account for 40–80% of the total copepod population by number (Jardzewski et al. 1982; Chojnacki and Weglenska 1984; Hopkins 1985a; Schnack et al. 1985; Montu and Oliviera 1986; Almeida Prado-Por 1989). *Oithona similis* prefers the upper 200 m; whereas, *Oncaea* spp. are bathypelagic (Schnack et al. 1985; Zmijwska 1988b). Among the calanoid species *Metridia gerlachei, Microcalanus pygmaeus*, and *Ctenocalanus citer* are the most numerous, and they occur throughout the area (Jazdzewski et al. 1982; Hopkins 1984; Schnack et al. 1985). *Microcalanus pygmaeus* and *Metridia gerlachei* together made up 70% of all the calanoids in Croker Passage between Gerlache Strait and Bransfield Strait (Hopkins 1985a) and up to 90% in the northern Bransfield Strait and south of Elephant Island (Schnack et al. 1985). Small copepod species (calanoid and cyclopoid) predominated by number, but large species such as *Calanoides acutus, Calanus propinquus, Rhincalanus gigas*, and *Metridia gerlachei* generally made up a large proportion of the total biomass (about 50–90%) (Chojnacki and Weglenska 1984; Hopkins 1985a; Hopkins and Torres 1986; Boysen-Ennen et al. 1991).

4.2.1.2 Salps

Salpa thompsoni is a dominant member of the zooplankton community in waters off the Antarctic Peninsula (Mujica and Asenio 1985; Piatowski 1985b). Nast (1986) counted a maximum of 889 individuals per 1000 m^{-3} north of Elephant Island in March 1985. On the other hand, salps were rarely found at stations influenced by Weddell Sea water (Mackintosh 1934; Nast 1986). Coinciding with the widespread occurrence of *S. thompsoni* in the austral summer 1983–1984, there was a strikingly low abundance of other zooplankton, including the larvae of Antarctic krill (Montu and Oliveira 1996).

Under favorable conditions, salps can rapidly respond to rises in phytoplankton stock, with rapid multiplication that can give rise to enormous concentrations (Foxton 1964). Grazing by *S. thompsoni* can remove a major part of the daily phytoplankton production (Huntly et al. 1989), thus depriving krill larvae of their food resource. *S. thompsoni* may also represent a significant predation pressure directly on krill larvae. In 1983–1984, over a 60-day period in the Antarctic Peninsula area, the salps removed 10–30% of the krill larvae in the upper 200 m; this would have serious effects on the larval stock and could account for the single order of magnitude reduction in krill larvae in 1984 relative to 1981 (Brinton et al. 1985).

4.2.1.3 Polychaetes

Polychaetes are permanent members of the zooplankton community (Mujica and Torres 1982; Mujica and Asencio 1985). The principal species is *Pelagobia longicittata* (Jadzewiski et al. 1982; Hopkins 1985a). Other common species are *Rhynchonerella bongraini* and *Tomopteris carpenteri.*

4.2.1.4 Pteropods

Among the pteropods, *Limacina helicina* is the dominant species. Off the Antarctic Peninsula, the highest concentrations occurred in the Drake Passage and in the waters of the Palmer Archipelago (Jazdzewski et al. 1982; Witek et al. 1985). *Clione limacina*, a predator of Limacinidae, was equally common but less abundant (Witek et al. 1985). *Clione pyramidata* is a characteristic member of the oceanic community.

4.2.1.5 Appendicularians

Appendicularians were found to be mainly concentrated in the upper 100 m at stations on the Antarctic Peninsula shelf and near the northern slope of the South Shetlands and the Palmer Archipelago (Jazdzewski et al. 1982).

4.2.1.6 Ostracods

Four species of pelagic ostracods (*Alacia belgicae, A. hettacra, Conchoecia isochiera*, and *C. skotsbergi*) often occur in zooplankton assemblages. However, they usually occur in low numbers.

4.2.1.7 Gelatinous Zooplankton

If one surveys the literature on Antarctic zooplankton, one is stricken by the remarkable lack of data about the so-called gelatinous zooplankton, aptly called "the forgotten fauna" by Pugh (1989). The early publications dealing with this group were mainly concerned with species descriptions. Some years later, the Discovery Reports provided data on abundance and distribution (Totton 1954; Kramp 1957; Foxton 1966) and established their presence and importance in Antarctic waters. Later publications on the gelatinous zooplankton dealt mainly with the salps, which were shown to be highly abundant in the spring, coinciding with the phytoplankton bloom (e.g., Nast 1986).

Recently, the ecological role of the gelatinous zooplankton has been reappraised. Some considerations from an energetic point of view (Clarke and Peck 1991) and data on its proximate and elemental composition (Clarke et al. 1992) have been published, but data about species composition, abundance, and distribution are still scarce. Recently, Pages and Lurbjewtt (1994) published data on the composition, abundance, and vertical distribution of mesoplanktonic cnidarians collected in the Weddell Sea. There is no doubt that the role of gelatinous zooplankton in the Antarctic pelagic food web has been underestimated, as the work of Larson (1986) on scyphozoan medusae has shown.

4.2.2 ZOOPLANKTON PROVINCES

In Chapter 1 and Chapter 2, the distribution of oceanic fronts and water masses in the Southern Ocean were discussed. These play an important role in the distribution patterns of the zooplankton. Three different latitudinal zones for zooplankton communities (northern, intermediate, and southern zones) coincide with the distribution of water masses and ice cover (Voronina 1971; Hempel 1985b; Smith and Schnack-Schiel 1990). The northern zone occupies the ice-free part of the oceanic Antarctic Circumpolar Current and is relatively poor in biomass and production (Maruyama et al. 1982; Hempel 1985b). Within the Antarctic Circumpolar Current, higher zooplankton biomass occurs near the Polar Front and decreases towards the south (Foxton 1956; Hopkins 1971; Yamada and Kawamaru 1986). Copepods, salps, small euphausiids, chaetognaths, and amphipods dominate the zooplankton, with copepods constituting more than 60% of the biomass in most parts and seasons (Seno et al. 1963; Hopkins 1971; Maruyama et al. 1982).

The northern zone occupies the oceanic part of the Antarctic Circumpolar Current and is relatively poor in biomass and production (Maruyama et al. 1982; Hempel 1985b). Within the Antarctic Circumpolar Current, higher zooplankton biomass is found near the Polar Frontal Zone, and it decreases towards the south (Foxton 1956; Hopkins 1971; Yamada and Kawamura 1986). Copepods, salps, small euphausiids, chaetognaths, and amphipods dominate the zooplankton, with copepods constituting more than 60% of the biomass in most parts and seasons (Seno et al. 1963; Hopkins 1971; Maruyama et al. 1982). *Calaniodes acutus, Calanus propinquus, Rhincalanus gigas*, and *Metridia gerlachei* constitute the bulk of the copepod biomass. Among the chaetognaths, *Sagitta gazella* and *Eukronia hamata* are common, and swarms of *Sala thompsoni, Thermisto gaudichaudii*, and *Thysanoessa* spp. are frequent. Krill are mostly absent except near South Georgia (Hempel 1985b).

The seasonal pack-ice zone constitutes the intermediate zone, which is ice-covered in winter and spring but ice-free in summer and autumn. This zone encompasses most of the Antarctic Circumpolar Current, the northern branch of the Weddell Gyre, and the Antarctic Peninsula region. This zone is the most productive region of the Southern Ocean with the highest annual primary production (Hempel 1985b). *Euphausia superba* is the dominant species, and large concentrations occur where water masses of different origins mix or where sharp changes in bottom topography occur.

The southern zone is the permanent pack ice zone occupying cold waters along the continental shelf, especially in the inner parts of the Ross Sea (Hempel 1985b). Phytoplankton production is limited to a short intense period; however, there is a much longer ice algal production period (Hempel 1985b). Zooplankton abundance and biomass are low. The small neretic euphausiid, *Euphausia crystallorophias* (Thomas and Green 1988), and juveniles of the pelagic silverfish, *Pleurogramma antarcticum*, are typical species of this zone (Boyen-Ennen and Piatkowski 1988).

4.2.3 COPEPODS

Copepods are the most diverse group of zooplankton in the Southern Ocean, accounting for more than 70 species in the upper 1000 m of the water column in the western Wedell Sea (Hopkins and Torres 1989). In the upper 200 m in the Bransfield Strait, approximately 30 species were reported (Zmijewska 1985). Many species are uncommon. The copepod assemblages are often dominated by cyclopoid copepods; *Oithona* spp. and *Oncaea* spp. account for 40–80% of the total copepod population by number (Jazdewski et al. 1982; Chojnacki and Weglenska 1984; Hopkins 1985a; Schnack et al. 1985; Almeida Prado-Por 1989). *Oithona similis* prefers the upper 300 m, whereas *Oncaea* spp. are bathypelagic (Schnack et al. 1985; Zmijewska 1985). Among the calanoid species *Metridia gerlachei, Microcalanus pygmaeus*, and *Ctenocalanus citer* are the most numerous ones and occur throughout the area (Jazdzewski et al. 1982; Hopkins 1985a). *Microcalanus pygmaeus* and *Metridia gerlachei* make up 70% of all calanoids in the Croker Passage (Hopkins 1985a) and up to 90% in the northern Bransfield Strait and south of Elephant Island (Schnack et al. 1985). Small copepod species (calanoid and cyclopoid) predominate in number, but large species such as *Calanoides acutus, Calanus propinquus, Rhincalanus gigas*, and *Metridia gerlachei* generally make up a larger proportion

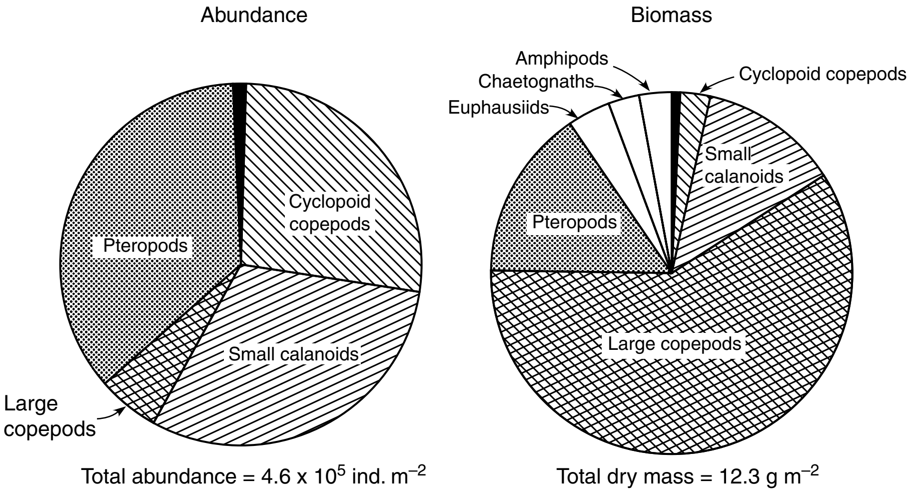


FIGURE 4.3 Composition of the zooplankton community within the top 200 m, compiled from mean values across 7 LHPR hauls. Large copepods are defined as all copepodite stages of *Calanoides acutus, Calanus propinquus, Rhincalanus gigas, Calanus simillimus, Metridia lucens, M. gerlachei*, and *Pleuromamma robusta.* Unidentified nauplii are included in the small calanoid group. Solid segment represents remaining taxa. (From Atkinson, A., Shreene, R.S., Pakhomov, E.A., Priddle, J., Blight, S.P., Ward, P., *Marine Ecology Progress Series*, 144, 195–210, 1996. With permission.)

of the total biomass (about 50–90%) (Chojnacki and Weglenska 1984; Hopkins 1985a; Hopkins and Torres 1988; Boysen-Ennen et al. 1991).

Most studies of Southern Ocean copepods have addressed the large biomass-dominant species such as *Calanoides acutus, Calanus simillius, Calanus propinquus, Rhincalanus gigas*, and, to a lesser extent, *Metridia gerlachei*. However, increasingly it is becoming clear that the smaller, numerically dominant genera such as *Oithona, Oncaea*, and *Ctenoclanus* are also important. For instance, mass specific ingestion rates of *Oncaea curvata* were found to be ten times greater than those of large Antarctic calanoids (Swadling et al. 1997; Metz 1998).

Atkinson et al. (1996) investigated the response of zooplankton to a phytoplankton bloom near South Georgia. Figure 4.3 depicts the total abundance and biomass of the zooplankton community that they found. In terms of copepod abundance, the dominants were small calanoids and cyclopoids. In contrast, the copepod biomass was dominated by large copepods (*Calanoides acutus, Calanus propinquus, Rhincalanus gigas, Calanus simillimus, Metridia lucens, M.gerlachei,* and *Pleurogramma robusta*) with the small calanoids and cyclopoids having much lower biomasses.

4.2.4 SALPS

Salps are a dominant component of the zooplankton of the Southern Ocean (Brinton 1984; Witek et al. 1985; Nast 1986; Lancraft et al. 1989; Boysen-Ennen et al. 1991; Quetin et al. 1996). Because the rate of increase of salps is much higher than in either copepods or euphausiids, they can respond quickly to improved environmental conditions. Thus, their grazing impact can be strong and ephemeral. There has been much discussion of the interrelationship between salps and euphausiids. Where salps are abundant, krill are generally rare. In an investigation of the distribution of salps near the South Shetland Islands, Nishikawa et al. (1996) found that *Euphausia superba* occurred abundantly in the high-chlorophyll areas. In contrast, salps exhibited high biomass in the oceanic area of low chlorophyll *a* concentrations.

The two principal species of salps are *Salpa thompsoni* (the most abundant) and *Salpa gerlachei*. A third species is *Ihlea racovitzia*. In the vicinity of the Antarctic Peninsula, *Ihlea racovitzia* occurred in the northern Bransfield Strait (Nishikawa et al. 1995), while the first two species, especially *S. thompsoni*, were more widespread. All share a life history characterized by alternating sexual and asexual (budding) generations (see Section 4.3.2) and a spring or summer maximum in abundance. Salps show a distinct and deep ontogenetic migration. In general, the solitary form, not the aggregate form, is found in the deeper layers of the water column (Foxton 1966). The ontogenetic vertical migration occurs after sexual reproduction and is undertaken by the solitary form to depths of 250 to 1500 m in the autumn (Foxton 1966; Ainley et al. 1991), leaving the aggregate form in the surface waters. Timing in the reproductive cycle determines when the vertical maximum in the salp population moves from the upper 250 m to deeper waters.

4.2.5 CHAETOGNATHS

Chaetognaths are one of the most numerous groups (9.8% of the overall mesoplankton biomass) in the Southern Ocean zooplankton. According to Alvarino (1964), the following species are typical of Antarctic waters:

- Epiplanktonic (200-0 m): *Eukronia hamata* and *Sagitta gazellae*

- Mesoplanktonic (600-150 m): *Sagitta marri, Sagitta maxima,* and *Sagitta planktonis*
- Bathypelagic (below 1,000 m): *Eukronia bathypelagica.*

Of the above, *E. hamata* and *S. gazellae* are the most common.

4.2.6 SOME REGIONAL DISTRIBUTION PATTERNS

4.2.6.1 The Scotia Sea, the Bransfield Strait, and the Waters Adjacent to the Antarctic Peninsula

This is one of the most intensively investigated areas of the Southern Ocean. The Scotia Sea is bordered to the south by the Weddell Sea, to the west by the Drake Passage, and on all the other sides by the Scotia Arc. The major oceanographic feature in the Scotia Sea is the Weddell-Scotia Confluence separating the cold water of the Weddell Sea from the warm water of the Antarctic Circumpolar Current.

Euphausiids and copepods dominate the zooplankton assemblages (e.g., Jazdzewski et al. 1982; Montu and Oliviera 1986). Among the euphausiids, *Euphausia superba* dominates with major concentrations in areas where water masses of different origin mix (Witek et al. 1981; Nast et al. 1986). However, they can be outnumbered by salps, mainly *Salpa thompsoni* (Witek et al. 1985; Montu and Oliviera 1986). Salps, however, were not found at all or were very scarce at stations influenced by water from the Weddell Sea (Piatkowski 1985a, 1985b).

Subantarctic and Antarctic species are typical components of the zooplankton community around South Georgia (Hardy and Gunther 1935; Atkinson and Peck 1990). The Weddell-Scotia Confluence is the southern limit of subantarctic species such as *Calanus simillimus*. The zooplankton population in the Antarctic Circumpolar Current consists of more advanced development stages of copepods and euphausiids than those which occur in the Weddell Sea (Makarov 1979a, 1979b, 1979c; Brinton 1985; Marin 1987).

When *E. superba* is absent, copepods constitute 40–90% (by numbers) of the total zooplankton population of the Scotia Sea and Bransfield Strait (Mujica and Torres 1982; Mujica and Asencio 1985). Cyclopoid copepods (*Oithona* spp. and *Onacea* spp.) often dominate the copepod assemblages and account for 40–80% of total numbers (Hopkins 1985b; Schnack et al. 1985). Among the calanoid species, *Metridia gerlachei* is the most numerous, occurring throughout the area (Jzdzweski et al. 1982; Zmijewska 1985). *M. gerlachei* and the small calanoid species, *Microcalanus pygmaeus*, made up 70% of the total calanoids in Croker Passage (Hopkins 1985b) and up to 90% in northern Bransfield Strait and south of Elephant Island (Schnack et al. 1985). Other abundant calanoid species are *Calanus acutus, C. propinquus, Rhincalanus gigas, Ctenocalanus* sp., *Clausocalanus* sp., *Stephos longipes,* and *Euchaeta antarctica,* all having large spatial and temporal variability.

Thysanoessa macrura is the second dominant euphausiid species (Kittel and Stepnik 1983), occasionally being more abundant than *E. superba* (Mujica and Asencio 1985; Piatkowski 1995a). *E. crystallorophias* is a neritic species that occurs over the shelf of the Bransfield Strait and west of the Antarctic Peninsula (John 1936; Piatkowski 1985a). *E. frigida* and *E. tricantha* are found only in areas of the Antarctic Circumpolar Current that have not been influenced by the Weddell Sea (Kittel and Stepnik 1983).

Zooplankton assemblages can be distinguished by differences in species composition and abundance and are associated with different water masses (Jazdzewski et al. 1982). Radiolarians, the polychaete *Tomopteris carpenteri*, and the crustaceans *Rhincalanus gigas* and *Thermisto gaudichaudii* are dominant members in the southern Drake Passage and Scotia Sea influenced by the West Wind Drift (Jazdzewski et al. 1982). Many species are abundant in the shelf waters west and north of the Palmer Archipelago influenced by Bellingshausen Sea water (Witek et al. 1985). Zooplankton is sparse in the waters of the Bransfield Strait (Witek et al. 1985) where *O. curvata* and *Pelagobia longicirrata* are typical inhabitants (Jazdzewski et al. 1982). Areas influenced by water from the Weddell Sea are characterized by the occurrence of rare copepod species such as *Paralabidocera antarctica* and by the scarcity of *R. gigas, E. frigida, T. gaudichaudii, Vibalia antarctica,* and *S. thompsoni* (Piatkowski 1985a; Schnack et al. 1985).

Based upon the analysis of copepod samples taken by the *Discovery* Expeditions from the 1920s to the 1950s in the Scotia Sea, Atkinson and Sinclair (2000) identified three assemblages associated with three different water masses. These water masses from north to South were: (1) the Subantarctic Front and the Polar Frontal Zone; (2) the Polar Front; and (3) the Antarctic Zone and the Weddell Sea Confluence (Figure 4.4). Small copepods (*Microcalanus pygmaeus, Ctenocalanus* spp., *Oncaea* spp., and *Oithona* spp.) formed approximately 75% of total copepod abundance in the top 1000 m across all major zones. *Oithona* spp. comprised approximately 40% of copepod numbers in the Polar Front area and to the south; further north, their importance declined. All mesopelagic taxa, except the warmer-water species *Metridia lucens*, and *Pleuromamma robusta*, extended throughout the entire study area with smaller regional differences than those for the shallower-living species. There was no evidence that the Polar Front was a major biogeographic boundary to their distribution. Indeed, several important species, including *Oithona* spp., *Metridia lucens*, and *Rhincalanus gigas*, reached maximum numbers in this area. Total copepod abundance was therefore higher in the vicinity of the Polar Front than in any other region.

4.2.6.2 Weddell Sea

The Weddell Sea is bordered by the Antarctic Peninsula, the Antarctic Continent (including the Larsen Ice Shelf and

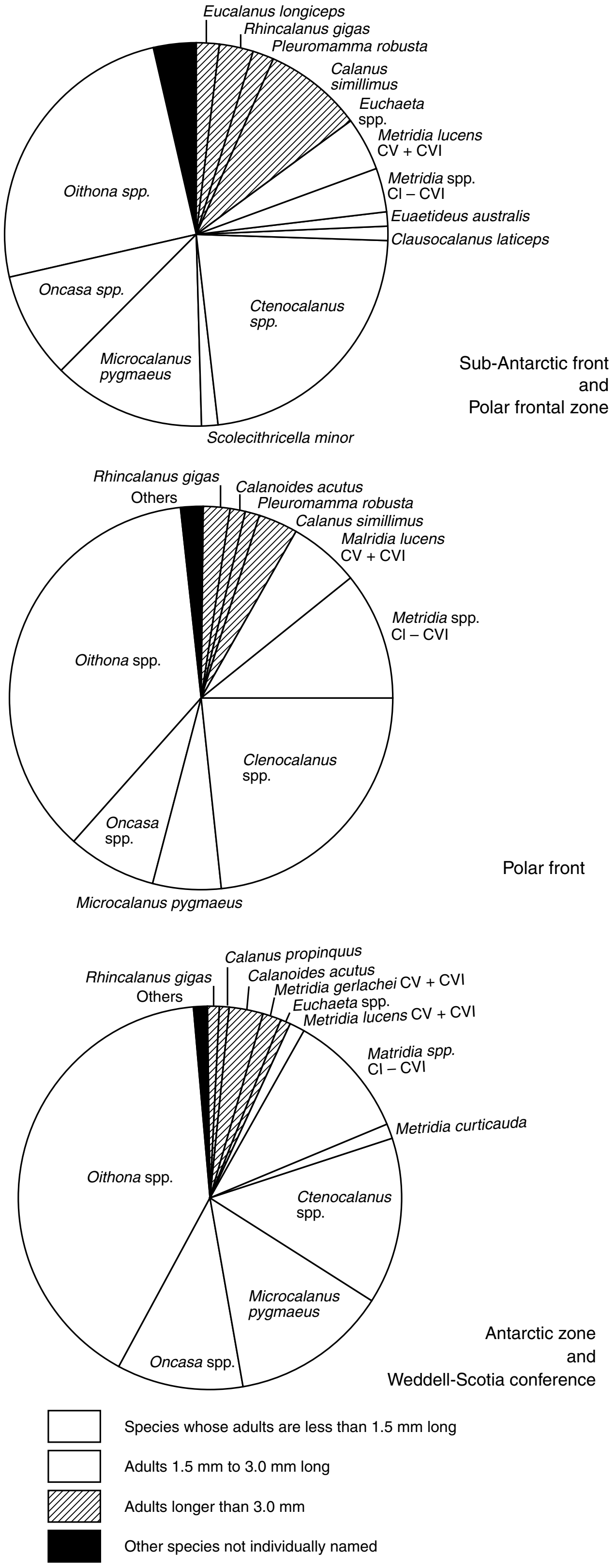


FIGURE 4.4 Contribution of species to median total abundance of copepods, integrated throughout the top 1,000 m layer by season in three water zones of the Scotia Sea. Unshaded: species whose adults are less than 1.5 mm long; stipled: adults 1.5–3.0 mm long; diagonal lines: adults longer than 3.0 mm; black: other species not individually named. (From Atkinson, A., Sinclair, T.D., *Polar Biol*., 23, 47, 2000. With permission.)

the Filchner-Ronne Ice Shelf), and the Scotia Ridge. It is part of the permanent ice zone (Hempel 1985). Ice-free polyna areas are a characteristic feature along the coast. These coastal polyna have relatively high phytoplankton stocks and productivity (El-Sayed and Taguchi 1981; von Bodungen et al. 1988). The northern Weddell Sea is ice-free for several months.

Siegel et al. (1992) investigated the community structure of the epipelagic zooplankton community in the zone of open water and under the sea ice in the northern Weddell Sea. They identified three hydrozoans, one scyphozoan, three siphonophores, one cephalopod, four pelagic mollusca, 11 pelagic polychaetes, 14 copepods, two decapod larvae, five euphausiids, 12 amphipods, one mysid, four ostracods, four chaetognaths, one salp, and nine fish larvae, a total of 85 species. This compares with 114 species found by Hopkins and Torres (1989) in the oceanic area of the Weddell Sea and 61 species recorded by Boysen-Ennen and Piatkowski (1988) in the eastern Weddell Sea, while Hopkins (1985) reported 106 species for the neretic area of the Croker Passage, Antarctic Peninsula. The standing stock estimated by Siegel et al. (1992) was only about a third to a half of that measured for areas such as the Antarctic Peninsula (Hopkins 1985) and the Ross Sea (Hopkins 1987).

Menshenina and Melnikov (1995) investigated the under-ice zooplankton in the under-ice surface (0-m layer) and at a depth of 5 m in the western rim of the Weddell Sea Gyre. Larva and postlarvae of *Euphausia superba* (Euphausidae), *Oithona similis, Stephos longipes, Paralabidocera antarctica, Pseudocyclopina belgicae, Microcalanus pigmaeus*, and *Ctenocalanus citer* (Copepoda) were the most abundant in both layers. Differences in the stage composition and abundance of these species between the two layers were found. *E. superba, S. longipes, P. antarctica*, and *P. belgicae* were most numerous near the under-ice surface and scarce at 5 m. *O. similis* density was greater at 5 m than at 0 m. *M. pigmaeus* and *C. citer* were comparatively greater in number at 5 m.

In the northern Weddell Sea, Siegel et al. (1992) found significant differences between the upper 60-m layer of the open sea and the upper 60 m layer of the closed pack ice. Abundance and biomass was highest in the surface layer of the open water while both variables decreased dramatically under the ice. Copepods dominated numerically in open water while salps dominated in biomass. *Euphausia superba* and *Thysanoessa macrura* were the dominant species in the upper water column of the closed pack-ice zone. Krill was the only species with increasing abundance in the sub-ice area and a dominance in biomass of more than 91% demonstrated the unique importance of this sub-ice habitat.

Studies by Hubold et al. (1985) and Boysen-Ennen and Pistkowski (1988) have identified three distinct communities of epipelagic zooplankton in the summer in the eastern Weddell Sea. These are southern shelf, northeastern shelf, and oceanic (Figure 4.5). The coastal convergence separating warm deep water from the cold shelf water can be considered the distributional border for the oceanic community. The oceanic taxa include gelatinous species such as: the hydromedusae, *Calycopsis borchgrevinki*; the scyphozoan, *Atolla wyvillei;* the siphonophore, *Vogata serrata;* the salp, *Salpa thompsoni;* the pteropod, *Clio pyramidata;* the copepods, *Rhincalanus gigas, Euchirella rostromagna, Gaidius* sp., *Scaphoclanus vervoorti, Racovitzanus antarcticus, Heterorhabdus* sp., *Haloptilus ocellatus*, and *H.oxycephalus*; the euphausiid, *Thysanoessa macrura*; the hyperiid amphipod, *Primno macropa;* and the chaetognath, *Sagitta marri* (Siegel 1982; Hubold et al. 1985; Boysen-Ennen and Piatkowski 1988). Within the oceanic community no single species predominates, but more species account for about two-thirds of the total abundance. Omnivorous and carnivorous species account for about two-thirds of the total abundance. The circumpolar species *M. gerlachei, Ctenocalanus* sp., *Oithona* spp., and *Oncaea* spp. dominate numerically. Biomass values are 3.5 and 19.7 mg dry weight m^{-3} (mean 9.4).

The divergence near Halley Bay divides the shelf zooplankton communities in the eastern Weddell Sea into southern and north–eastern communities. The north–eastern community consists of neritic and oceanic species. Total abundance is high, mainly copepodite stages of *C. acutus* and *C. propinquus.* Five species (the copepods, *C. acutus, C. propinquus, M. gerlachei,* and *Ctenocalanus* sp. and larvae of the euphausiid, *E. crystallorophias*) constitute 95% of total abundance. Filter feeding species predominate, and diversity is low. Euphausiids (*E. superba* and *E. crystallorophias*) are major constituents of the macrozooplankton (Siegel 1982; Boysen-Ennen and Piatkowski 1988). Biomass values of the northeastern community are between 1.1 and 29.0g dry wt^{-3} (mean 11.2).

In the southern shelf community, standing stock varied between 1.4 and 10.9 g dry wt m^{-3} (mean 4.0). It was therefore the community with the lowest biomass. Apart from copepods (18.2%), the zooplankton was mainly composed of shelf species, e.g., *Euphausia crystallorophias* (22.7%) and *Limacina helicina* (16.6%). *Salpa thompsoni* (21.8%) was also an important component; although, its occurrence was very patchy. Low in biomass (2.5%) but characteristic of this community was the gammaridean amphipod, *Eusrirus propeperdentatus. E. superba* was virtually absent from this community.

4.2.6.3 The Ross Sea

The bathymetry, water masses, and circulation patterns in the Ross Sea have been discussed in Chapter 1 and Chapter 2. A characteristic feature along the Ross Ice Shelf is the extensive Ross Sea Polyna (see Chapter 1, Section 6.3.5). This polyna is characterized by extremely high phytoplankton biomass and productivity (Biggs 1982). Zooplankton biomass in this polyna is low, and an inverse relationship between chlorophyll *a* and zooplankton biomass is a feature (Biggs et al. 1983).

Ross Sea zooplankton is dominated by copepods, followed by pteropods, euphausiids, ostracods, polychaetes, and radiolarians (Hopkins 1987; Forster 1989). Copepod biomass is higher near the Ross Ice Shelf than at offshore

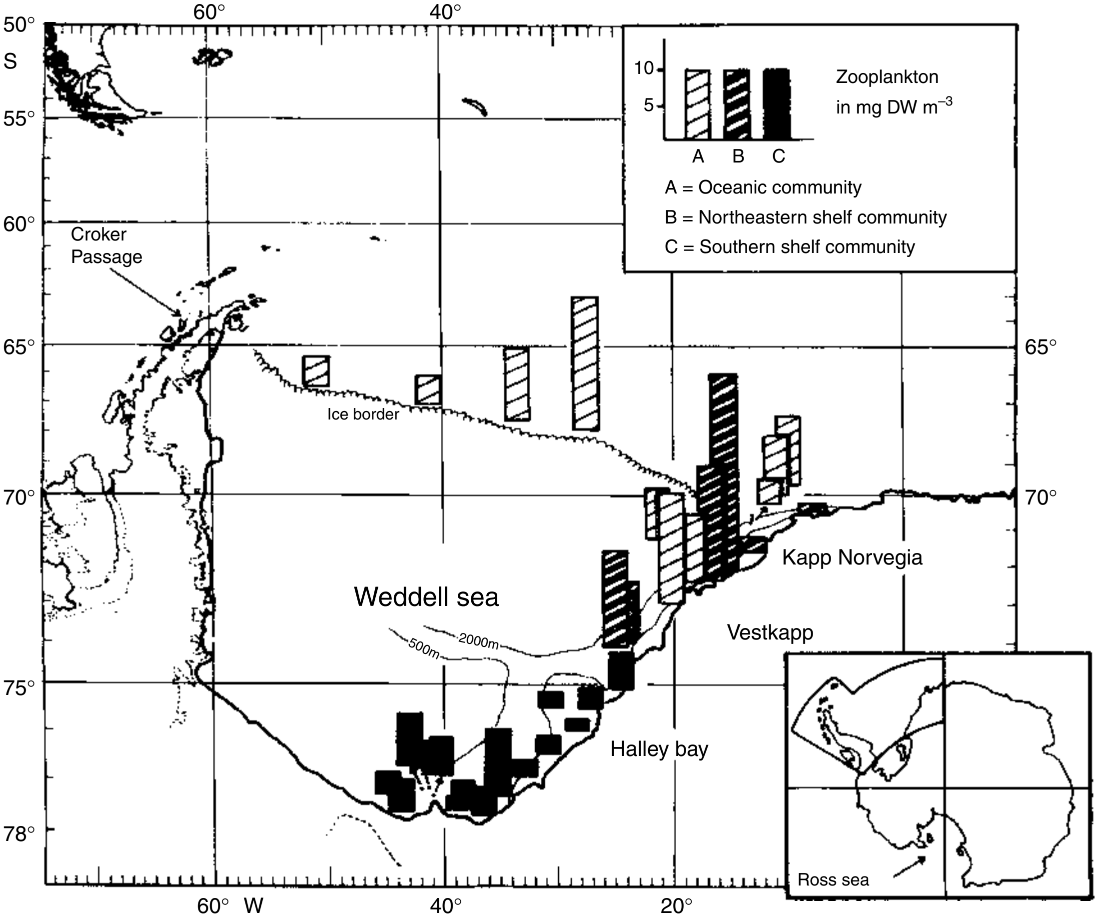


FIGURE 4.5 Zooplankton biomass in the Weddell Sea. (From Boysen-Ennem, E., Hagen, W., Hubold, G., Piatkowsk, U., *Mar. Biol.*, 111, 229, 1991. With permission.)

stations (Biggs 1982). *Oithona similis, Ctenocalanus* sp., *C. acutus, Metridia gerlachei*, and *Oncaea curvata* form the bulk of the Ross Sea copepods (Hopkins 1987). The outer Ross Sea (northern and northeastern part) has many faunal members of the Antarctic Circumpolar Water, with large numbers of deep, warm-water species (e.g., *Rhincalanus gigas, Metridia curticauda, Onchocalanus wolfendeni, Heterorhabdus austrinus, H.farrani, Haloptilus ocellatus*, and *Racovitzanus antarcticus*) which are found only seaward of the 500-m isobath. The inner portion in the southwest corner of the Ross Sea is not directly influenced by the Antarctic Circumplolar Water, which is reflected in the scarcity of *R. gigas* and the occurrence of neritic species such as *Aetideopsis antarctica* and *Paralabidocera antarctica* (Bradford 1971). The neritic nature of the southwest corner is also seen in the presence of numerous invertebrate larvae: polychaetes, barnacles, nemerteans, ascidians, decapod crustaceans, and echinospira larvae of a lamellibranch gastropod (Forster 1989).

Hopkins (1987) carried out a detailed study of the zooplankton in McMurdo Sound in February, after the break-up of the sea ice. The zooplankton was dominated by copepods and the pterood *Limacina helicina*. Among the copepods, the species *Calanoides acutus, Ctenocalanus citer, Euchaeta antarctica, Metridia gerlachei, Oithona similis,* and *Oncaea curvata* contributed all but a small fraction of the numbers and biomass. Other important taxa were *Euphausia crystallorophias* (furcilia), large radiolarians, and the polychaete *Pelagobia longicirrata*. Zooplankton biomass was estimated at 1.5–3.4 g dry wt m^{-2}.

The most important macrozooplankton–micronekton species were: (1) *Euphausia crystallorophias* (postlarval stages); (2) the amphipods *Orchomene plebs, Epimeriella macronyx,* and *Eusiris tridentatus*; (3) the mysid shrimp *Antarctomysis ohlinii*; (4) the chaetognaths *Sagitta gazellae* and *Eukronia hamata*; (5) the pteropod *Clione antarctica*; (6) the siphonophores *Diphyes arctica* and *Pyrostephos vanhoeffeni*; and (7) larval and postlarval stages of the midwater nototheniid fish, *Pleurogramma antarcticum*. The biomasses of the postlarval *E. crystallorophias* and *P. antarcticum* were estimated, respectively, at 0.21 (0.16–0.33) and 0.82 (0.18–3.68) g dry wt m^{-2} of sea surface.

Hopkins (1987) has compared the zooplankton communities of McMurdo Sound and Croker Passage, Antarctic

Peninsula (Hopkins 1985a, 1985b). While the two areas have many species in common, the biomass composition was different. Croker Passage is a Southern Ocean high-biomass area dominated by krill, *Euphausia superba*, with a zooplankton–euphausiid fish combined biomass of 58.0 g dry wt m^{-2} (Hopkins 1985a). McMurdo Sound has a much lower standing stock with a total zooplankton-euphausiid-fish biomass of only 3.5 g dry wt m^{-2} (Hopkins 1987). Furthermore, the ratio of these biomass components differ radically, with the zooplankton-euphausiid-fish ratios of Croker Passage and McMurdo Sound being 1.0:19.0:0.3 and 1.0:0.1:0.3, respectively. These ratios reflect the abundance and overwhelming dominance of krill in the vicinity of the Antarctic Peninsula (Marr 1962; Amos 1984) and the lesser importance of the ice krill (*E. crystallorophias*) in McMurdo Sound. This points to the reduction of the significance of the niche occupied by large-sized particle grazers in McMurdo Sound. This is supported by the fact that salps, which were a major biomass component in Croker Passage, were absent from McMurdo Sound. Fish biomass was comparable in the two systems, but while *Pleurogramma antarcticum* and the myctophid *Electrona antarctica* shared dominance in Croker Passage, myctophids were absent in McMurdo Sound. DeWitt (1970) attributed the absence of myctophids and other characteristic mid-water fishes to the cold temperature (less than −1.5°C) in the deeper waters over the shelf.

Until recently, it was believed that krill (*E. superba*) was absent for most of the Ross Sea. However, as detailed in the next Chapter, this has been shown to be erroneous, and, in fact, substantial krill populations do occur. The zooplankton assemblage in the north–eastern Ross Sea is similar to the oceanic community of the northern Weddell Sea, whereas the zooplankton assemblage of the inner Ross Sea corresponds to the shelf communities of the south–western Weddell Sea (Boysen-Ennen and Piatkowski 1988).

4.2.6.4 The Prydz Bay Region

Zooplankton communities in the Prydz Bay region have been investigated by Yamada and Kawamura (1986), Hosie and Stolp (1989), Hosie (1991,1994, 1997), Hosie and Cochram (1994), Hosie et al. (1997), and Chiba et al. (2001). These investigators all identified a strong latitudinal zonation of the zooplankton communities. These communities are: (1) the neritic community; (2) the main oceanic community; (3) the northern oceanic community; and (4) a *Euphausia superba* community (Figure 4.6). Chiba et al. (2001) also identified a northern subantarctic community north of the Polar Front.

The neritic, or shelf community, was characterized by the euphausiid *Euphausia crystallorophias*. When present, gammarids and larvae of *Pagetopsis macropterus* formed a close association with the euphausiid. This assemblage

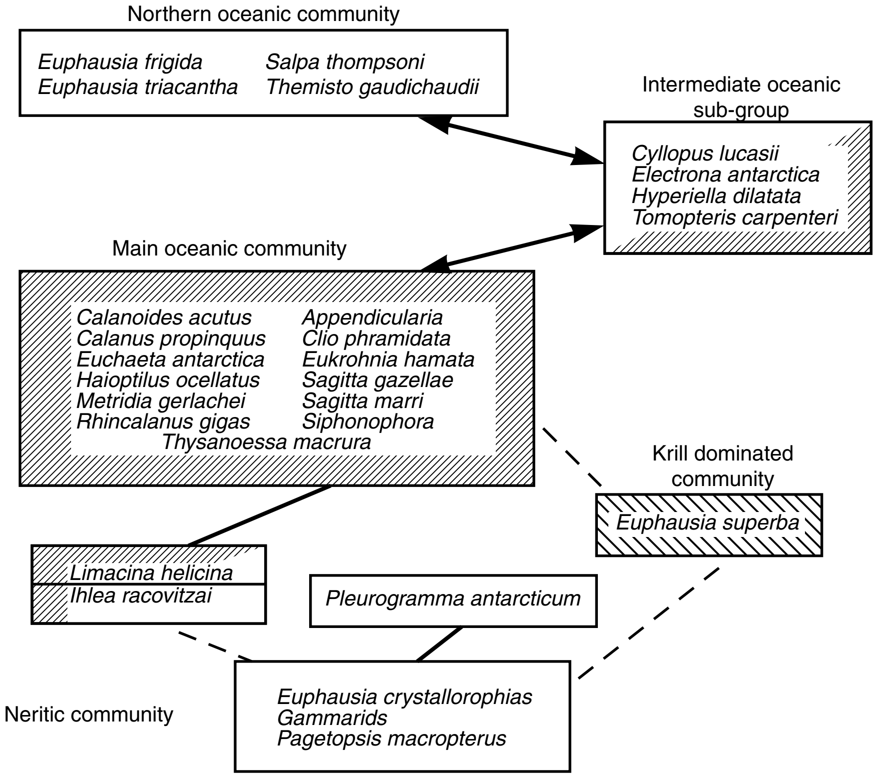


FIGURE 4.6 Zooplankton communities defined for the Prydz Bay region, based on macroscale surveys. (From Hosie, G.W., Cochram, T.G., *Mar. Ecol. Prog. Ser.*, 106, 35, 1994. With permission.)

dominated the inshore region in Prydz Bay south of 57°30′S. The pelagic fish *Pleurogramma antarcticum*, another neretic species, had only a partial association with the other three species. The salp *Ihlea racovitzai* and the pteropod *Limacina helicina* were two species that were not distinctly associated with either the neretic or oceanic communities. Both species were associated primarily with the main oceanic community but were also abundant indicators of the neretic community in 1981.

The main oceanic community included all the abundant copepod species, particularly the herbivores *Calanus propinquus, Calanoides acutus,* and *Rhincalanus gigas,* as well as the associated carnivores, such as chaetognaths (*Euchronia hamata, Sagitta gazellae,* and *S. marri*). Included in this assemblage are the euphausiid *Thysanoessa macrura,* the pteropod *Clio pyramidata,* and appendicularians and siphonophores. All of these species have wide circumpolar distributions. While copepodites of the dominant copepod species have been found to be widely distributed over the shelf region, the copepods are generally more abundant and dominate the region between the continental shelf edge and 62–63°S. The northern limit approximates the southern boundary of the Antarctic Circumpolar Current.

Difference in species abundances is the main feature distinguishing the northern oceanic community, rather than differences in species composition. This northern assemblage comprises four main species: the euphausiids *Euphausia frigida* and *E. tricantha,* the hyperiid *Thermisto gaudichaudii*, and the salp *Salpa thompsoni*. *Electronia antarctica, Cyllopus lucasii, Hyperiella dilatata*, and *Tomopteris carpenteri* form an intermediate oceanic subgroup that, at different times, is associated with either the northern assemblage or the main oceanic group.

A krill-dominated community can also be distinguished. While *Euphausia superba* may form a distinct association with both the neretic and main oceanic communities, it often is an important abundance indicator of geographic areas distinct from the main oceanic and neretic communities. Krill are primarily localized and dominant near the continental shelf edge in a transition zone between the neretic and oceanic assemblages. In such areas, the non-krill zooplankton abundance is consistently lower.

Chiba et al. (2001) identified a northern subantarctic community north of the Polar Front. Indicator species of this community were the copepod *Eucalanus longiceps* and the pteropod *Limacina retroversa.* These are both typical subantarctic species.

4.2.6.5 The Polar Frontal Zone

The Southern Ocean Polar Frontal Zone (PFZ) is a region of high physical and biological variability. In the west Indian Ocean, the two major fronts bounding the PFZ, the Subantarctic Front (SAF) to the north and the Antarctic Polar Front (APF) to the south, exhibit meanders (Froneman et al. 1997) and eddies. These features facilitate the transfer of plankton across the main frontal systems. As a consequence, the zooplankton species composition of the PFZ is highly variable with communities comprising species from a variety of origins, including Subtropical species (e.g., *Ctenocalanus vanus, Pleuromamma abdominalis*), Subantarctic species (e.g., *Metridia lucens, Scolecithricella minor, Calanus simillimus*), and Antarctic species (e.g., *Oithona frigida, Rhincalanus gigas, Limacina* spp., *Clausocalanus laticeps, C. citer*) (Fronemann et al. 1997; Pakhomov and Froneman 1999).

The mesozooplankton community is dominated both numerically and in biomass by copepods of the genera *Oithona, Ctenocalanus, Calanus,* and *Clausocalanus* (Pakhomov et al. 1997; Bernard and Bernard 2003; Pakhomov and Froneman 2004). Estimates of grazing within the PFZ rage from less than 1 to approximately 50% of the available chlorophyll in the water column (Bernard and Froneman 2003; Froneman et al. 2003). Bernard and Froneman (2003) have emphasized the importance of grazing by small copepods, particularly the calanoid copepods, *Ctenocalanus* spp., and the cyclopoid copepod, *Oithona similis*. They found that these copepods were responsible for between 15 and 92% of the total grazing impact. Other groups, such as pteropods, may at times contribute up to 10% of total numbers (Bernard and Froneman 2002) and up to 35% of the standing stock (Pakohomov and Froneman 2004). Pakohomov and Froneman (2004) showed that in the Spring Ice Edge Zone in the Atlantic sector pteropods were responsible for up to 53% of the total grazing impact during the austral summer.

In the west Indian sector of the PFZ Bernard and Froneman (2005) found that mesozooplankton abundances ranged from 2,478 individuals m^{-2} to 163,84 individuals m^{-2} and biomass between 6.70 and 23.40 mg dry wt m^{-2}. The mesozooplanktn community was dominated almost entirely by copepods, which contributed between 35 and 79% of the total numbers. The pteropod, *Lamacina retroversa*, contributed up to 35% of the total numbers. Two distinct mesozooplankton communities separated by an intense frontal feature were identified, namely, the Antarctic and Subantarctic Zone groups. Ingestion rates of the four numerically dominant copepod species (*Calanus simillinus, Clausocalanus* spp., *Ctenocalanus* spp., and *Oithona similus*) and the pteropod *L. retroversa*, ranged from 0.156 to 2.958 mg (pigm) m^{-2}, or between 1 and 29% of the available chlorophyll *a* per day. The four copepods contributed approximately 36% of the total daily grazing impact, while the pteropod contributed to a mean of 64%. In general, the highest daily grazing impact was exhibited in the Antarctic Zone group (mean 12% of the phytoplankton standing stock per day).

4.2.7 ABIOTIC AND BIOTIC FACTORS AFFECTING DISTRIBUTION PATTERNS

A range of abiotic and biotic factors influence the distribution pattern of Southern Ocean zooplankton.

4.2.7.1 Abiotic Factors

The distribution and abundance of the zooplankton is influenced by variations in the distribution and intensity of ocean currents, variability in the position of the frontal systems, and the nature of the different water masses. Of particular relevance to the macrozooplankton is the variation that occurs in the location of the Polar Frontal Zone. In the Weddell Sea region, this feature may move hundreds of kilometres north or south over a period of weeks (Whitworth 1980), resulting in a shift of populations associated with frontal systems. Smaller features such as gyres, both permanent and temporary, meanders, and eddies (Hoffmann et al. 1996) can redistribute populations of zooplankton in a particular location over shorter time periods.

Some changes in macrozooplankton distribution and abundance are not caused by population changes but by circulation patterns acting directly on individuals in the population. For example, Zmijewska and Yen (1993) suggest that seasonal pulses of the copepod *Rhincalanus gigas* in shelf waters west of the Antarctic Peninsula are a function of the interaction of ontogenetic migration and seasonal changes in circulation patterns. On a larger scale, global meterological conditions, such as the Southern Ocean Oscillation, may also affect oceanic conditions and result in changes in the patterns of macrozooplankton populations. Various authors have suggested that variations in atmospheric circulation can lead to changes in the Weddell Sea Confluence and that this could explain the paucity of krill around South Georgia in certain years (e.g., Sahrhage 1988a, 1988b). Years of low krill abundance and coincident poor breeding success in the land-based predators (birds and seals) often follow strong ENSO events (Croxall et al. 1988a).

In contrast, years when salps are abundant appear to follow strong ENSO events (Hofmann and Huntley 1991), resulting in an alternating dominance between krill and salps. Coincident with abundant salp years is a change in the distribution of other macrozooplankton taxa (Mujica and Asencio 1985), resulting in a change in community composition. This shift in community composition impacts on the apex predators in the system, and it also affects other aspects of trophic dynamics, including the dominant pathways for carbon transfer through the food web and carbon flux to the benthos.

4.2.7.2 Biotic Factors

One of the major biotic factors affecting zooplankton distribution is the abundance and composition of the phytoplankton upon which they feed. In Chapter 5, the positive association of krill with high phytoplankton concentrations will be discussed. In addition to the potential influence of phytoplankton biomass on zooplankton distribution patterns, phytoplankton community composition may also affect these patterns. Differences in size and nutritional value of the various species groups, such as diatoms and pyremnesiophytes, may impact distribution directly for motile organisms that search out food patches and indirectly through effects on population dynamics and recruitment success for non-motile species. Many species may alter their vertical distributions in response to phytoplankton community composition. Schnack et al. (1985) sampled the top 100 m of the Bransfield Strait in an area dominated by *Phaeocystis antartica* and found low copepod biomass. On the other hand, in an adjacent area dominated by diatoms, a relatively high copepod biomass was found.

4.3 LIFE HISTORY AND GROWTH

4.3.1 COPEPODS

Fertilized copepod eggs hatch into the free-swimming nauplius. Successive moults of the nauplius add more appendages. There are commonly six naupliar instars, after which the body form changes to one similar to the adult form, the copepodite. Usually, there are five or more moults giving rise to copepodites I to VI. The major events in the life cycles of Antarctic copepod species have been known since the work of Ottestad (1932), Ommaney (1936), and Mackintosh (1937), and are summarized by Vervoort (1957) and Andrews (1966). More recent studies include those of Voronina (1978), Atkinson and Peck (1988), Marin (1988a, 1988b), Atkinson (1989), and Huntley and Escritor (1991).

The life cycles of Antarctic copepods can be summarized as follows. These copepods are seasonal migrants that overwinter at depth as late copepodites. Spawning is associated with their ascent in the spring, and the new generation grows within the surface water layers in summer. The later copepodites progressively and gradually descend later in the year until the overwintering depth is reached. Voronina (1970, 1978) noticed that the migration and spawning cycle of the dominant species was asynchronous and followed the following order: *Calanoides acutus, Calanus proquinuus*, and *Rhincalanus gigas*. She postulated that this was a mechanism for reducing interspecific competition for food during the summer growing season. However, Marin (1988a, 1988b) has challenged this conclusion.

The life cycles of *Calanoides acutus, Calanus simillimus,* and *Rhincalanus gigas* have been investigated by Atkinson (1991) in the Scotia Sea. The predominantly Antarctic species *C. acutus* mates below 250 m in middle to late winter, and the summer generation develops rapidly to either Calyptopus CIV or CV (Figure 4.7). The life span typically seems to be one year, but some of the CV's that fail to moult and spawn in the winter survive to the second summer. *C. simillimus* is a Subantarctic species that mates in the top 250 m, mainly in the spring. The rapid development of the summer generation may allow a second mating period and a smaller second generation to appear in late summer. *C. simillimus* remains in the surface layers for a longer period than *C. acutus* and *R. gigas,* and its depth distribution is bimodal throughout the winter. *R. gigas* is most abundant in sub-Antarctic waters to the north of the Polar Front. It mates within the top 750 m, later in the spring than the other two species, and its development seems less synchronized, with

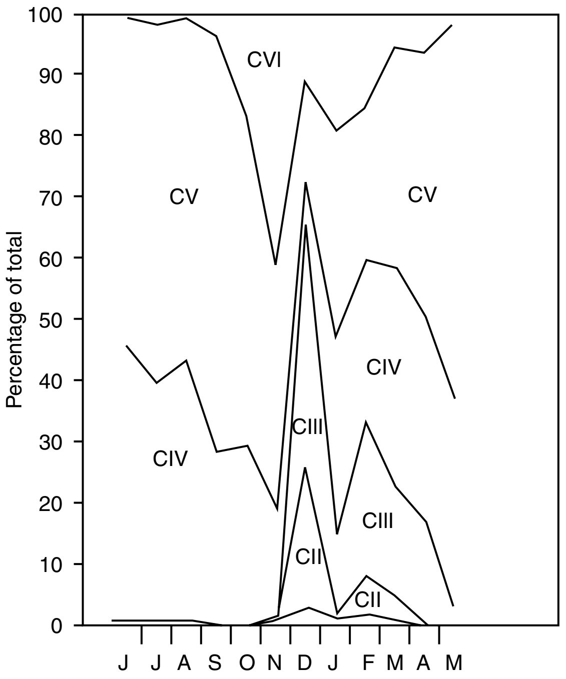


FIGURE 4.7 Seasonal changes in the relative abundance of the copepodite (development stages I–VI) composition of the copepod *Calanoides acutus* in the top 100 m of the water column. (From Everson, I., *Antarctic Ecology*, Vol. 2, Laws, R.M., Ed., 463, 1984; based on data from Andrews, K.J.H., The distribution and lifehistory of *Calanoides acutus* (Giesbrecht), *Discovery Reports*, 34, 117–162, 1966. With permission.)

egg laying and the growth season being more protracted. Stages Calyptopus CIII and CIV are reached in the first autumn, and further development resumes very early in the following spring. A striking feature is the rapid growth attainable by these cold water species.

The amphipod *Parathemisto gaudichaudii* (Figure 4.8) exhibits a peak of growth during the summer period (Kane 1966), but during the winter when food supplies are low, there is practically no growth at all. Mating animals in the early spring release large numbers of juvenile stages that feed on the early life history stages of the herbivorous zooplankters when they appear at the commencement of the spring phytoplankton growth. Kane (1966) considered that, in general, *P. gaudichaudii* has a life cycle span of one year but that a very small number of individuals survive to breed again in a second year.

4.3.2 SALPS

The life cycle of the salps is complex, consisting of alternating sexual (production of embryos) and asexual (budding) generations (Figure 4.9). In the solitary form, chains of the aggregate form are produced by budding from the stolon. Individuals in a recently released chain are only 4.5 mm long. These hermaphroditic individuals continue to grow. Once they are about 25–30 mm long, each individual releases a fertilized embryo (oozooid) 3–4 mm in total length and then functions as a male. Budding, release of aggregates, and swarm production are zero in winter, and the aggregate form is at minimum abundance. In winter solitary individuals are also generally small, but some growth may occur. In the spring there is an increase in the relative proportion of aggregate forms, with a maximum in the summer and autumn. The aggregate form dominates when swarms are found. Sexual reproduction occurs at the end of a salp bloom.

4.3.3 ONTOGENETIC MIGRATION AND LIFE SPAN

Antarctic zooplankters exhibit a pronounced seasonal vertical migration pattern with biomass maxima concentrated in the surface layers in the summer but in deeper layers in the winter. These so-called ontogenetic migrations are well documented. The ontogenetic migrations of the major copepod species have a pronounced influence on the standing stocks in the surface layers (Mackintosh 1937; Voronina 1972; Atkinson and Peck 1988). Between 4% and 33% of the total biomass is concentrated in the winter in the top 250 m of the water column (Hopkins 1971), while below 200 m 35–55% of the biomass is found in the 500–1000-m layer. For the chaetognaths, *Sagitta gazella* (David 1955, 1958) and *Euchronia hamata* (Mackintosh 1937; David 1958), and the salp, *Salpa thompsoni,* a different vertical distribution pattern is found in the summer and winter.

As recorded elsewhere (Longhurst 1976) Southern Ocean zooplankton species maintain their general oceanographic position by these directed seasonal vertical migration related to differential water mass transport with increasing depth. They concentrate near the surface in the Antarctic summer where the general flow is towards the north but descend into deep water in the winter, where the movement is to the south. They are thus maintained within the limits of their normal species distribution, as shown in Figure 4.10. The seasonal vertical movements of these species to depths between 500 and 1000 m result in horizontal displacements of many hundreds of meters (Mackintosh 1937). Examples of species which spend the summer months in the surface waters and descend to deep water in the winter are:

- Copepoda: *Rhincalanus gigas* (Ommaney 1936), *Calanoides acutus* (Andrews 1966)*, Calanus propinquus* (Voronina 1972)
- Amphipoda: *Parathemisto gaudichaudii* (Kane 1966)
- Chaetognatha: *Eukrohonia hamata* (David 1958, 1965), *Sagitta gazellae* (David 1958)*, Sagitta marrii* (Mackintosh 1937).

The three copepods show different intensities of ontogenetic migration (Table 4.1). *Calanoides acutus* migrates to the deepest depths and ascends first from depth in the spring. Both *Calanus propinquus* and *Rhincalanus gigas* exhibit a partial ontogenetic migration, either dispersing throughout

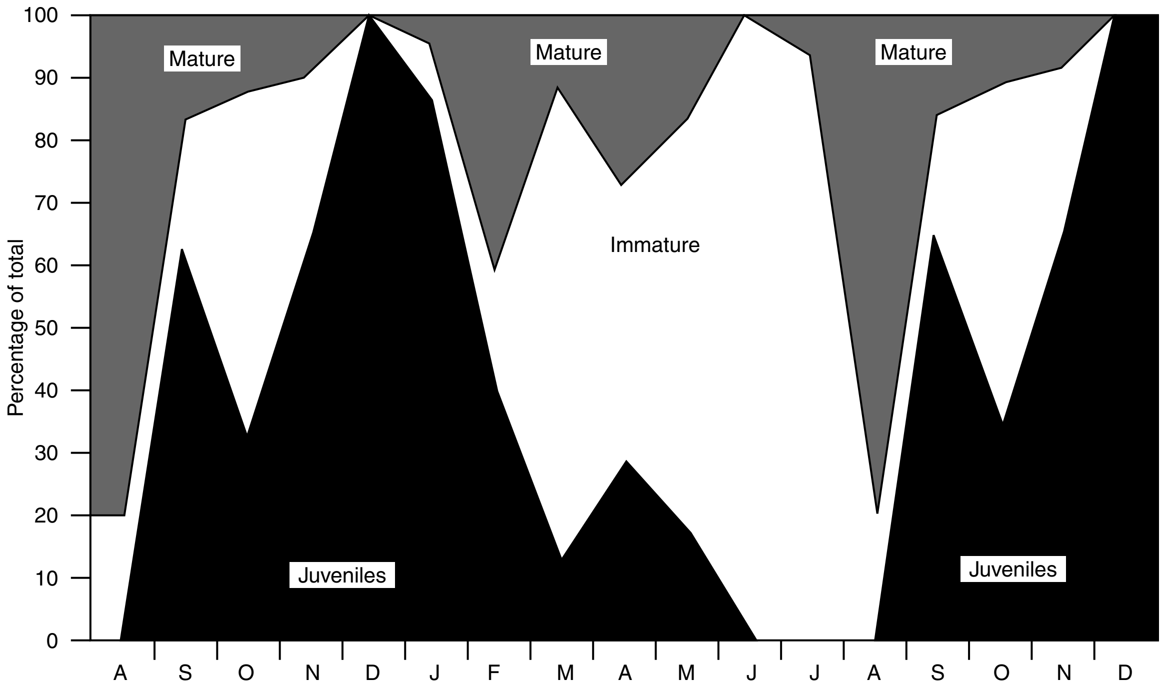


FIGURE 4.8 *Parathemisto gaudichaudi*: percentage frequency of juvenile, immature, and mature specimens in net hauls. (From Everson, I., *Antarctic Ecology*, Vol. 2, Laws, R.M., Ed., 463, 1984; based on data from Kane, J.E., *Discovery Reports*, 34, 163, 1966. With permission.)

the midwater or inhabiting an intermediate depth. They ascend and descend sequentially after *C. acutus*. No ontogenetic migration is found in the other common copepod, *Metridia gerlachei*.

Salps show a distinct and deep ontogenetic migration. Solitary forms dominate the population during the winter in deeper layers (Foxton 1966). Data suggests that it is only the solitary form and not the total population that undertakes the ontogenetic migration. This occurs after sexual reproduction when the solitary form migrates to depths from 250 to 1,500 m in the autumn (Foxton 1966), leaving the aggregate form in the surface waters.

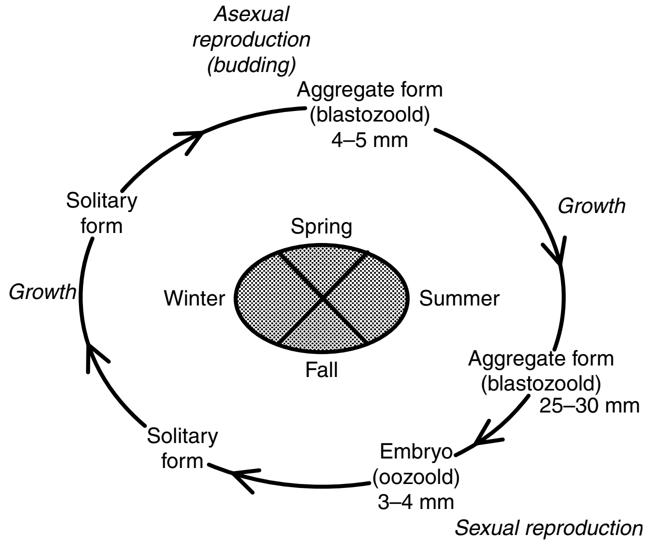


FIGURE 4.9 Conceptual life cycle of salps, with alternating generations of solitary and aggregate forms. Based on seasonal data from Foxton (1966). (From Quetin, L.B., Ross, R.M., *Ant. Res. Ser.*, 357, 1996; based on data in Kane, J.E., *Discovery Reports*, 34, 163, 1966. With permission.)

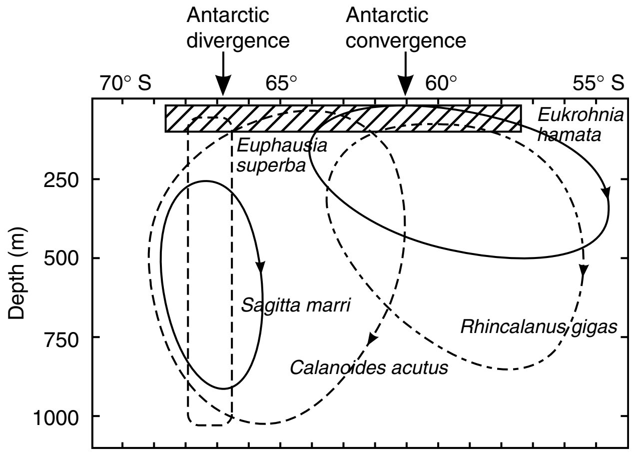


FIGURE 4.10 Seasonal vertical migration patterns of the zooplankton in Antarctic waters based on data in Mackintosh (1937) and Marr (1962). Summer feeding zone is shaded. (From Nemoto, T., Harrison, G., *Analysis of Marine Ecosystems*, Longhurst, A.R., Ed., 95, 1981. With permission.)

4.4 VERTICAL MIGRATION

Many zooplankton species exhibit a diel pattern of migration and feeding. The benefits of diel periodicity might be avoidance of predation by visual predators, advantages to energetics and growth, avoidance of light damage, and horizontal mixing of populations (Hardy and Gunther 1936). The link between upward migration and night-time feeding is obvious where plankton ascend from food-poor strata to feed at night in rich surface waters. Additional modifying factors include time of the year, food availability, and the physical structure of the water column. Atkinson and Sinclair (2000) investigated the vertical distributions and feeding cycles of four copepod species, *Calanus simillimus* CV, *Calanus propinquus* CV, and *Rhincalanus gigas* CIII, CV, and CVI, as well as those of dominant competitors and predators, at an oceanic site near South Georgia.

Planktonic predators, with the exception of the diel migrant *Thermisto gaudchaudii*, resided deeper than the herbivores. During the day and around midnight, when feeding rates were low, species and stages reached their maximum vertical separation. At these times, new generation copepodites of the four species lived progressively deeper, and the overwintering generation (i.e., *R. gigas* Stages CIV, CV, and CVI) were progressively shallower. During the afternoon or evening (depending on the species), all stages older than CII, as well as *Euphausia frigida* and *T. gaudchaudii*, migrated upwards to amass in the surface mixed

TABLE 4.1
Life Cycle Characteristics of Four Mesozooplanktonic Copepods: Life Span, Ontogenetic Migration, Timing and Duration of Spawning, and Winter Strategy and Depth

Species	Life Span	Ontogenetic Migration	Spawning	Copepodite 1 Appearance	Winter
Calanoides acutus	1 year	Strong	Early spring	Late spring	Diapause as late stage copepodites (CIV–CVI) >500 m^a
Calanus propinquus	1^a or 2^b	Partial	Late spring to early summer, extended	Summer	Active, no diapause disperse <500 m^b
Rhincalanus gigas	1 or 2^a	Partial	Fall ^{a,d} Spring and fall^e, Dec^c	Fall	Active, no diapause mid-depth
Metridia	Unknown	No^f	Spring/summer extended	Summer/fall	Active; surface

Information from Schnack-Schiel and Hagen (1994) unless otherwise indicated. (a) Marin (1988), (b) Dritz et al. (1993), (c) Zmijewska (1987), (d) Marin and Schnack-Schiel (1993), (e) Atkinson (1991), (f) Atkinson and Peck (1988), (g) Huntly and Escritor (1992), (h) Zmijewska and Yen (1993), (i) Lopez et al. (1993).

[a] In shallow water *C. acutus* winters near the surface.

Source: Schnack-Schiel, S.B. Hagen, W., *J. Plankton Res.*, 65, 1994. With permission.

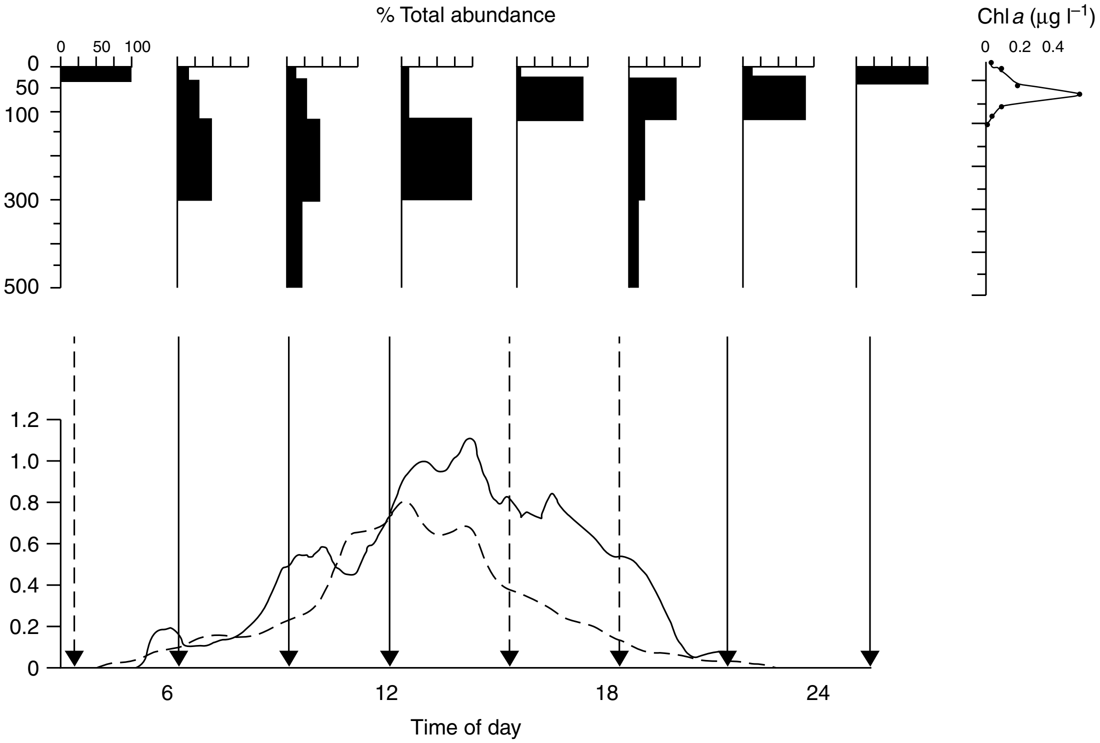


FIGURE 4.11 Vertical distribution (*Salpa thompsoni*) (*upper*) and solar radiation (*lower*) as a function of time of day. "Salp abundance" indicates its relative abundance in each sampling period. The *continuous* and *broken line*, the *solar radiation curves* indicate data taken on December 23 and December 24, 1994, respectively. Total chlorophyll *a* concentration is indicated on the *right* side of vertical distribution. (From Nishikawa, J., Tseuda, A., *Polar Biol.*, 301, 2001. With permission.)

layer. Intraspecific competition can be reduced by vertical separation of copepodite stages. The commonest pattern, one seen in the four species in Atkinson and Sinclair's (1992) study, is for the older stages to live deeper and migrate further than early copepodites. A pattern of later stages of Antarctic copepods living progressively deeper is well documented (Voronina 1972; Atkinson 1991).

Feeding was restricted to darkness; although, *R. gigas* commenced feeding several hours before dusk. The results of gut pigment analyses suggested that: (1) feeding could occur during sinking, as well as during upward migrations; (2) upwards migrations were not always associated with feeding increases; and (3) individuals appeared to descend after filling their guts.

Nishikawa and Tsuda (2001) investigated diel vertical migration in the tunicate, *Salpa thompsoni*. *S. thompsoni* began migration to the subsurface at midday when the solar radiation was largest, stayed in the phytoplankton-rich and rather bright layer (30–120 m) for a relatively long time, and then moved up to the surface during complete darkness (Figure 4.11). This diel vertical migration pattern would have an advantage in increasing the feeding opportunities for the salps. Although the longer stay in the bright layer may also increase the risk of predation by potential visual predators, the overlap of the depth between salps and visual predators was considered to be low during the stay in the shallow layer. The unique diel vertical migration of *S. thompsoni* may be an adaptation to the oligotrophic environment of the oceanic region of the Southern Ocean and one of the characteristics that enable them to maintain their large population stocks.

4.5 SWARMING

The trophic importance of zooplankton in the Southern Ocean is enhanced by their habit of forming dense swarms. Swarming behaviour is particularly pronounced in the euphausiids where *Euphausia superba, E. crystallorophias*, and *Thysanoessa macrura* the principal swarming species in Antarctic waters and *E. tricantha* in the sub-Antarctic. Swarming in euphausiids will be discussed in Chapter 5.

Dense swarms of calanoid copepods are common, especially in Subantarctic waters. Kawamura (1974) has described such swarms of *Calanus tonsus* from waters where Sei and Right whales feed on them. Such swarms, or patches, maintain their shape close beneath the surface even in rough conditions, and they may be some hundreds of meters across. Densities of *C. tonsus* in such swarms range from 300 to 3,860 individuals m^{-3} with their biomass reaching 34 g m^{-3}. Other zooplankters that frequently occur in large swarms are the salp, *Salpa thompsoni,* and the amphipod, *Parathemisto gaudichaudii*.

In the summers of 1983–1984 *Salpa thompsoni* was a dominant member of the zooplankton community in waters near the Antarctic Peninsula, with biomasses in mid-March ranging from 49 to 671 mg C m^{-2} and 9.6–136 mg N m^{-2} (Huntley et al. 1989). Direct measurements suggested that fecal production by 23 mm blastozoids was equivalent to 10.2% body C day^{-1} and 6.6% body N day^{-1}. Grazing by *S. thompsoni* removed the bulk of the daily primary production in March but less than 1% in January at the peak of the phytoplankton bloom. It is clear that dense swarms of zooplankton can have a profound effect on the structure of plankton communities.

4.6 FEEDING

Traditionally, Antarctic krill, which often occur in large swarms of high biomass, have been identified as the major grazers on phytoplankton in the Southern Ocean. However, research on Antarctic zooplankton have shown that they are not the only important and dominant zooplankters in this ecosystem. Sometimes, mesozooplankton, such as copepods, can form the bulk of the phytoplankton biomass, exceeding that of krill (Hosie et al. 1997; Swadling et al. 1997). It has been shown that they can consume at least three times, perhaps as much as eight times, the primary production that is eaten by krill (Conover and Huntley 1991).

The interaction between zooplankton and phytoplankton in the Southern Ocean has been the subject of much extensive research. Questions addressed include: (1) the diets and quantities consumed by various species; (2) the sizes of the phytoplankton species consumed by individual species; (3) the quantities consumed by individual species; (4) the biomass of phytoplankton consumed by zooplankton communities; (5) seasonal variation in phytoplankton consumption; (6) the impact of zooplankton consumption on the phytoplankton community composition; (7) overwintering strategies of zooplankton when phytoplankton production is low, including lipid storage; (8) the extent to which some zooplankton feed on sea ice microalgae; (9) the extent to which some herbivorous zooplankton are also carnivorous; and (10) the impact of phytoplankton consumption on the sedimentation of organic carbon.

In recent years, new information suggests that microzooplankton also play an important role as grazers in Southern Ocean food webs, especially in controlling nano- and picophytoplankton, which are typically smaller than the phytoplankton grazed efficiently by larger zoolankton (Hewes et al. 1985; Garrison et al. 1993; Pakhomov and Perissinotto 1996; Fronemann et al. 1997).

4.6.1 HERBIVOROUS ZOOPLANKTON

A number of recent publications have addressed the range of questions listed above (e.g., Pakhomov et al. 1994; Ward et al. 1995; Atkinson et al. 1996; Swadling et al. 1997; Pakhomov and Froneman 1999).

Ward et al. (1995) investigated the grazing impact of the summer zooplankton community off SouthGeorgia. The zooplankton community comprised the copepods *Calanoides acutus, Rhincalanus gigas, Calanus simillimus, Calanus propinquus, Ctenocalanus* sp., *Oithona* spp., *Onacea* spp., *Metridia* spp., *Metridia curticauda, Euchaete* spp., and *Pleuromamma robusta,* the amphipod *Thermisto gaudichaudii*, two euphausiids, ostracods, and chaetognaths. The grazing rate of the epipelagic community (copepods and small euphusiids) was estimated to remove 3–4% of the microbial standing stock day^{-1} and a conservative 25% and 56% of the daily primary production at the oceanic and shelf stations, respectively (Table 4.2). Thus, following the spring, phytoplankton bloom zooplankton grazing may account for a considerable proportion of the primary production.

Studies of zooplankton grazing impact carried out in the Southern Ocean suggest that grazers are not food limited and that losses due to vertical flux and phytoplankton respiration or excretion generally exceed those due to zooplankton grazing (Schnack et al. 1985; Hopkins 1987; Huntley et al. 1991). Schnack et al. (1985) found that during the early part of the bloom, copepod grazing accounted for less than 1% of the primary production in the Bransfield Strait and the waters adjourning the ice edge near Joinville Island, rising to 55% in the Drake Pasage where the copepod biomass was higher and the phytoplankton production lower. Hopkins's (1987) sampling in McMurdo Sound during a bloom estimated total zooplankton consumption to be on the order of 2% of phytoplankton standing stock day^{-1}, while Huntley et al. (1991), studying the declining phase of the spring bloom in the Gerlache and Bransfield Straits, estimated that the grazing could account for 1–5% of production in January through March. The ingestion rate in Ward et al.'s 1995) study, expressed as a percentage of zooplankton body carbon, was 9–11%. Schnack (1985a) found the same percentage at two of their stations; although, it was higher (32%) at another station. Pakhomov et al. (1997), in the vicinity of South Georgia, found that grazing rate varied

TABLE 4.2
Grazing Impact of Major Zooplankton Groups Near South Georgia in February–March, 1994

Grazing Rate of Zooplankton Groups (mg(pigm) m^{-2} day^{-1})	
Large copepods	0.710–1.562
Small copepods	0.019–0.450
Cyclopoid copepods	<0.001–0.314
Euphausiids	0.185–0.730
Pteropods	0.072–3.997
Total ingestion rate	
Mg(pigm) m^{-2} day^{-1}	1.234–5.985
% of chl *a* biomass	0.5–3.411
Mg C m^{-2} day^{-1}	61.7–170.5
% of primary production	5.0–102.3

Source: Pakhomov, E.A., et al., *Polar Biol.*, 18, 180–192, 1997, see also page 187. With permission.

widely from less than 1–8% (mean 3.5%) of phytoplankton standing crop and from 5% to 102% (mean 36%) of primary production.

Swadling et al. (1997) investigated the grazing of phytoplankton by copepods at a coastal site near Davis Station. Copepods accounted for at least 65% of the zooplankton biomass before the sea ice breakout, whereas larval polychaetes and ctenophores dominated after ice breakout. *Onacea curvata* was the numerically dominant species throughout the study. The highest grazing rate (8.7 mg C m^{-3} day^{-1}) was recorded on December 21 when *O. curvata* accounted for more than 50% of the total ingested. Grazing had decreased markedly by December 28 (0.9 mg C m^{-3} day^{-1}); again *O. curvata* accounted for more than 50% of the total ingested. Copepod grazing increased again after the ice breakout. The main species responsible for grazing were *O. curvata, Oithona similis, Calanoides acutus,* and the unidentified copepod, nauplei (Figure 4.12). It was estimated that copepods removed between 1% and 5% of primary productivity.

It has often been stated that there is a relationship between the size of an animal and the size of its food; large animals feeding on large particles, and small animals feeding on small particles (e.g., Freyer 1957; Parsons et al. 1967). For marine environments, Gamble (1978) and Harris (1982) have described rather similar particle-size feeding by copepods differing considerably in size (ca. 10–20 times, in terms of body weight). In feeding experiments carried out by Schnack (1985b), the differences in body weight between ecologically similar copepod species ranged between 89 and 505 μg C $individual^{-1}$ in November through December and between 59 and 392 μg C $individual^{-1}$ in February. The ratios of these differences (5.7 and 6.6) are between values given by Gamble (1978) and Harris (1982). From Figure 4.13, it can be seen that in spite of the considerable size differences between the zooplankton species (e.g., a mean dry weight of 185 μg for copepodites and 1102 μg for *Rhincalanus gigas*) the relative proportions of the different phytoplankton species consumed was approximately the same as the ambient food supply. In the enriched food supply experiment (Figure 4.13b) the proportion of the diatom *Corethron criophilum* was 67% compared to only 28% in the ambient food supply. All zooplankton species showed a positive selectivity index for *C. criophilum*, its proportion in the diets of all species increasing considerably. There was no evidence for large copepod species feeding preferentially on large particles. All animals fed most efficiently when food was most abundant, irrespective of the size and shape of the food particles (Figure 4.13). This type of feeding behavior has been described as opportunistic by Poulet and Chanut (1975), and Schnack's results agree with those of Poulet (1978) who reported opportunistic feeding in five small copepod species.

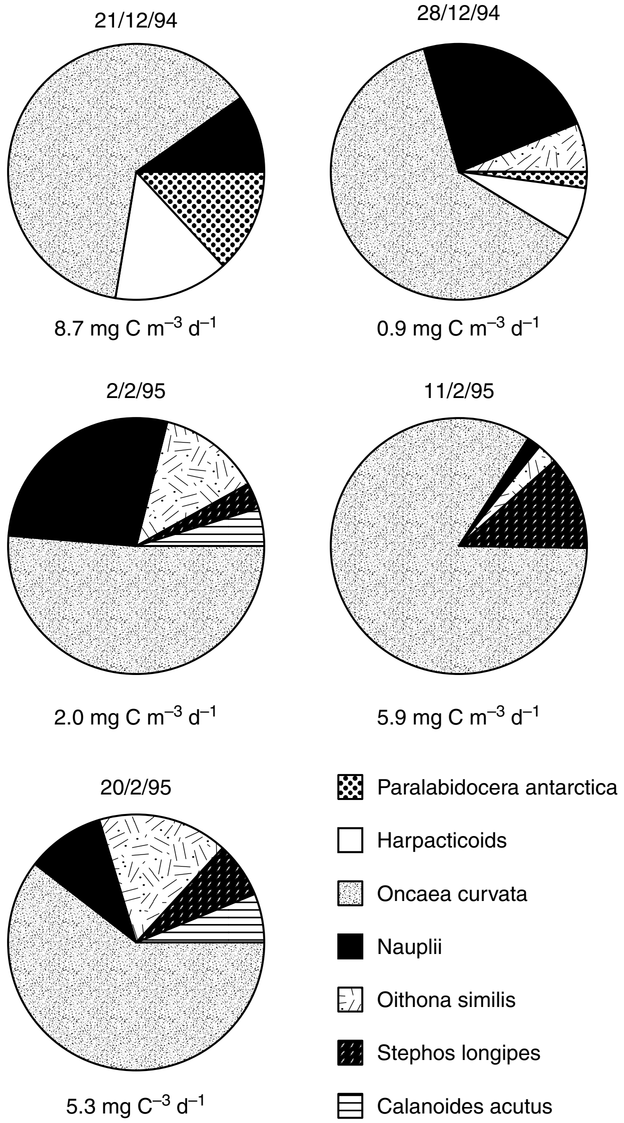


FIGURE 4.12 Partitioning of grazing by copepods on each sampling date. Percentage of grazing by each taxa is represented by pie areas: total daily grazing is shown below each pie chart. (From Swadling, K. M., et al., *Mar. Biol.*, 301, 1997. With permission.)

Hopkins (1987) examined the trophic structure of the midwater pelagic ecosystem in McMurdo Sound in February through the analysis of 35 species of zooplankton and micronekton. Ten feeding groups were suggested through cluster analysis. They can be grouped into three categories with respect to diet: small particle grazers, omnivores ingesting a variety of food types, and carnivores specializing on one or several types of metazoan prey. The results of diet analysis can be summarized as follows.

4.6.2 COPEPODS

These were principally small-particle grazers. Some grazing species, such as *Aetideopsis antarctica, Calanus propinquus, Metridia gerlachei, Oithona frigida,* and *Oncaea antarctica* ingested metazoans in addition to phytoplankton. The principal phytoplankton in the copepod diets were

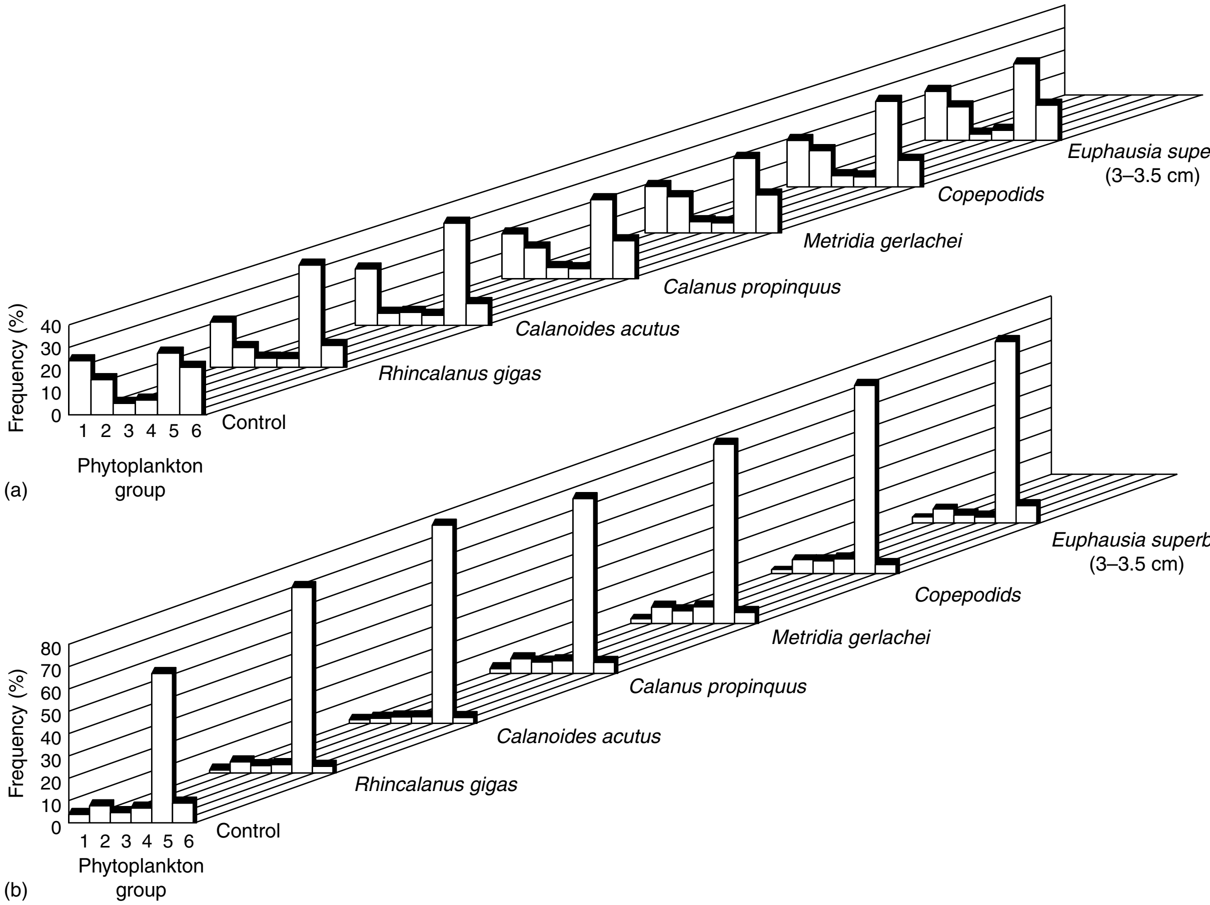


FIGURE 4.13 Relative proportions of six different phytoplankton groups: (1) nanoflagellates; (2) pennate diatoms; (3) centric diatoms; (4) *Disteophamus speculum*; (5) *Corehron criophyllum*; and (6) remainder, in relation to ingestion in the diets of *Euphausia superba* and copepods, which fed either on an ambient food supply (72 μg C l^{-1}; top diagram) on an enriched food supply (177 μg C l^{-1}; bottom diagram). Control is the percentage composition of the food supply. (From Schnack, S.B., *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*, Gray, J.S., Christiansen, M.E., Ed., Wiley, Chichester, Ed., 45, 1985. With permission.)

species of the *Nitzschia* group (predominantly *N. curta*), species of coscinodiscoid diatoms, and peridian dinoflagellates. Tintinnid ciliates and, to a lesser extent, radiolarians, and the heliozoan *Stichlonche* sp. were also common in the diets. The three species of tintinnids abundant in the stomach contents were *Codonellopsis gausii, Laakmaniella naviculaefera*, and *Cymatocylis antarctica* f. *vanhoeffeni*. The predatory copepods were *Euchaeta antarctica, E. erebi*, and *E. similis*. Their diet was primarily copepods, the pelagic mollusc *Limacina helicina*, and the pelagic polychaete *Pelagobia longicirrata*. Changes in diet with ontogeny were indicated for both small particle grazers and the carnivores, with the ingestion of an increasing proportion of protozoans and metazoans with age (Figure 4.14).

4.6.3 OSTRACODS

The ostracods *Conchoecia belgicae* and *C. isocheira* were omnivorous. Their guts contained phytoplankton, protozoans, and metazoans.

4.6.4 EUPHAUSIIDS

Euphausis crystallorophias was abundant, and *Thysanoessa macrura* was rare. The latter species was omnivorous, its diet being composed of phytoplankton, protozoans, and metazoans. All three major food groups (phytoplankton, protozoans, and metazoans) occurred in the diets of 5.5–7.5 mm furcilia and 28–33 mm postlarvae of *E. crystallorophias*. The incidence of phytoplankton was proportionately higher in the furcilia. Proportionately, more tintinnids and metazoans occurred in the guts of postlarvae.

4.6.5 AMPHIPODS

Although phytoplankton occurred in the diet of the three hyperiid species, *Hyperiella dilatata, H. macronyx*, and *Hyperia macrocephala*, the diet diversity was low, and the principal food item in terms of bulk was coelenterates. The gammarids had more diverse diets, which included more protozoans and an array of metazoans. Phytoplankton was an important dietary component of the four gammarids, *Epimeriella macronyx, Eusirus tridentatus, Orchomene plebs*, and

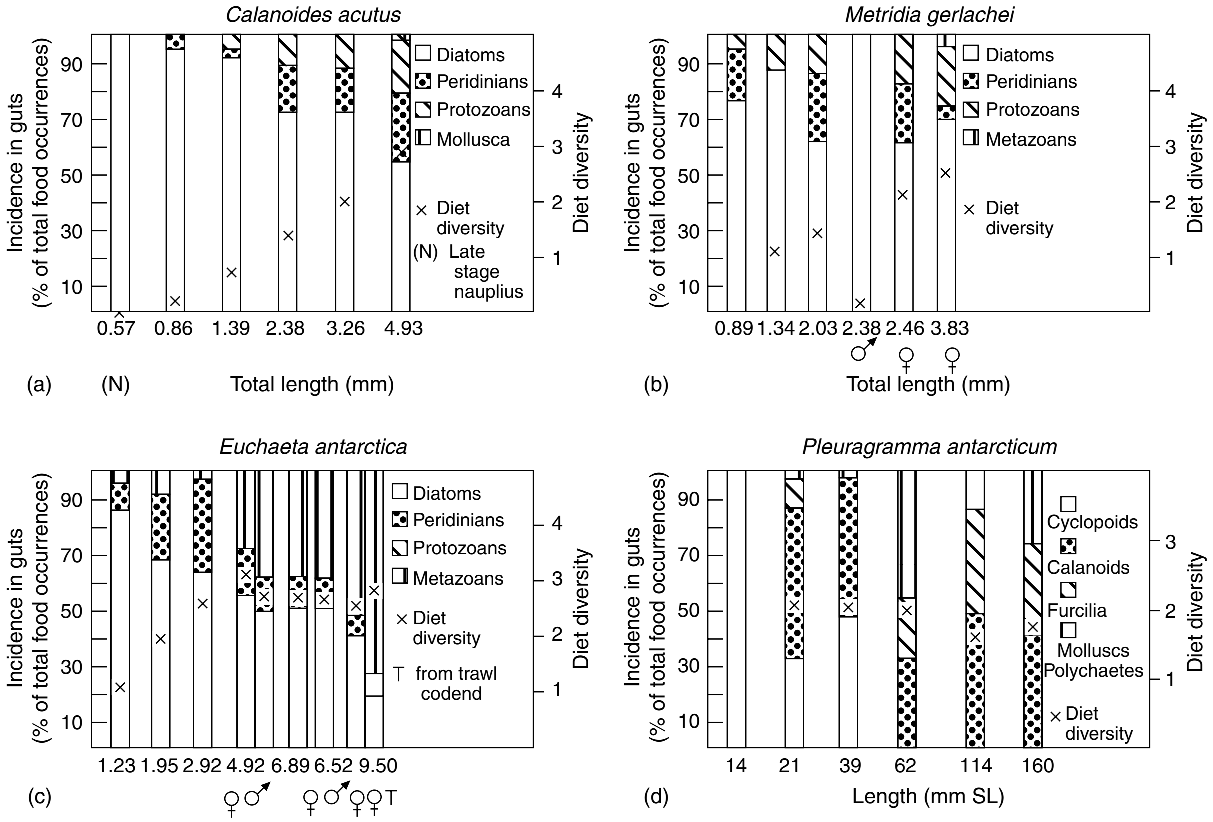


FIGURE 4.14 Diet trends of three copepod species and the pelagic fish *Pleurogramma antarcticum* with respect to ontogeny in McMurdo Sound. (a) *Calanoides acutus*; (b) *Metridia gerlachei*; (c) *Euchaeta antarctica*; (d) *Pleurogramma antarcticum*. Diet diversity is indicated on a diversity scale of 0–4 by a cross for each size class. (From Hopkins, T.L., *Mar. Biol.*, 96, 197, 1987. With permission.)

O. rossi. Coelenterates occurred in the diets of all the gammarids.

4.6.6 MYSIDS

The mysid *Antarctomysis ohlinii* was a generalist, with its diet closely resembling that of the gammarids.

4.6.7 CHAETOGNATHS

Eukrohania hamata fed on copepods, most frequently on *Calanoides acutus*. Incidence of food in the gut of *Sagitta gazellae* was low, with *C. acutus* being the most frequently ingested copepod species. The polychaete *Pelagobia longicirrata* was also included in the diet.

4.6.8 POLYCHAETES: MOLLUSCS

The polychaete *Pelagobia longicirrata* and the pteropod *Limacina helicina* both fed exclusively on phytoplankton. *Clione antarctica* fed on *L. helicina.*

4.6.9 FISH

Larvae of *Artedidraco* and *Chionodraco* fed mostly on the furcilia of *E. crystallorophias*, while the guts of macrourid larvae contained mostly ostracods. Larval *Pleurogramma antarcticum* fed on copepods, pelagic molluscs, and polychaetes.

A comparison of the diets of the McMurdo Sound zooplankton (Hopkins 1987) with those of the krill dominated Croker Passage (Antarctic Peninsula) (Hopkins 1985a, 1985b) indicated that species common to the two areas occupied approximately the same trophic position (Table 4.3). The major difference was that detritus in the form of moult debris was a major food resource in Croker Passage.

The impact of small-particle grazers on the phytoplankton bloom dominated by *Nitzschia curta* in McMurdo Sound was considered by Hopkins (1987). The principal small-particle grazers among the zooplankton in McMurdo Sound were the copepods *Calanoides acutus, Meridia gerlachei, Ctenocalanus vanus, Oncaea curvata*, and *Oithona similis*, the furcilia of *Euphausia crystallorophias*, the polychaete *Pelagobia longicirrata,* and the cosomatous pteropod *Limacina helicina*. Together, these constituted over 80% of the biomass of net-caught zooplankton, with the small-particle grazing copepods alone totalling 50%. These taxa have the greater impact on the phytoplankton. Average particulate concentrations in the upper 150 m off Victoria Land, 80–160 km northeast of McMurdo Sound, in a bloom that covered considerable areas of the Ross Sea, was

TABLE 4.3
Major Components of the Diets of Species Common to McMurdo Sound, Ross Sea and Croker Passage, Antarctic Peninsula

Diet Composition	McMurdo Sound	Croker Passage
Phytoplankton >90%	*Ctenocalanus vanus (?)*	*Ctenocalanus vanus (?)*
	Microcalanus pygmaeus	*Metridia gerlachei*
	Oithona frigida	*Microcalanus pygmaeus*
	Oithona similis	*Oithona frigida*
	Oncaea curvata	*Oithona similis*
	Stephos longipes	*Oncaea curvata*
	Pelagobia longicirrata	*Oncaea antarctica*
		Stephos longipes
Phytoplankton + Protozoans >90%	*Aetideopsis antarctica*	*Calanus propinquus*
	Calanoides acutus	*Pelagobia longicirrata*
	Calanus propinquus	
	Metridia gerlachei	
Metazoans 20–40%	*Oncaea antarctica*	*Aetideopsis antarctica*
	Conchoecia isocheira	*Conchoecia isocheira*
	Thysanoessa macrura	
	Epimeriella macronyx	
	Orchomene plebs	
Metazoans 40–80%	*Conchoecia belgicae*	*Euchaeta similis*
	Antarctomysis ohlinii	*Conchoecia belgicae*
		Thysanoessa macrura
		Epimeriella macronyx
		Hyperiella macronyx
		Orchomene plebs
		Antarctomysis ohlinii
Coelenterates > 40%	*Hyperiella dilatata*	*Hyperiella dilatata*
	Hyperiella macronyx	
	Orchomene rossi	
Metazoans > 80%	*Euchaeta Antarctica*	*Euchaeta antarctica*
	Euchaeta simils	*Eukrohnia hamata*
	Eukrohnia hamata	*Sagitta gazellae*
	Sagitta gazellae	
Not feeding	—	*Calanoides acutus*

Comparisons are on groups of individuals of each species taken with the same type of net.

Source: From Hopkins, T.L., *Mar. Biol.,* 93, 1987. With permission.

191 μg C L^{-1} (=28.7 μg C m^{-2}) (Smith and Nelson 1985a, 1985b). At such carbon levels, the dominant Antarctic copepod particle-grazers, e.g., *Calanus acutus, C. propinquus,* and *Metridia gerlachei*, ingest up to 35% of body weight, in terms of carbon, per day (Schnack 1985b). The biomass of particle grazing copepods in McMurdo Sound was estimated at 50% of the standing crop, or 2.45 g dry wt m^{-2} of grazer copepod carbon. Maximum possible impact would be obtained if copepods and other small grazers were concentrated in the upper 150 m, i.e., in the zone of primary production. On this basis, 0.6 g C m^{-2} of grazing copepods potentially could remove 0.21 g C m^{-2} of the particulate standing crop. If it is assumed that *Limacin helicina* and the remaining particle grazers remove a similar amount then total zooplankton, consumption would be roughly 2% of the phytoplankton biomass per day. Thus, about 98% of the standing crop possibly remains uneaten by grazers. This removal estimate does not include daily phytoplankton growth, which ranges from 0.1 to 0.6 doublings per day (Sakahaug and Holm-Hansen 1986; Vargo et al. 1986). In addition, the abundant protist and other heterotrophic organisms present in the water column could also have a considerable impact on the phytoplankton. Even taking this into account, it is evident that at least 90% of the phytoplankton potentially is not consumed and is either mineralized within the water column or sediments to the bottom (see Chapter 14).

4.6.10 Carnivorous Zooplankton

The role played by the carnivorous zooplankton has been comparatively neglected. However, recent research has filled in the gaps in our understanding of the role that they play (e.g., Oresland 1990; Oresland and Ward 1993; Metz and Schnack-Schiel 1995).

Metz and Schnack-Schiel (1995) investigated carnivorous feeding in four calanoid copepods, *Calanoides acutus, Rhincalanus gigas, Metridia gerlachei,* and *Calanus propinquus*. These four species dominate the zooplankton biomass in many areas. Gut content analyses indicate that all four species are predominately small-particle grazers feeding on zooplankton and protozoans (Hopkins 1985b, 1987; Hopkins and Torres 1989; Hopkins et al. 1993). However, there is increasing evidence that some of these species, especially during the winter period, are opportunistically carnivorous (Schnack-Schiel and Hagen 1995).

Metz and Shnack-Schiel (1995) found that adult females of the diapause species *Calanoides acutus* and *Rhincalanus gigas* did not feed on females of the poecilostomatoid *Oncaea curvata*. In contrast, adult *Calanus propinquus* and *Metridia gerlachiei* females, which remain active during winter, fed on *Oncaea curvata* females. This suggested that, while carnivorous feeding was not vital for these species, it might be very important in winter when phytoplankton is extremely scarce.

In an investigation of feeding of the copepod *Euchaeta antarctica*, Øresland (1991) found that copepods made up 80 to 90% of all food items by number. *Metridia gerlachiei, Calanoides acutus, Euchaeta* spp, other large copepods, *Oncaea* spp., and other small copepods were the main prey. These findings were confirmed by Øresland and

Ward (1993) who investigated the summer and winter diets of adult female *Euchaeta antarctica, E. farrani, E. rasa*, and *E. biloba* around South Georgia. Copeods of variable size dominated the diet of all predators during both seasons (46–99% of all food items). The mean number of prey per predator (0.9–8.6), as well as the distribution of predators with different numbers of prey in the gut, indicated no general decrease in feeding by *Euchaeta* spp. during the Antarctic winter. During summer, copepod nauplii and the small copepod *Drepanopus forcipatus* and *Oithona* spp. dominated the diet of CV *E. antarctica* in the upper 200 m. During winter, *D. forcipatus* dominated the diets of both CV and adult *E. antarctica* and *E. biloba.*

An investigation of the feeding dynamics and predation impact of the hyperiid amphipod *Themisto gaudichaudi* in the South Georgia region by Pakhomov and Perissinotto (1996) showed that it was a visual opportunistic predator, consuming primarily the most abundant species of copepods, euphausiids, and pteropods. In situ estimated daily rations were equivalent to 6.3% of body dry weight. In vitro estimates produced daily rations higher than these, ranging from 8.5 to 21.8% of body dry weight. The predation impact of *T. gaudichaudi,* averaged over a 0–200 m or 0–100 m layer, never exceeded 2.1% of mesozooplankton standing stock per day but accounted for up to 70% of the daily secondary production. This suggested that in the vicinity of South Georgia *T. gaudichaudi* adults are able to control the local mesoplankton community and may contribute significantly to the downward flux of biogenic carbon.

Chaetognaths comprise a significant proportion of the zooplankton standing stock and are considered important predators in the Southern Ocean (Oresland 1990a, 1990b; Hosie 1994; Tarling et al. 1995). In the vicinity of the Antarctic Peninsula, the dominant chaetognath, *Euchronia hamata*, has been shown to consume up to 3% of the total copepod standing stock per day (Oresland 1995). In an investigation of feeding and predation impact of two chaetognath species, *Euchronia hamata* and *Sagitta gazellae*, in the vicinity of Marion Island, Froneman et al. (1998) found that copepods (mainly *Oithona* spp., *Calanus* spp., and *Rhincalanus gigas*) and ostracods were the main prey of both species, accounting for 87 and 61% of the total number of prey in *E. hamata* and *S. gazellae* stomachs. In the guts of *S. gazellae*, pteropods (*Limacina* spp.) and chaetognaths were also well represented. The mean number of prey items for *E. hamata* range from 0.02 to 0.06 prey items individual^{-1}, which corresponds to an individual feeding rate of between 0.05 and 0.12 prey day^{-1}. For *S. gazellae* the mean number of prey items values were higher, varying between 0.04 and 0.20 prey individual^{-1}, or between 0.15 and 0.76 prey day^{-1}. The daily predation impact of the two chaetognaths was estimated at between 0.3% and 1.2% of the copepod standing stock or between 7% and 16% of the daily copepod production. Predation by *S. gazellae* on chaetognaths accounted for up to 1.6% of the chaetognath standing stock day^{-1}.

It is thus clear that predatory zooplankton can have significant impacts on the composition and biomass of zooplankton communities. In the past, this impact has been underestimated in the compilation of planktonic energy budgets.

4.7 BIOMASS AND PRODUCTION

Due to the enormous differences in size, depth distribution, diurnal and seasonal migrations, and absolute density of the considerable number of species that make up the zooplankton of the Southern Ocean, there are enormous problems in making realistic estimates of the standing stock. For the most part, estimates that have been made exclude the physically large animals, such as medusae and salps, which generally are not caught by plankton nets. Since their biomass may be considerable, their omission can give an unrealistic picture of the total biomass. In addition, species which are known to be fast swimmers, such as krill, are certainly able to avoid plankton nets with efficiencies that vary with the type of net used and the conditions under which the samples were taken.

Foxton (1956) summarized the then available information on the zooplankton standing crop in various latitudinal zones of the Southern Hemisphere (Table 4.4). It can be seen that the Antarctic waters have a significantly higher standing crop than the tropical and temperate regions. It also showed that, although there was a clearly marked seasonal cycle in Antarctic seas, with a peak during the summer for zooplankton in the top 50 m, the biomass over the top 1,000 m was more or less constant throughout the year due to the seasonal vertical migration and the fact that most of the species have a life span of one year. Voronina (1960) has given estimates of the standing crop based on the results of the first and second cruises of the Soviet Antarctic Expedition. In a profile along 20°46′S–36°30′S taken from February 21 to March 11, 1957, it was found that the copepods constituted the greater part of the biomass in Antarctic waters. Below 100–200 m, the mean biomass of the zooplankton was 10–50 mg wet wt m^{-3} along most of the length of the profile, with the exception of stations in the vicinity of the Polar Front (300 mg m^{-3}) and the Antarctic Divergence (80 mg m^{-3}). In the upper levels, there were a number of clearly defined maxima with biomasses of more than 100 mg m^{-3}. The three copepod species, *Rhincalanus gigas, Calanus propinquus,* and *Calanoides acutus,*

TABLE 4.4
Standing Crop of Zooplankton in (mg m^{-3}) in the Southern Ocean

Depth(m)	Antarctic	Sub-Antarctic	Tropical	Subtropical
0–50	55.2	55.8	33.1	40.5
0–1000	25.6	20.9	9.8	9.0

Source: After Foxton, P., *Disc. Rep.*, 28, 1956.

contributed 72.8% of the biomass. The averaged results from the profiles gave estimates of a similar order to those of Foxton (1956).

Boysen-Ennen et al. (1991) have published data on zooplankton biomass in the ice-covered Weddell Sea during the summer and reviewed data on zooplankton biomass in the Southern Ocean. Mesozooplankton ($<$ 14.5 mm) biomass in the Southern Ocean is generally between 0.8 and 3.6 g dry wt m^{-2}. High values have been measured in the Croker Passage near the Antarctic Peninsula (Hopkins 1985b), and low values in the oceanic northern Weddell Sea (El-Sayed and Taguchi 1981). Calanoid copepods clearly dominated the biomass. It is only in the high Antarctic shelf regions that copepods are partly replaced by smaller gastropods (*Linacina helicina*). The copepods *Calanoides acutus, Calanus propinquus,* and *Metridia gerlachei* are responsible for a biomass peak in the 1–5 mm size range. A second biomass peak in the 7.0–8.5 mm ranges is sometimes caused by the salp *Salpa thompsoni* (Everson 1984a; Piakowski 1985b; Boysen-Ennen et al. 1991).

Published data on zooplankton biomass in the Southern Ocean are on the order of 0.2–2.4 g dry wt m^{-2}, excluding studies which are focussed on krill. Macrozooplankton biomass is lower than mesozooplankton biomass at all latitudes and also decreases from lower to higher latitudes. Krill are often considered to be the most important zooplankton species in the Southern Ocean, and on occasions in specific locations they can dominate the zooplankton biomass, e.g., in the Croker Passage, krill biomass outnumbered that of other zooplankton by an order of magnitude (Hopkins 1985a). However, the results of the intensive "BIOMASS" investigations gave average densities of krill in its principal areas of distribution of 1–2 g dry wt m^{-2} (Siegel 1986a). This is the same order of magnitude as that of the mesozooplankton biomass, even in areas of main krill occurrence. It is clear that the overall contribution of krill to Southern Ocean zooplankton biomass has often been overestimated.

Taking into account the higher production to biomass ratio of copepods (4.5:1, Voronina et al. 1981) over krill (1.0, Everson 1977b), copepods contribute most to total zooplankton production in the Southern Ocean. Boysen-Ennen et al. (1991) have listed estimates for mesozooplankton production in the Atlantic sector of the Southern Ocean, and based on these estimates they concluded that in this sector mesozooplankton production exceeds that of macrozooplankton production by a factor of 8–14. However, these copepods, with few exceptions, do not constitute a major food resource for the large predators of the Southern Ocean. The main predators on these copepods are mesopelagic fish, such as the Myctophidae (Rowedder 1979). These fishes are absent from the shallower waters over the high Antarctic shelf where the holopelagic fish *Pleurogramma antarcticum* dominates and feeds on copepods throughout its life cycle (Eastmam 1985b; Hubold and Ekau 1987).

To the copepod biomass must be added that of other herbivores, such as the euphausiids and salps, and the

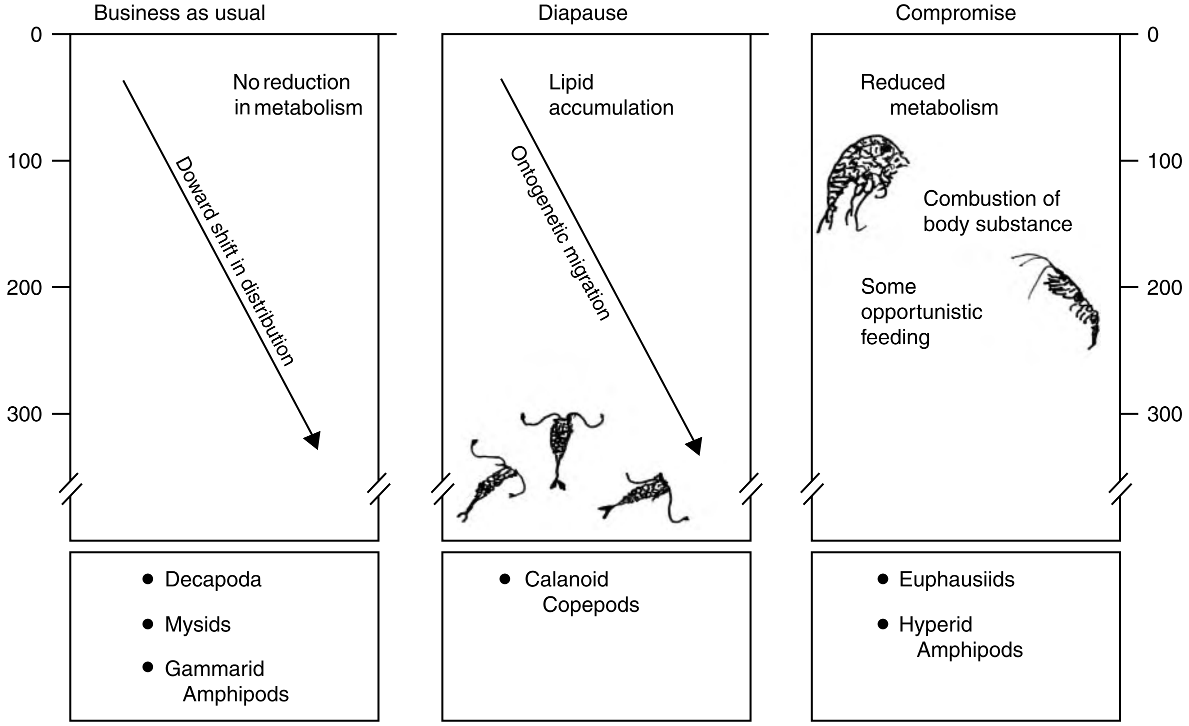


FIGURE 4.15 Winter-over strategies for pelagic crustaceans in the Southern Ocean. Based on description in Torres et al. (1994). (From Quetin, L.B., Ross, R.M., *Ant. Res. Ser.*, 70, 363, 1996. With permission.)

carnivorous zooplankton, which includes the carnivorous copepods, the pelagic amphipods, the chaetognaths, the pelagic polychaetes, and the medusae and siphonophores. The available data base is inadequate at present to accurately estimate the secondary production of these groups. However, from an ecological point of view, global estimates of global secondary production are not of a great deal of value. In the Southern Ocean, production is characterized by a great amount of variability, both geographically and seasonally, and, in addition, within any given region it can be very patchy.

4.8 ECOPHYSIOLOGY

Antarctic zooplankton exhibit several physiological characteristics that appear to be adaptations to or consequences of the cold water temperatures and extreme seasonality in food availability (Clarke and Peck 1991; Quetin and Ross 1991). For Antarctic crustaceans, these include: low metabolic rates, low annual growth rates, high lipid stores, long life spans, and delayed reproductive maturity. In contrast, low lipid stores in carnivores (ctenophhores, chaetognaths, and polychaetes) (Smith and Schnack-Schiel 1990) may be a consequence of

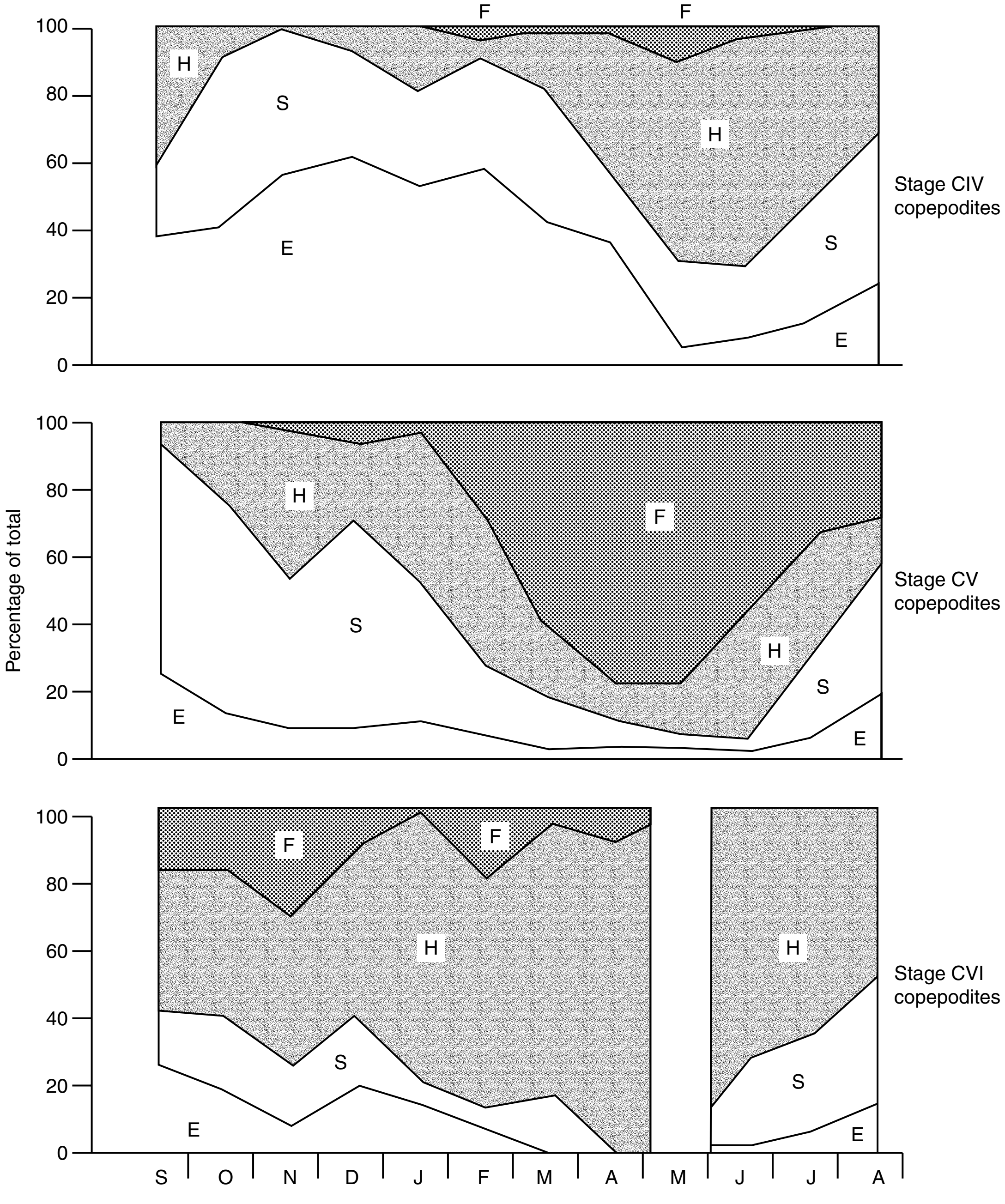


FIGURE 4.16 The copepod *Calanus acutus*: Monthly variation in oil contained within the oil sac by four subjective categories; E, empty; S, very little; H, half full; F, full. (From Everson, I., *Antarctic Ecology*, Vol. 2, Laws, R.M., Ed., Academic Press, London, 463, 1984. Based on data from Andrews, K.J.H., *Discovery Reports*, 34, 117–162, 1966. With permission.)

their feeding on zooplankton, which is less seasonal than phytoplankton. Although annual growth rates are low, in areas of high primary productivity the instantaneous growth rates of herbivores can be seasonally high (Clarke and Peck 1991). Both euphausiids and some gelatinous zooplankton can utilize their body tissues during periods of low food availability. This results in shrinkage or "degrowth."

Clarke and Peck (1991) point out that gelatinous zooplankton occupy a special niche in the Southern Ocean pelagic ecosystem. Because they are neutrally buoyant, their metabolic costs are generally less than those for crustaceans. Thus, when food conditions are favourable, populations of some gelatinous zooplankton can grow and reproduce rapidly. This results in the peaks in abundance for gelatinous zooplankton, such as salps, being higher and occurring on shorter time scales than those for crustaceans.

4.9 STRATEGIES FOR WINTER SURVIVAL

Several strategies for winter survival when food resources are low have been proposed and evaluated for Antarctic zooplankton (Quetin and Ross 1991; Schnack-Schiel and Hagen 1994; Torres et al. 1994). Quetin et al. (1996) have reviewed these strategies. Identification of the strategy used by a particular species is based on the following: (1) seasonal changes in metabolic rates; (2) type and amount of lipid reserves; (3) seasonal changes in water and lipid content indicating mobilization of internal tissues; (4) indicators of net production such as growth and reproduction; and (5) indicators of ingestion such as stomach fullness and contents and rate of ingestion in the field.

Three main strategies have been proposed (Figure 4.15):

1. *Business as Usual*. Torres et al. (1994) suggest that one extreme is a "business as usual" strategy, where metabolic activity remains the same, and energy requirements during the winter months can be satisfied by opportunistic feeding combined with some combustion of tissue. This option is open to carnivores and omnivores. These can survive over the winter because the presence of zooplankton provides a year-round food source. One species that is known to use this strategy is *Metridia gerlachei*, an omnivorous copepod that feeds actively in winter in the upper layers of the water column, has a moderate lipid content (both wax esters and tricylglycerols), and does not enter a period of diapause (Schnack-Schiel and Hagen 1994). This strategy is also used by species that live below the epipelagic zone, such as gammarid amphipods, decapods, and mysids (Torres et al. 1994) where food supply is not significantly affected by season. During the winter, these crustaceans have access to the bulk of the zooplankton biomass, which generally occurs below 300 m (Hopkins et al. 1993).
2. *Lipid Stores and Diapause*. Another strategy that is used by herbivorous copepods is to accumulate large lipid reserves, generally wax esters, and, in winter, to enter a diapause or dormant state triggered by photoperiod (Hagen 1988). In the Southern Ocean, one copepod, *Calanoides acutus*, follows this strategy, with a strong ontogenetic migration downwards in winter, high storage of wax esters, and a definite diapause (Schnack-Schiel and Hagen 1994). *Rhincalanus gigas* may also follow this strategy, although the evidence is not definite (Schnack-Schiel and Hagen 1994).
3. *Compromise Between Busines as Usual and Shut Down*. The third alternative is a mixture of the above two strategies. Metabolic activity decreases to some degree, either because of starvation or an environmental cue, and energy requirements are met by a combination of opportunistic feeding and mobilization of body tissue. Both hyperiid amphipods and euphausiids appear to follow this compromise strategy.

The development of oil sacs of copepods and the storage of oil by euphausiids is illustrated by the copepod *Calanoides acutus* (Figure 4.16) and the copepod *Paraeuchaeta antarctica* and the euphausiid *Euphausia crystallorophias* (Figure 4.16). Figure 4.17 depicts the variation in oil content contained in the oil sacs of Copepodites VIV, CV, and CVI of *C. acutus* (Andrews 1966). The overwintering strategies of CVI and CV show some interesting differences. Relatively few Stage CIVs achieved a full oil sac before the onset of winter. This is because they continued to divert energy to growth rather than to building up maximum food reserves. In Stages V and VI, the relatively high oil content remaining in the spring probably aids in the production of eggs coincident with the spring phytoplankton bloom.

The establishment of lipid stores during the summer has also been demonstrated for the copepods *Rhincalanus gigas*

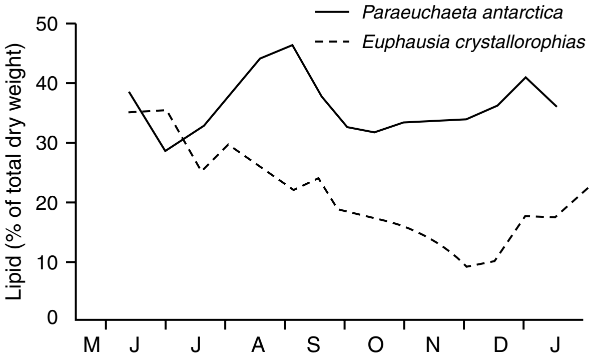


FIGURE 4.17 Seasonal changes in the lipid content of two Antarctic crustaceans, the copepod *Paraeuchaeta antarctica* and the euphausiid *Euphausia crystallorophias*. (From Everson, I., *Antarctic Ecology*, Vol. 2, Laws, R.M., Ed., Academic Press, London, 463, 1984; based on data from Littlepage, J.R., *Biologie Antarctique*, Carrrick, R., Holdgate, M.W., Prevost, J., Ed., Herman, Paris, 163, 1964. With permission.)

TABLE 4.5
Estimated Clearance of the Copepod Community in Relation to Abundance and Biomass within the Surface Mixed Layer

			Percentage of Surface Mixed Layer Cleared Daily		
Species Group	**Mean no. (m^{-3})**	**Mean Dry Mass ($mg\ m^{-3}$)**	**Dinoflagellates Plus Ciliates**	**Mean for Counted Diatom Taxa**	**Total chl *a***
Species/copepodites included	1517	88	1.4	0.93	0.79
Large species only	444	95	0.89	0.87	0.65
Total copepods	3785	112	2.8	1.3	1.2

Clearance values are percentages determined for the different food sources and measurement methods. The large copepods are defined as all copepodite stages of *Calanoides acutus, Rhincalanus gigas, Calanus simillimus,* and *C. propinquus.*

Source: From Atkinson, A., et al., *Mar. Ecol. Prog. Ser.,* 144, 1996, see also page 205. With permission.

and *Paraeuchaetea antarctica* and the euphausiid *Euphausia tricantha*. As *P. tricantha* is a carnivore, it is capable of obtaining food year-round and thus shows little fluctuation in its seasonal lipid content (Figure 4.17). This difference between carnivorous and herbivorous zooplankton is also reflected in the type of lipid used as an energy source. Species capable of feeding year-round (such as *Paraeuchaetantarctica*) tend to store glycerides, whereas those that fast overwinter (such as *Calanoides acutus*) tend to store less readily mobilized lipids, such as wax esters (see Benson and Lee 1975; Sargent 1976). It is of interest that *Euphausia superba* has generally been found to contain very little, if any, wax esters, and this may indicate that krill feed year-round.

The carnivorous zooplankton, with the exception of the amphipod *Parathemisto*, do not tend to lay down lipid deposits because the biomass of small zooplankton in the upper 1000 m, which is more or less constant throughout the year (Foxton 1956), ensures a constant food supply. Thus, they do not need to rely on food reserves to live through periods of food shortage. The continuous feeding of such species throughout the winter results in the release of large quantities of detritus that may provide an alternative food source for other species (Everson 1984a) (Table 4.5).

5 Krill

CONTENTS

5.1 INTRODUCTION

As we have seen euphausiid crustaceans are conspicuous members of the Southern Ocean plankton community. Collectively they are referred to as “krill,” although the term is frequently reserved for the dominant species *Euphausia superba* (Figure 5.1). This species, because of its widespread distribution and abundance and its central position in the food web, has attracted much attention. During the interwar period, *E. superba* was studied intensively by many investigators, especially the scientists of the *Discovery* Expeditions (e.g., Rudd 1932; Fraser 1936; Marr 1962; Mackintosh 1972), where the main interest was the importance of krill as food for baleen whales. In recent years an added dimension has been the commercial potential of krill as food for humans. *E. superba* has also been the focus of intensive research during the 10-year BIOMASS Programme. As a result there has been a considerable volume of publications on many aspects of krill biology, ecology, behaviour, physiology, and biochemical adaptations (e.g., Ross 1982; Ross and Quetin 1983a, 1983b; Schnack 1985b; George 1984a; Quetin and Ross 1985, 1991; Siegfried et al. 1985; Sahraghe 1988a; Miller and Hampton 1985; Daly and Macauley 1991; Quetin and Ross 1991; Everson and Miller 1996; Quetin et al. 1994, 1996; Siegel and Kalinowski 1996; Azzali and Kalinowski 1998; Nicol et al. 2000; Murphy and Reid 2001; Quetin and Ross 2001).

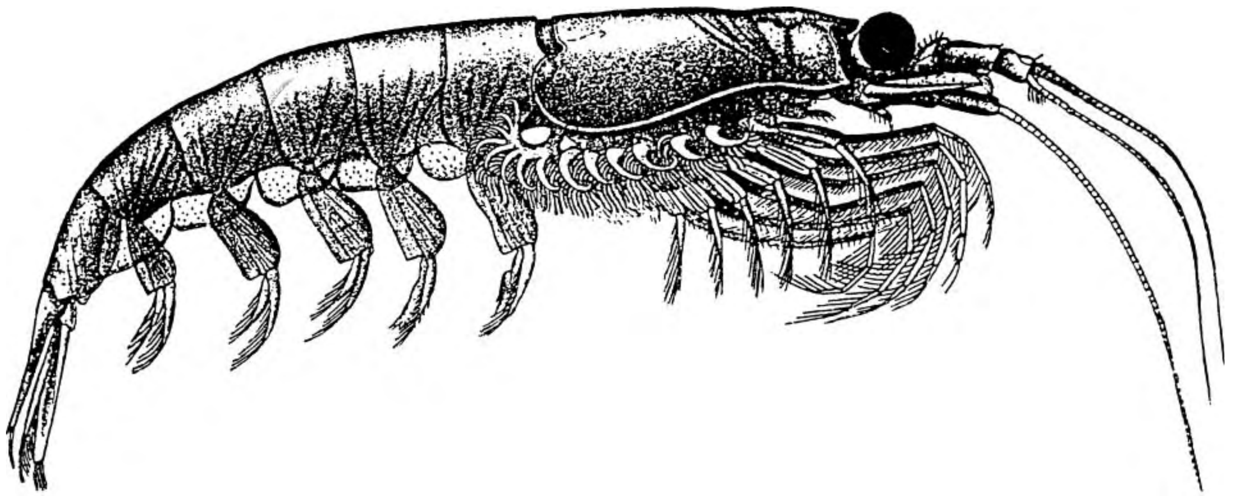


FIGURE 5.1 *Euphausia superba*, the Antarctic krill.

In comparison with other euphausiids, *E. superba* has a number of unique characteristics (Kils 1983), including:

1. An unusually high body weight (e.g., 60 times that of *Euphausia pacifica*).
2. An unusually high metabolic rate for a euphausiid of its size living in a low-temperature environment (reflected in a respiration rate of 1 mg O_2 (g dry wt) h^{-1}, swimming speeds of 60 cm s^{-1}, and a reaction time of 40 ms).
3. A large size ratio between krill and their food (e.g., the ratio between the length of a typical diatom (6 μm) and a 60 mm *E. superba* is 1–10,000), while the weight ratios are 1:7 million.
4. An unusual relationship between energetics and size. Normally larger animals have a lower specific metabolism (energy per body unit and time unit) than smaller ones. However, in *E. superba* this does not vary with body size. The significance of this is discussed below.

To these, the following may be added (Quetin and Ross 1991):

5. The ability to find concentrations of food in several types of habitat and efficiently exploit whatever food is available.
6. The close correspondence of life cycle with seasonal food availability.
7. A combination of physiological and behavioral mechanisms which enable krill to survive the long winter period when food resources are low.

5.2 SPECIES OF EUPHAUSIIDS

There are eleven species of euphausiids which occur in the waters of the Southern Ocean, but only six of these are important and endemic south of the Polar Front. All eleven species have circumpolar distributions. The latitudinal distributions of the species are shown in Figure 5.2.

5.3 LIFE HISTORY AND GROWTH

5.3.1 INTRODUCTION

As a result of the early work on *E. superba*, particularly that of *Discovery* Expedition scientists (Bargmann 1945; Marr 1962; Mackintosh 1972), the broad outlines of the life history and growth patterns of *E. superba* became known. However, a number of questions remained unanswered, and further

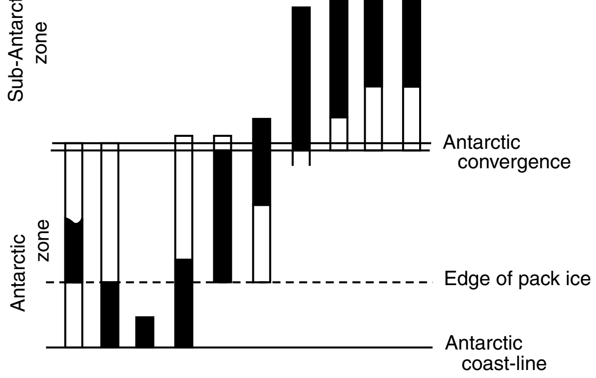


FIGURE 5.2 Latitudinal distribution of Antarctic euphausiids. The dark areas represent the main distributional range of the species.

uncertainties have arisen as a result of recent work. Recent research has been directed at finding answers to the following questions:

- What are the factors influencing spawning in krill, where are the spawning grounds located, and how many times may a female spawn in a season?
- At what depth does spawning take place?
- Do females spawn in one season only, or can they spawn in successive seasons?
- What is the relationship between pressure and krill embryology and larval development?
- What are the factors responsible for the distribution of krill larval stages?
- What are the growth rates of larval and adult krill in relation to food supply and environmental factors?
- What are the factors involved in krill swarming behaviour?
- What is the feeding mechanism of krill and what kinds and quantities of food are consumed?
- What is the growth strategy of krill during the winter months (i.e., do they continue to feed and grow during the winter, or do they cease feeding but continue to moult and decrease in size)?
- How long do krill live, and how can the age of krill be determined?

Information gathered over the period since the publication of the first edition of *The Biology of the Southern Ocean* has gone some way toward answering the questions listed above, but gaps in our knowledge still remain.

5.3.2 REPRODUCTION AND FECUNDITY

A species reproductive potential is governed by two integral factors: the energy cost of reproduction and the energy transferred to successive generations (i.e., its fecundity) (Miller and Hampton 1985). We need to consider the cost of producing eggs and the calorific losses incurred during spawning activities.

Ross and Quetin (1986) define fecundity as

$$F = E(T \cdot \mathrm{SF}),$$

where F is fecundity, or total number of eggs released by an individual in a spawning episode, E is the total number of eggs per spawning episode, T is the length of the spawning season, and SF is the proportion of mature females releasing eggs per day. Krill fecundity has been determined in a variety of ways, including counts of all or part of the eggs present in the ovary, counts of the number of eggs spawned, measurements of the ratio of ovarian to body volume, and analysis of body lipid content. In spite of recent research, there is a degree of uncertainty regarding the number of times a female spawns and the number of eggs released (Miller and Hampton 1985).

Estimates of the number of eggs produced by a single female vary widely from a low of 310 to 800 (Mauchline and Fisher 1969) to 20,000 (Ross and Quetin 1983a, 1983b, 1986). The mean of these estimates falls within the range of 2,200–8,000 assessed by Denys and McWhinnie (1999). Estimates of the number of spawning episodes also vary considerably. El-Sayed and McWhinnie (1979) supported the view advanced by Makarov (1972, 1979b) that krill possibly spawn twice over a period of two seasons. Contrarily, Ettershank (1983) considered that spawning might extend over four or five seasons. Ross and Quetin (1983a, 1983b) assumed that spawning took place nine to ten times per season with a mean interval of 6.7 days. Subsequent research does not support these assumptions (Siegel 1985). Siegel contended that the spawning season assumed by Ross and Quetin was too long. Spawning frequency also varies strongly, not only over the season, but also among schools sampled simultaneously a short distance from one another. In investigations west of the Antarctic Peninsula over the period 1993–1999, Quetin and Ross (2001) found that spawning frequencies varied from 5% to 25%, and that the proportion of the females reproducing varied from 10% to 98%.

5.3.3 ENERGY COSTS OF REPRODUCTION

The major energy cost of reproduction in female krill is the accumulation of the large, lipid-rich yolk mass of eggs (Clarke and Morris 1983a, 1983b). Since krill spawn in the summer, or, at the earliest, during the spring phytoplankton bloom (Hart 1934; Bargman 1945; Marr 1962), latitudinal variation in spawning times suggests that ovarian development is promoted by an increased availability of food rather than lipid reserves laid down the previous summer (Clarke and Morris 1983a, 1983b).

Clarke and Morris (1983a) considered the minimum cost of egg production to be 46% of total production based on the assumption that a female matures one single ovary. Ettershank (1983), on the other hand, presents some evidence that mature females may not grow, so that production would go primarily into eggs, not tissue. Based on work with other euphausiids, Ross and Quetin (1986) have considered the ratio between the energy costs of reproduction to growth and moulting to be 4:1 (Figure 5.3). Nicol et al. (1995) estimated that a female Antarctic krill loses 34% of its body mass when it lays a batch of eggs. This represents a considerable input of energy which was estimated using a combination of measured mass and energy differences in female krill and from the measured energetic content of ovarian tissue. Large (approximately 50-mm) female krill were estimated to lose 2.9–3.8 kJ each time a batch of eggs is laid. Ross and Quetin (1986) estimated that a female would need to ingest more than 300 μg of chlorophyll *a* to produce the predicted number of eggs. On this basis *E. superba* would require relatively high average concentrations of phytoplankton (approximately 1.5 g chl $a\,\mathrm{l}^{-1}$) to reproduce if all the energy for reproduction comes from feeding during the spawning season. Nicol et al. (1995) calculated that multiple spawning by Antarctic krill in a season would require above average phytoplankton concentrations (>0.5 μg chl $a\,\mathrm{l}^{-1}$) and filtration rates which are close to the maximum reported ($>10\,\mathrm{l\,h}^{-1}$). Even if the number of eggs produced were half of the estimate,

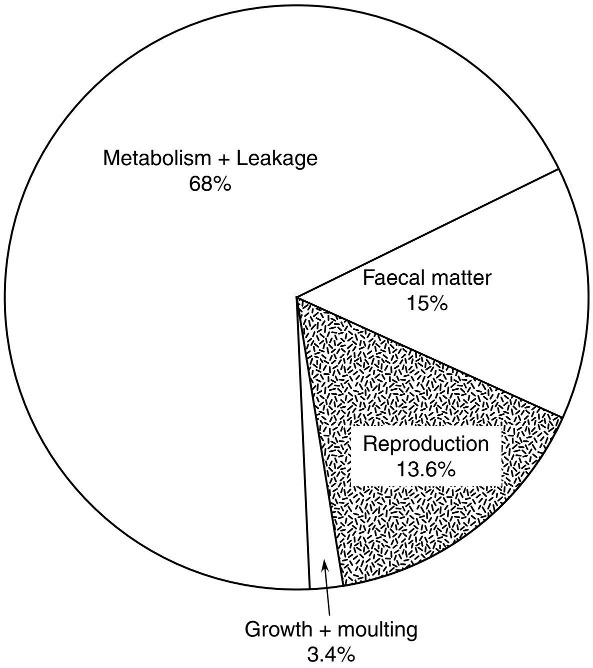


FIGURE 5.3 Proportional allocation to metabolism plus leakage, faecal matter, reproduction, and growth plus moulting of the total food ingested by a female, *Euphausia superba*, based on the standard energy budget, where ingestion is faecal matter + metabolism + leakage + moulting + growth + reproduction. The following assumptions were made to derive the portion allocated to each activity: assimilation efficiency = 85% (Ross 1982); metabolism + leakage = 80% of assimilation (Clarke and Morris 1983a; Ikeda 1984b), and production (what remains after metabolism and leakage) = 20% of assimilation; reproduction = 80% of production. (From Ross, R.M., Quentin, L.B., *Bioscience*, 36, 264, 1986. With permission.)

the phytoplankton concentrations required would still be high. Such concentrations do not commonly occur in oceanic waters, but do so in bays around the Antarctic Peninsula and shallow areas near the Scotia Ridge (Bienati et al. 1977; Holm-Hansen and Huntley 1984) and in ice edge blooms (Smith and Nelson 1986). Thus patches of phytoplankton in high concentrations and/or food sources other than phytoplankton may be important for reproductive success.

There has been a paucity of studies addressing the energetic costs of reproduction in male krill. One exception is that of Virtue et al. (1996). They found that mortality was significantly higher for reproductive males than for females in the first three days after capture. Also, all reproductive males had low lipid levels (1–3% dry wt) with negligible triacylglycerol stores (0–2% total lipid). In sampling krill in the Prydz Bay region, they found a sharp decline in the numbers of male krill once they attained a length of 51–55 mm. They concluded that the low lipid levels in reproductive male krill and their high mortality may be due to reproductive costs.

5.3.4 LIFE HISTORY

Spawning is generally believed to take place in the upper 0–100 m layer (Fraser 1936; Marr 1962). According to Makarov (1983) there is evidence for this occurring in *E. frigida* and *T. macrura* off South Georgia, as at night most of their eggs are found in this layer. After spawning the eggs sink, undergoing development on the way. However, one of the problems involved in studying the breeding patterns and development of euphausiids is the comparative rarity of eggs in plankton net hauls due to a combination of the patchy distribution of the spawning females, the vertical dispersion of the eggs, and their low catchability (Hempel 1978; Hempel et al. 1979; Marschall 1983).

Euphausiids pass through a series of larval stages, as shown in Figure 5.4, known as nauplius, metanauplius, calyptopus, and furcilia. These larval types and their nomenclature have been discussed and defined in Mauchline and Fisher (1969). The early life history has been described by Marr (1962) and the morphological structure of the larval stages discussed by Fraser (1936). Descriptions of the larval stage of other Southern Ocean euphausiids has been provided by John (1936). After hatching at a depth of several hundred metres, stage two of nauplius and one of metanauplius are passed through as the larvae ascend in the water column (Marr 1962; Hempel 1983, 1985a; George 1984b; Hempel and Hempel 1986) (Figure 5.5). Feeding commences in the next phase, the calyptopus, when it enters the surface waters. This occurs at about 30 days after spawning according to Kikuno (1981), or after 21–55 days according to Ross and Quetin (1983a). Investigations by Makarov (1978, 1979b, 1983b) have also shown that the sinking of eggs and the developmental ascent of the larvae are characteristic for all species of Antarctic euphausiids except for *E. crystallorophias*, and not, as originally believed, for *E. superba* only. According to Makarov (1978, 1983b) there are species differences in the depths to which the eggs sink and in the ontogenetic migration. With increase in age, the larvae of *E. superba* and *T. macrura* rise to the surface and concentrate in the subsurface layers, whereas those of *E. tricantha* and *E. frigida* tend to sink again after some time.

Growth rates of krill larvae from calyptopus onward are not well known. Witek et al. (1980) attempted an analysis using mid-points that limit the varying periods during which the different development stages have been collected in the field. For example, they estimated 15–30 days from calyptopus 1 to calyptopus 2, and 135–240 days for the full duration of larval life. On the other hand, Brinton and Townsend (1984) found five larval stages in high abundance (>10 per 1,000 m^{-3}) north of the south Orkney Islands in March 1981, indicating that the spawning season must have been at least as long ago as five development stages. Based on their data, Brinton and Townsend estimated a spawning period of 40 days, with an average of 8 days per development stage. This stage duration is shorter than that proposed by other investigators; Mauchline (1980a) gives 8.5–11.5 days (based on theoretical reasoning), Ross and Quetin (1983b) at least 15 days (laboratory rearing), and Ikeda (1984a) suggests 9–14 days for calyptopus stages and 11–15 days for furcilia stages (laboratory rearing). Ikeda (1984a, 1985) estimated a total development time from egg to larval stage of 150 days.

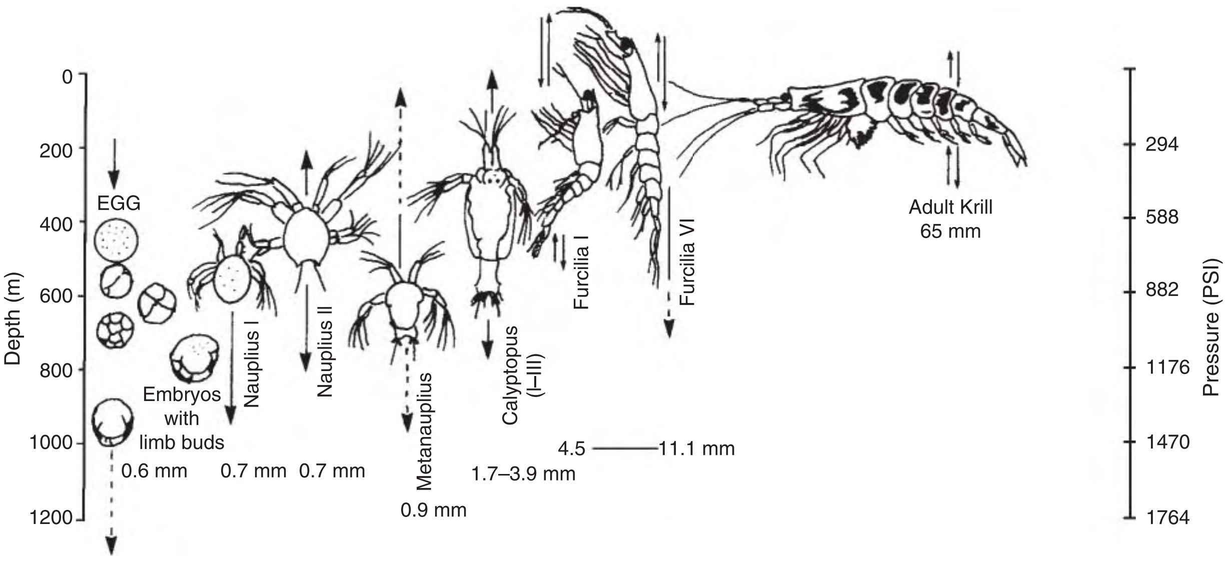


FIGURE 5.4 Vertical distributions of the various ontogenetic stages of *Euphausia superba*, depicting the phenomenon of "developmental descent" and "developmental ascent." Arrows indicate the depth distribution of the ontogenetic stages. (From George, R.Y., *J. Crust. Biol.*, 4, 252, 1984. With permission.)

Figure 5.6 depicts the life cycle of Antarctic krill. Quetin and Ross (1996) point out that there are distinct times when critical interactions with the environment occur during this life cycle, influencing both recruitment potential and larval survival. West of the Antarctic Peninsula the spawning season normally begins on mid-December and lasts through March (Ross and Quetin 1986; Quetin et al. 1994). Depending on the growth rates during the previous two years,

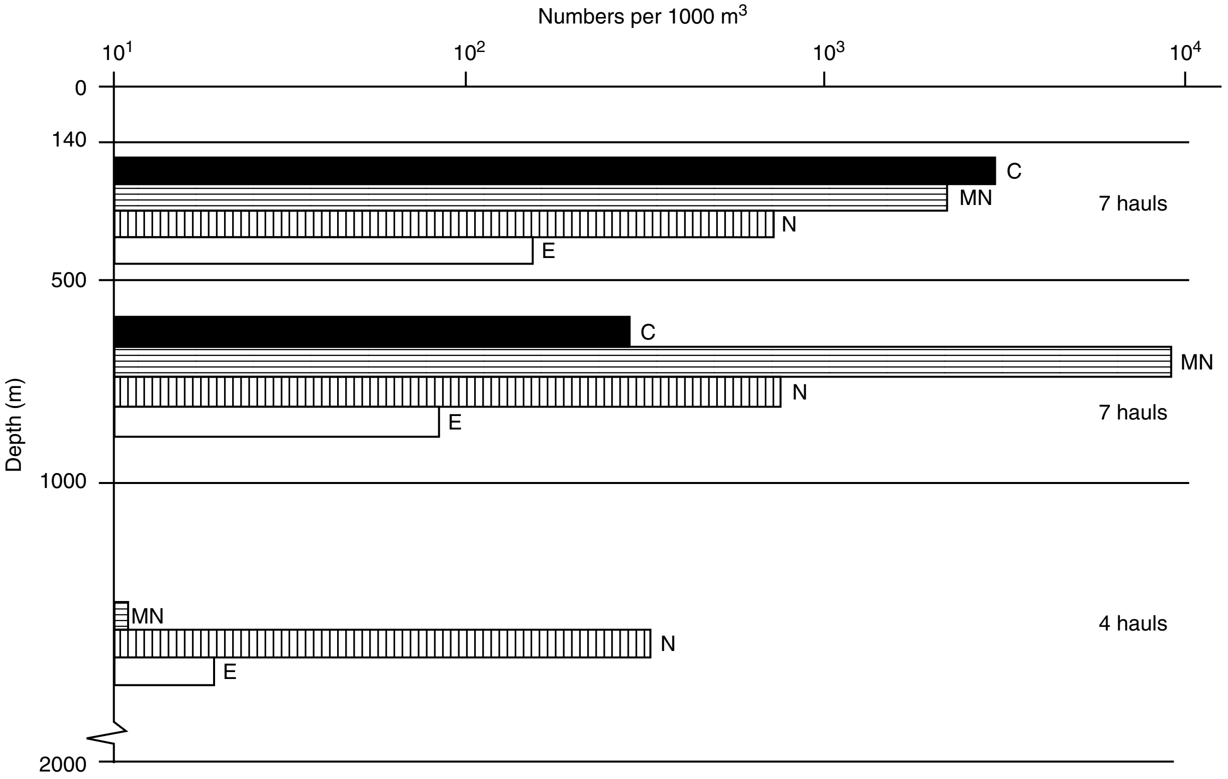


FIGURE 5.5 Abundance of *Euphausia superba* eggs (E), nauplii (N), metanauplii (MN), and calyptopus stages (C) in relation to depth in the Bransfield Strait and the Scotia Sea, January 1981. (From Hempel, I., *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds. Springer, Berlin Heidelberg, 93, 1985.)

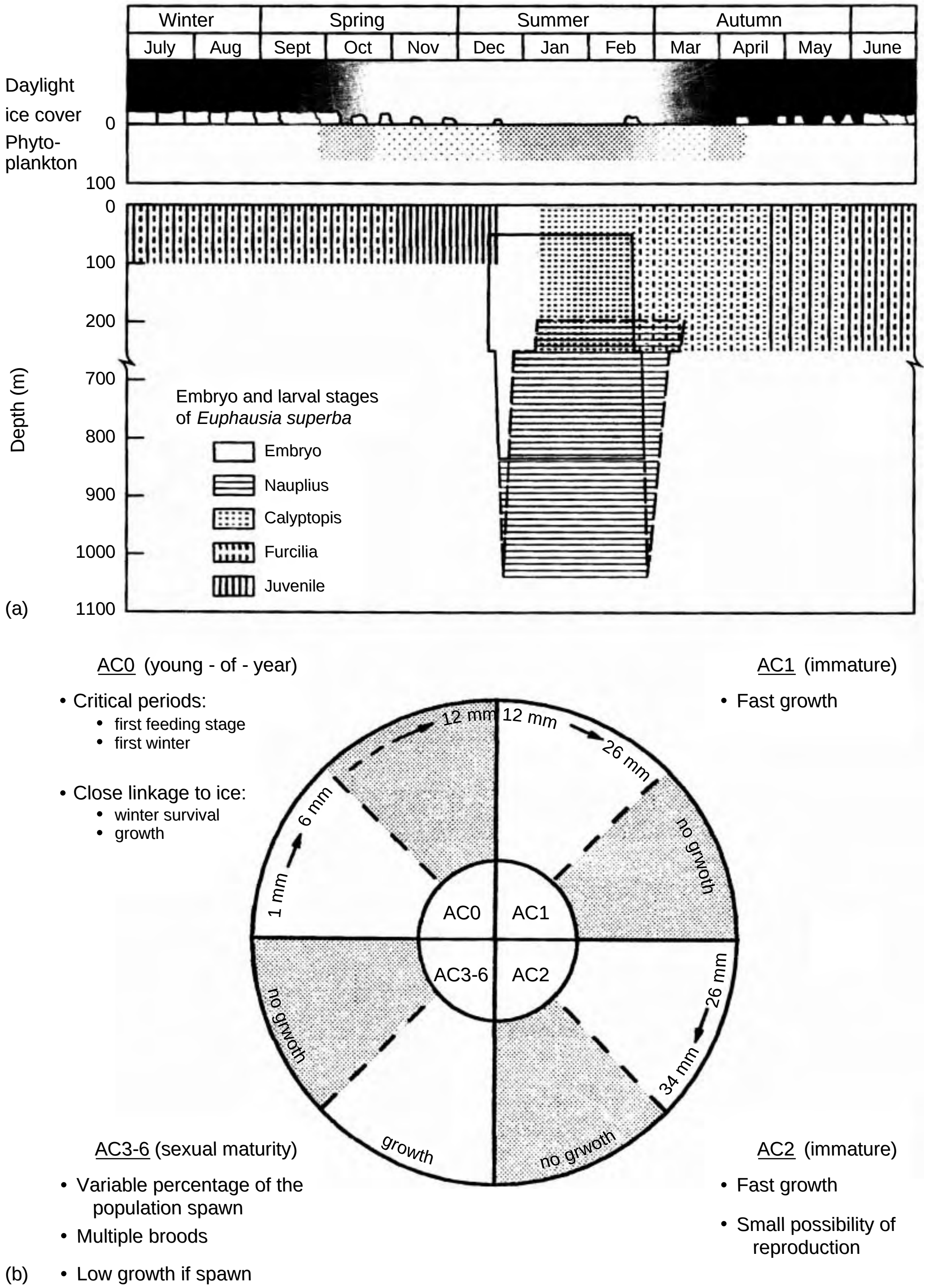


FIGURE 5.6 Life cycle of Antarctic krill, *Euphausia superba*: (a) Vertical distribution and timing of early life history stages in relation to seasonal cycles of daylight; ice cover and phytoplankton concentrations. From Quetin and Ross (1991); (b) Pattern of growth and reproduction with age: ACD (young-of-year) is age class 0 from January to September, AC1 and AC2 (immature) are age classes 1 and 2, AC3-6 (reproduction) includes age classes 3 through 6. The two growth periods for ADC are January to June and June to September. For age classes 1 through 6, growth periods are divided into Spring/summer (October through March, white area) and fall/winter (April through September, shaded area). Characteristics of each age group(s) are to the side. (From Quetin, L.B., Ross, R.M., *Ant. Res. Ser.*, 70, 365, 1996.)

a small proportion of the female krill will reproduce during their third growing season (AC2, Figure 5.6). Minimum size at spawning is about 33 mm (Cuzin-Roudy 1987), although most spawning individuals are 38–50 mm (Ross and Quetin 1983a, 1983b). Age classes 3 through 6 are characterized as sexually mature (AC3-6, Figure 5.6) because individuals of this size range (35–60 mm) have developed gonads and will reproduce under favorable environmental conditions.

Oocytes begin to develop in September, with the rates of development being dependent on spring and summer food resources. Food intake required for fecundities observed west of the Antarctic Peninsula is high (Ross and Quetin 1986), suggesting that a combination of ice biota, ice edge blooms, and open water phytoplankton blooms may be necessary to meet the spring and summer food requirements of reproducing female krill. Food availability is a factor not only in the timing of reproduction but also in the proportion of the population reproducing and the number of broods per female (Quetin et al. 1994). As discussed above, multiple spawning requires above average phytoplankton concentrations.

There are several critical periods for larval survival (Quetin and Ross 1996). The first feeding stage, Calyptopus 1, initially appears in the surface waters in January and may continue to appear for the next 4 or 5 months. Immediately after reaching the surface there is a critical period when the Calyptopus 1 must find adequate food within 10–14 days or die. The first winter in the life cycle of krill is another critical period because the larvae cannot survive the prolonged winter period of very low food availability in the water column without an alternative food source (Ross and Quetin 1991). In the winter, even with extensive sea ice cover, larvae continue to grow and reach an average of 12 mm by September (Fraser 1936), with a maximum length of 16 mm. In winters with no sea ice cover, larval growth rates are zero or negative (Ross and Quetin 1991). An alternative food source during the winter is the sea ice microalgae. This enables the larvae to grow and survive. Growth rates of krill during their second growing season (end of AC0, and AC1, Figure 5.6) are generally rapid, and average total lengths increase from approximately 12 mm in September to 26 mm in the following autumn (Siegel 1987; Quetin and Ross 1991). After the first two growing seasons, immature and mature adult krill do not grow throughout the winter, but either shrink or stay the same size, using a suite of winter-over mechanisms to survive the period of low food availability (Quetin and Ross 1991).

5.3.5 General Distribution of the Larvae and Breeding Grounds

The occurrence of larval euphausiids generally follows the pattern of latitudinal distribution of the adults (Lomakina 1964). Larvae of *E. frigida* and *E. tricantha*, as a rule, have a more northerly distribution than those of the other euphausiid species. Larvae of *E. superba* and *E. crystallorophias* tend, to a large extent, to be distributed to the south, while those of *T. macrura* occur at almost all latitudes. The general pattern is substantially modified by the distribution of the water masses of different origins (Bogdanov et al. 1980; Maslennikov 1980). The situation becomes extremely complicated in the Atlantic sector, in particular in the Scotia Sea, due to the convergence of the water masses of the Antarctic Circumpolar Current and the Weddell Drift.

E. frigida, *E. tricantha*, and *T. macrura* breed over the whole of their habitat range, whereas *E. crystallorophias* in general breeds in the shallow waters in the vicinity of the Antarctic Continent. The breeding sites of *E. superba* are unique among Southern Ocean euphausiids. Marr (1962) discussed the probable localities of spawning and concluded that the vicinity of the continental shelf was the most important factor in locating the spawning areas. Mackintosh (1972) implied that spawning in oceanic areas as well as in the shelf areas was of major importance. Makarov (1972, 1973) described a major spawning area in the frontal zone between the Weddell Sea and the Antarctic Circumpolar Current, thus confirming that spawning does take place in the open ocean. Recent studies in the Scotia Sea, Bransfield Strait, and Drake Passage (Guzman and Marin 1983; Hempel 1983; Mujica and Asencio 1983) have confirmed the importance of convergence zones as breeding locations of *E. superba*.

Evidence is accumulating that spawning in *E. superba* may be highly variable from year to year. Hempel (1985b) found striking differences in the overall abundances of krill larvae (mainly calyptopes) in the Scotia Sea and adjacent waters over the period January–March in 1976, 1978, and 1982. Larval abundance was highest in 1981, generally low in 1978, and intermediate in 1976. Maximum abundance varied by three orders of magnitude. It is thus clear that larval abundance in the western part of the Atlantic sector of the Southern Ocean is subject to marked annual fluctuations.

5.3.6 Summary of the Life Cycle of *E. superba*

Details of the life cycle of *E. superba* are best known from the Scotia Sea region. Based on studies carried out since the *Discovery* Expeditions (Fraser 1936; Marr 1962; Mackintosh 1972; Makarov 1972, 1973; Dolzhenkov 1973; Vorinina 1974; Everson 1976, 1977b, 1981; Hempel 1978; Hempel and Hempel 1978; Nast 1978; Witek et al. 1980) the life cycle of *E. superba* can be summarized as follows (Figure 5.4 and Figure 5.6).

1. Females spawn somewhere in the upper 200 m, probably mostly below 80 m.
2. Immediately after spawning, the eggs sink at a rate 150–250 m per day. The sinking rate of the eggs will be governed by their density and that of the surrounding water.
3. Spawning, as well as sinking, seems to occur over relatively short periods for individual swarms and egg batches.
4. As the eggs sink they undergo development and hatch at variable depths, depending on the bathymetric and hydrological conditions.
5. Although eggs under laboratory conditions will develop and hatch at atmospheric pressure, greater pressure may be necessary for normal development under natural conditions.

6. The sinking of the developing eggs culminates in the hatching of the short-lived Nauplius 1. The depth of hatching is conditioned by the bottom water, where the upper boundary will become the lower boundary for egg sinking (according to Vorinina 1974), or will be the actual place of hatching.
7. After hatching, the larvae ascend to the surface passing through a number of stages, and as they do, lead to the stratification of the larvae in oceanic samples, with nauplei generally below 150 m, metanauplei concentrated below 150 m, and calyptope stages towards the surface (see Figure 5.6).
8. From the calyptope stages onward, *E. superba* lives in the surface water, exhibiting diel vertical migrations. Horizontal migrations of late larval stages and adults will be considered later.

5.3.7 GROWTH, MOULTING, AND LONGEVITY

Despite considerable effort to elucidate the life cycle and ecology of krill, the results to date have given a range of estimates for growth rates and longevity. The question of longevity is fundamental to the management of any commercial fishery; both the growth rate to maturity, and the number of eggs each adult can produce will directly affect estimates of production and hence safe harvesting rates. Growth can be estimated from the relationships between various body length measurements (e.g., Rudd 1932; Bargmann 1945; Marr 1962; Ivanov 1970; Siegel 1982; Miller 1986a), or from laboratory experiments on growth rates (e.g., Mackintosh 1972; Murano et al. 1979; Ikeda and Dixon 1982a, 1982b; Poleck and Denys 1982; Morris and Keck 1984; Ikeda et al. 1985; Ross et al. 2000; Quetin et al. 2003), or from model studies (e.g., Asheimer et al. 1985; Siegel 1987; Priddle et al. 1988). From the viewpoint of production, krill body length measurements need to be related to growth in terms of dry weight increase or energy fixed. Various authors have derived expressions for the relationships of krill body length to dry weight (Clarke 1976; Kils 1981), fresh weight (Heyerdahl 1932; Lockyer 1973; Jazdzewski et al. 1978; Sahrhage 1978; Stepnik 1982; Miller 1986a; Siegel 1986b), and volume (Kils 1979a, 1981); see review by Morris et al. (1988).

Growth in various species of euphausiids has been reviewed by Mauchline and Fisher (1969), Mauchline (1980a), and Siegel (1987). Mauchline (1980a) points out that the growth rate, maturation, and life span of euphausiid species is extremely difficult to determine, primarily due to the difficulty of validating field data through the maintenance of animals under laboratory conditions (cf. Baker 1963; Komaki 1966).

Ettershank (1983, 1984), Siegel (1986b, 1987), and Nicol (1990) have reviewed earlier work concerning growth and age determination in krill. Earlier opinions of a two-year life cycle (Rudd 1932; Mackintosh 1972) conflicted with the conclusion of Bargmann (1945) and Marr (1962) that krill breed only in their third year of life, spending the first two years as larvae and juveniles. Ivanov (1970) on the basis of modal size-class analysis concluded that there were five-year classes. Other analyses of modal length classes have given contradictory results because of different interpretations of strongly overlapping size classes of the older age groups (Aseev 1983). As noted above, evidence has accumulated to show that krill may spawn in successive seasons (Makarov 1975; Ross and Quetin 1983b). This led Kock and Stein (1978), Fevolden (1979), and Makarov (1979a) to postulate that krill may live for three years or more. The general consensus is that krill live for at least five years and that the life span may in some populations extend to seven.

Much recent research has been directed towards resolving the impasse concerning growth rates and longevity. Such research has involved laboratory rearing experiments to determine moulting frequencies and growth rates and the exploration of new methods of age determination.

Growth in euphausiids, as in other arthropods, is dependent on moulting, which continues in basically identical cycles during the greater part of the life span. Results of laboratory observation on moulting have been published by Mackintosh (1972), Clarke (1976), Murano et al. (1979), Ikeda and Dixon (1982a, 1982b), Poleck and Denys (1982), Buchholz (1983, 1985), Segawa et al. (1983), Morris and Keck (1984), and Ikeda et al. (1985). The intermoult periods reported by these authors range from 13 to 30 days. These laboratory experiments require the maintenance of krill under controlled environmental conditions for prolonged periods. Such experiments are subject to considerable difficulty (Buchholz 1983). First, as pelagic animals, krill live in an environment without boundaries. Hence, they are maintained in a highly unnatural situation in maintenance chambers. Secondly, there are difficulties in providing the krill with the right amounts and kinds of phytoplankton as food.

In laboratory studies Ikeda and Dixon (1982a, 1982b) found that the intermoult period of specimens kept at 0.5°C ranged from 22.0 to 27.5 days for females (mean 25.5 ± 3.2), and from 25.7 to 29.8 for males (mean 27.6 ± 3.9), with an overall mean of 26.6 ± 4.1 days. Observed changes in body length included increase (positive growth), decrease (negative growth), and no change (zero growth). Buchholz (1982, 1985) developed a more sophisticated flow-through system for keeping krill in the laboratory that reduced handling and furnished a constant supply of natural phytoplankton. Morris and Keck (1984) later modified the Burchholz system and found a positive growth of 8.0% and a mean intermoult period of 14.3 days. The average growth rate obtained by Buchholz was 0.132 mm day^{-1}; this agrees with the 0.142 mm day reported by Morris and Keck (1984) and is higher than that recorded by Ikeda and Dixon (1982a).

Pakhomov (1995) listed the then available growth rates for *E. superba*. They ranged from lows of very small for feeding krill (Ikeda and Dixon 1982a), negative for nonfeeding krill (Ikeda and Dixon 1982a), and 0.025 for a field population (McClatchie 1988), to highs of 0.130

for a field population (McClatchie 1988), 0.190 for a field population (Ikeda 1985) and 0.220 for a field population (Pakhomov 1995). Thus there are wide variations in the growth rates that have been determined. Given the potential for pronounced regional variations in temperature and food conditions, as well as in the pattern of seasonal change in these factors (Whitehouse et al. 1996), it is perhaps not surprising that studies of krill growth rates and life cycle, using different methodologies and locations, have arrived at differing conclusions (see Ikeda 1985).

Reid (2001) investigated the growth of *E. superba* at South Georgia. The increase in length of krill he found there would appear to be much greater than that predicted by previous models of krill growth, in which krill of 42 mm would attain approximately 48–49 mm rather than the 52–56 mm estimated by Reid.

Ikeda and Dixon (1982a, 1982b) maintained krill in the laboratory for 211 days without food. During this time a significant reduction in body weight (32.1–56.1% of initial body weight) was observed. Ikeda and Dixon argued that body shrinkage might be a strategy for overwintering when the stocks of phytoplankton are scarce, or nil, and krill would need to burn up body tissue to fulfil energy needs. Shrinkage in the laboratory has been shown for five species of euphausiids. The capacity to shrink can be taken as a natural response by *E. superba* to sub-optimal feeding conditions, and shrinkage in the laboratory has been shown to have no adverse effects on the animals subsequent ability to grow and survive.

While shrinkage certainly does occur in some populations, it is by no means universal. Both Siegel (1986b) and Daly (1990) reported significant growth of young krill during the winter in the marginal ice zone. Growth rates (mm day^{-1}) are a combination of the growth increment (mm) at moulting and the moulting frequency (day^{-1}). The length increment at ecdysis is set several days before the exoskeleton is actually shed (Buchholz 1985) and, thus, reflects the nutritional environment and physiological status of the individual during the previous intermoult period. Growth and moulting frequency is thus dependent upon the availability of food.

Ross et al. (2000, 2001) investigated growth in *E. superba* near Palmer Station, Antarctic Peninsula, for over 4 years (1991–1992, 1993–1994, 1994–1995, and 1995–1996). They found that instantaneous growth rates reflected the in situ nutritional history of the previous intermoult period. The response of krill to the food environment was seen on temporal scales of days and weeks. Percent growth per intermoult period (percentage IMP^{-1}) varied significantly both within and between years, ranging from $\sim$2% to $\sim$10% IMP^{-1}. Percent growth IMP^{-1} increased with increasing chlorophyll *a*, reaching a maximum of 9.3% IMP^{-1} above a critical concentration of about 3.5 mg m^{-3}. Maximum growth was reached in only 2 years, 1991–1992 and 1995–1996. In a multiple regression analysis, total chl *a* and prymnesiophyte chl *a* explained over 71% of the temporal variance in growth. In general, highest growth was found toward the end of a diatom bloom and lowest during periods of low phytoplankton biomass, or blooms dominated by cryptophytes and prymnesiophytes. The results of the study supported the hypothesis that maximum growth rates are only possible during diatom blooms and that production in Antarctic krill is limited both by food quantity and quality. In a subsequent study, Ross et al. (2004) carried out instantaneous growth rate experiments on larvae collected from the under-ice habitat on the outer shelf, mid-shelf, and in the mouth of Marguarite Bay, western Antarctic Peninsula. For all experiments average growth increments were about 11.6% per intermoult period, with a medium intermoult period of 30.6 days.

There are two schools of thought regarding the feeding, growth, and metabolism of *E. superba* during winter. The first of these assumes that feeding ceases, and that krill must reduce their metabolism, utilize stored energy, and even shrink in size. Ikeda and Dixon (1982a, 1982b) point out that, even allowing for a considerable reduction in body lipid content (Clarke 1980a), *E. superba* could not survive the entire winter on lipid alone. They purposely starved individuals ranging is size from 22.7 to 49.6 mm for 211 days finding a significant reduction in body weight (32.1–56.1%), and concluded that starvation alone and utilization of body protein was the only mechanism necessary to survive the winter. Quetin and Ross (1991) concluded that in areas of annual ice, krill do not have an opportunity to feed on ice algae during the winter, and that in the winter adults do not feed, have lowered metabolic rates, and negative or zero growth rates.

The scenario outlined above is at odds with observations allied to the second school of thought, which hold that krill do feed and grow in the winter. Evidence is accumulating that food is available to krill throughout the winter. In situ observations of apparent feeding on ice microalgae by both larvae and adults (Garrison et al. 1986a, 1986b; Kottmeier and Sullivan 1987; Quetin and Ross 1988; Stretch et al. 1988; Hamner et al. 1989; Daly 1990; Daly and Macaulay 1991; Ross and Quetin 1991b; Quetin et al. 1994b; Fraser et al. 1997, 2002a) have been confirmed by examination of gut pigments, as well as by experiments (Marschall 1988). The guts of krill caught in the southern Weddell Sea in winter contained a variety of phytoplankton (Lancraft et al. 1989). Feeding on phytoplankton in the water column during the winter has been observed (Morris and Priddle 1984); however, given the paucity of phytoplankton they concluded that it is unlikely that krill will rely completely on phytoplankton throughout the year. Even for krill feeding on ice microalgae, Daly (1990) concluded that larvae must be obtaining carbon from heterotrophic and possibly detrital sources.

Feeding on detritus near the bottom has been observed in shallow waters (Kawaguchi et al. 1986), but the water depths over the greater part of the range of krill precludes this as a viable alternative. Experiments conducted by Price et al. (1988) during the summer indicate that krill are able to ingest zooplankton, but they concluded that this was insufficient to meet metabolic requirements. Copepods and other zooplankton have consistently been found among the gut contents of *E. superba* in summer (Hopkins 1985b), autumn (Hopkins and Torres 1989), and winter (Lancraft et al. 1991).

There are thus conflicting views on krill growth. It appears that krill can adjust to the food situation by changing the frequency of moulting. Thus, krill can apparently adjust their growth rate very sensitively to the specific environmental situation by both altering the frequency of moulting and growth increment between moultings. Krill are able to adapt to the strong regional and seasonal changes in feeding conditions that are typical for Antarctic waters. Krill grow fast, and in spite of being planktonic, attain a large size. This enables fast swimming, which facilitates the location of rich food resources. When these are encountered fast growth is initiated.

Siegel (1987) has studied the age and growth of five species of euphausiids from the Antarctic Peninsula region and the southeastern Scotia Sea. Figure 5.7 summarizes the minimum and maximum size of their development stages and the age of occurrence of each development stage for each species. Life spans range from two years for *E. frigida* to six years for *E. superba*. The latter was calculated to develop from the larval phase (nauplei, metanauplii, and calyptope stages) into the juvenile stage at a length of 15 mm, normally during the winter season in the first year of life. The juvenile stage covered the length classes of 14 to about 16 mm, while the smallest subadults already occurred at a length of 27 mm. The overlapping size distributions of the developmental stages were also found in the subadult and adult (reproductive) stages. The largest subadults measured 45 mm, while the smallest were around 35 mm. When taking the seasonal growth curve into account, the juvenile stage is continued throughout the second year (age group 1+). At the end of age 1+ the krill develop into the subadult stage which then dominates the age group 2+. During this year only a few individuals mature. From age group 3+ onwards all krill are adults. Siegel considered that *E. superba* spawned three times during its life cycle. The southern Weddell Sea krill showed the same pattern as those from the Antarctic Peninsula region.

5.3.7.1 Assessment of Longevity

Although the data have given conflicting results concerning both the growth rate and longevity of krill, a consensus has emerged for the view that krill are long-lived, living for at least five or six years. Both Ettershank (1983, 1984) and Rosenberg et al. (1986) have estimated a maximum age of six to seven years for krill to approach 60 mm in length. The solution to the problem of krill longevity lies in the interpretation of the number of year classes in the adult krill group. Siegel (1987) points out that his age group 5+, estimated as the oldest one, might possibly embrace one or more cohorts of very low abundance which cannot be separated by distribution mixture analysis. However, he noted that the largest krill found in all of his samples taken in October/November were 55 mm in length, indicating that all krill larger than 55 mm had died off during the preceding winter season.

Ettershank (1982, 1983, 1984) has reviewed the extensive literature on the relationship between size and age in *E. superba*. He discusses the use of an age pigment, lipofuscin, which has been found in all aerobically respiring invertebrates. Lipofuscin accumulates as a result of metabolic activities (Ettershank et al. 1982) and its assay by a fluorescence technique is thus a measure of the cumulative metabolism of an organism, or metabolic time. Ettershank (1984) analysed the lipofuscin content of adult female krill from a sample taken in Prydz Bay in 1981. Seven age classes could be distinguished on the basis of this analysis. Berman et al. (1989) determined the age of 252 mature female krill collected from Prydz Bay using length frequency analysis, combined with a computerized image analysis system, and the fluorescent age pigment technique. The results of both methods suggested six-year classes for adult krill. Correspondence between the ages determined by the two techniques was generally within one year. On the other hand Nicol (1990) states that the lipofuscin technique as it was initially applied was being questioned on a number of methodological and technical grounds (Eldred et al. 1982; Nicol 1987). Additionally, a number of studies of natural populations of crustaceans have failed to show a clear relationship between fluorescence and age (Hill and Radthe 1988; Mullin and Brooks 1989). Hill and Womersley (1991) reviewed the problems involved in fluorescent age pigment methodologies. They concluded that while the technique shows a great deal of promise, much further research is necessary.

5.3.8 MORTALITY

Data on krill mortality rates is relatively rare. Estimates obtained by different methods have been summarized by Miller and Hampton (1985) and discussed by Siegel (1992). A range of estimates is listed in Table 5.1.

Calculations based on length-at-age data are sensitive to the species' lifespan. As discussed above, estimates of the number of krill age groups range from 6, including the 0-age group (i.e., a lifespan of five years; Siegel 1987) to a maximum of 7 or 8 (i.e., longevity of 6–7 years; Ettershank 1984; Rosenberg et al. 1986). Based on this maximum range, krill mortality would then be expected to remain within the range $M=0.66$–0.92. This is concurrent with the range of recent estimates and corresponds to a survival rate of 40–51% for postlarval age groups from one year to the next.

5.3.9 RECRUITMENT

Studies have demonstrated that recruitment success in Antarctic krill is highly variable (Siegel and Loeb 1995; Siegel et al. 1998, 2002; Watkins 1999; Siegel 2000a; Quetin and Ross 2003), leading to significant seasonal interannual differences in the population structure and,

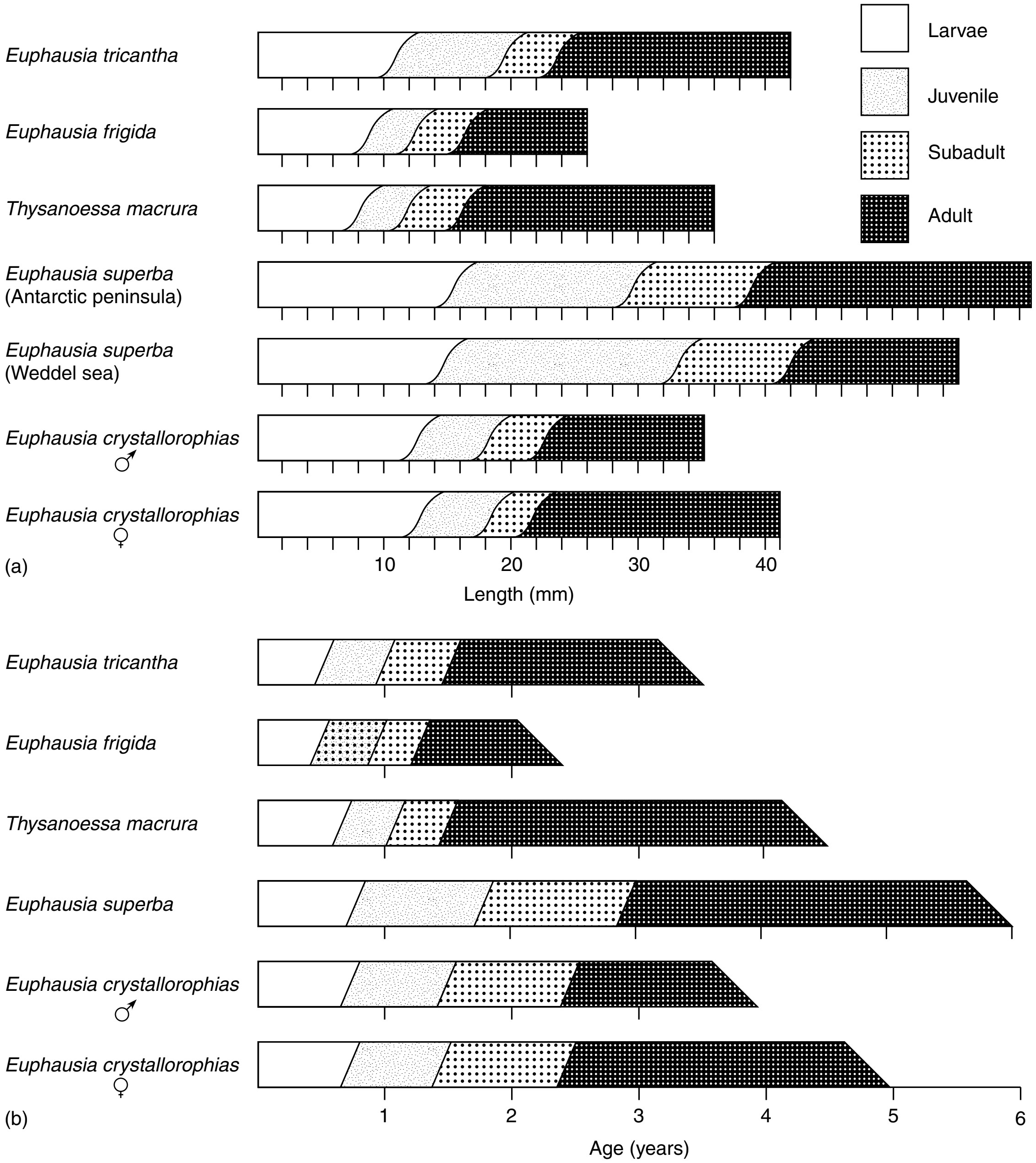


FIGURE 5.7 Life cycles of Antarctic Euphausiacea: (a) Minimum and maximum size of developmental stages for the different species. (b) Occurrence of the developmental stages at age of the species (Pen = Antarctic Peninsula, Wed = Weddell Sea). (From Siegel, V., *Mar. Biol.*, 96, 483, 1987.)

potentially, abundance. In the Palmer LTER study region west of the Antarctic Peninsula, interannual variability in intensity of reproduction has been over 10-fold (Quetin and Ross 2001). Priddle et al. (1988) suggested that a failure in recruitment in one year could result in a 3- to 4-fold variation in density of *Euphausia superba* and that recovery to initial densities might take several years of good recruitment. Based on the correlation of recruitment and seasonal sea ice dynamics (Siegel and Loeb 1995; Quetin and Ross 2003), and a warming trend in the Antarctic Peninsula (Smith and Stammerjohn 2001), Loeb et al. (1997) speculated that a warming climate might alter the population dynamics of Antarctic krill and its availability to predators in the region.

Data from studies of *Euphausia superba* in the Palmer LTER region over the period 1991–2002 (Quetin and Ross 2003) showed a pattern of episodic recruitment, with 2 strong year classes in succession followed by 3 or 4 moderate or poor year classes. The recruitment index was positively correlated with the absolute value of a seasonal El

TABLE 5.1
Estimates of Krill Natural Mortality

Mortality	Method	Area	Reference
5.5	Edmondson's method abundance data of length groups	Scotia Sea	Kawakhami and Doi (1979) Brinton and Townsend (1984)
2.31	Larval to subadults, 1–2 years old		
0.51	2–3 years old		
0.78–1.17	Linearized catch curve data	Ant. Peninsula	Siegel (1986)
0.88–0.96	Linearized catch curve data		Siegel (1992)
0.94–0.99	Pauly (1980) formula on VBGF and M relationship		Siegel (1986)
0.8–1.35	$M = 2 \times K$ of VBGF	Scotia Sea	Priddle et al. (1988)
0.5	1-Cumulative length-frequency	*Discovery* data	
0.45–0.65	Length-dependent Predation curve		

Source: From Siegel, V., Kalinowski, J., *Southern Ocean Ecology: The BIOMASS Perspective*, Cambridge University Press, Cambridge, 157, 1996. With permission.

Nino/Southern Oscillation (ENSO) index, with the strongest recruitment during the neutral or moderate periods of ENSO. The mechanisms underlying the strong link between the recruitment index and ENSO is most likely the effects of seasonal sea-ice dynamics on both reproduction and winter-over survival.

5.4 KRILL AGGREGATIONS

5.4.1 Introduction

The salient characteristic of euphausiid distribution in the Southern Ocean, especially that of *Euphausia superba*, is their patchiness. Throughout most of its life cycle, *E. superba* occurs near the surface of the sea in discrete swarms or schools (Marr 1962; Mauchline 1980b; Hamner et al. 1983), and reddish patches of krill are often visible from aboard ship (Marr 1962; Shust 1969). Marr (1962) has plotted such observations up to that date. An understanding of such processes underlying the formation and persistence of such aggregations is essential for the management of krill fisheries, since they define the site of fishing grounds, the major trophic relationships, and energy flow within the system.

Past attempts to correlate krill aggregations with physical and environmental factors have not been very conclusive. Hence recent research has focussed on the biological and behavioral processes involved in the formation and persistence of krill aggregations (e.g., Bidigare et al. 1981; Antezana and Ray 1983, 1984; Hamner et al. 1983; Everson 1984a; Watkins et al. 1986, 1990, 1992; Daly and Macaulay 1991). Increasingly attention is being paid to the relationships between feeding, vertical migration, moulting, and predator–prey interactions in swarming behaviour.

5.4.2 Types of Aggregation

The ability of *Euphausia superba* to aggregate in swarms is a feature that distinguishes this species from other Antarctic euphausiids, although *E. crystallorophias* may also occur in swarms (O'Brien 1987). The sizes and shapes of krill aggregations vary considerably. They vary in area, depth range, and in the sex ratios and age classes of the individuals in them (Marr 1962). The diameter, or length, of krill swarms is generally in the range of 0.5 m to over 100 m, but is sometimes considerably greater. The area covered ranges from a few square metres to over 600 m^2 and exceptionally may cover many square kilometres. Most swarms appear to be laminar in shape, ranging from a few centimetres to a few metres in thickness. They can also be ribbon-shaped from oval to circular.

Various terms ("swarm," "patch," "school," "layer," "super-swarm") have been used to describe the different types of krill aggregations. Classification schemes have been proposed by Mauchline (1980b), Kalinowski and Witek (1982, 1983, 1985), and Murphy et al. (1988). The scheme adopted here (Figure 5.8) is the modified version of Kalinowski and Witek's (1985) scheme, proposed by Miller and Hampton (1985) and used by Siegel and Kalinowski (1996). The three levels of organization shown in Figure 5.8 correspond to three horizontal spatial scales (i.e., macro, $>1{,}000$ km; meso, 10–100 km; and micro, <10 km). As proposed by Murphy et al. (1988), they have a corresponding time scale: "concentrations" at a scale of months, "patches" from days to months, and "aggregations" from hours to days.

Patches can be subdivided in several ways. One possibility is to follow a spatial and time scale classification which would lead to microscale aggregation (less than 10 km) superswarms, swarms, layers, and irregular forms. Behavioral mechanisms of the krill are probably more important

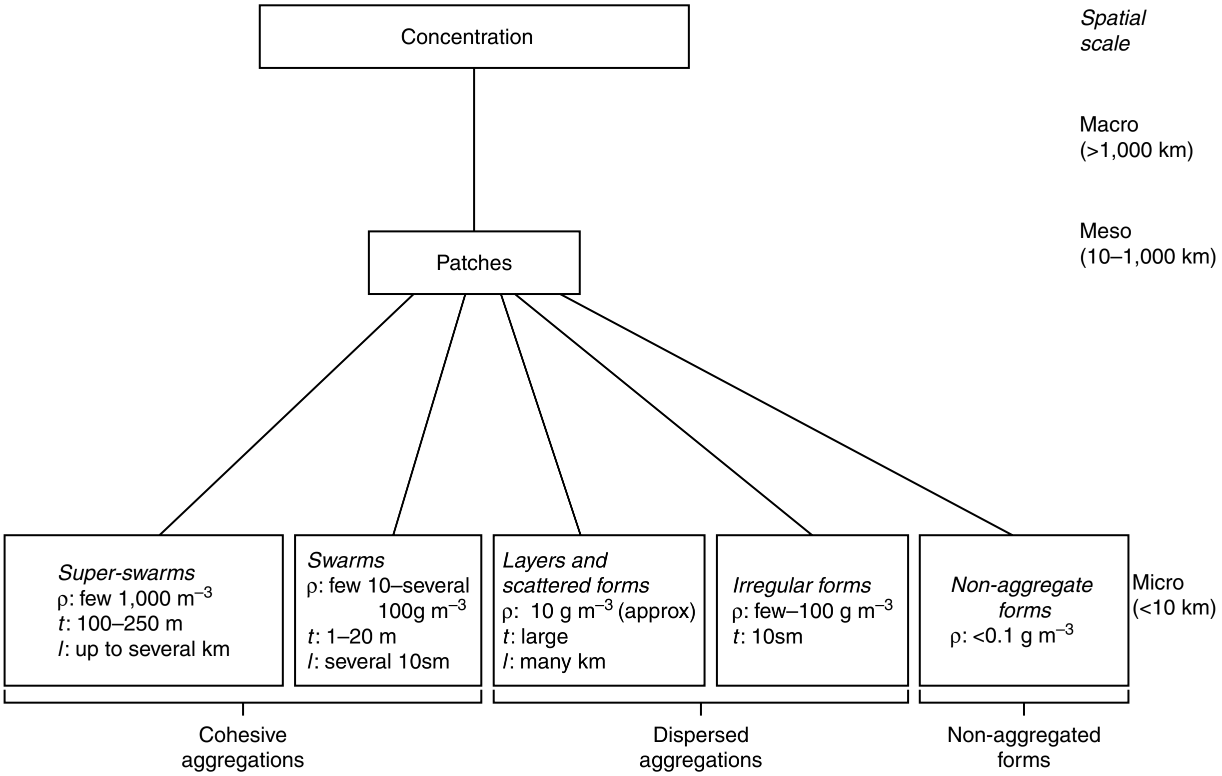


FIGURE 5.8 A classification scheme for krill aggregations (modified from Kalinowski and Witek 1985): *p*, density; *t*, thickness; *l*, length. (From Siegel, V., Kalinowski, J., *Southern Ocean Ecology: the BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, 145, 1996.)

in maintaining the patches, rather than environmental physical parameters.

5.4.3 PHYSICAL CHARACTERISTICS OF AGGREGATIONS

5.4.3.1 Swarms

Swarms are the commonest type of aggregation and they are characterized by relatively small dimensions and relatively uniform high density (Figure 5.9). They are described by Kalinowski and Witek (1985) as "being typically several tens of metres across, several metres to about 20 m thick, with densities generally between 100 and several 100 g m^{-3}" Miller and Hampton (1985) have summarized information on krill aggregation parameters detected in 1976–1977 and 1977–1978 summer seasons (Kalinowski and Witek 1982, 1985) and during the First International Biomass Experiment (FIBEX) (Table 5.3 and Table 5.4). FIBEX data were consistent with those obtained by Kalinowski and Witek. Aggregations (mostly swarms) were estimated to have been on average 73 m wide (along the widest dimension) and 5 m thick, with a mean density of 2.49 g m^{-3}. The swarm biomass ranged from 90 kg to 407 tons. From the BIOMASS data (Table 5.2) it is clear that there are regional differences in krill swarm dimensions, density, and biomass.

Acoustic work indicates that the distribution of swarm sizes tends to be highly positively skewed. Hampton (1985) studied acoustically the abundance, distribution, and behaviour of *E. superba* between 15° and 30°E and south of 60°S to the ice edge at about 69°S during February–March 1981. The krill were spread uniformly over the survey area, probably because of the absence of large-scale hydrodynamic features to concentrate them in any part of the region. The mean biomass and density of the 1304 swarms encountered were estimated by multi-channel echo location to be 0.139 tons and 31 g m^{-3} respectively. Ninety-eight percent of the swarms were estimated to have weighed less than 1 tonne. Most of the biomass was concentrated in a few large swarms. This agrees with data from the Antarctic Peninsula and Scotia Sea regions between 1976 and 1979 (Miller and Hampton 1985) where 665 of all swarms detected had a biomass of less than 1 ton.

In addition to acoustic measurements, various estimates of swarm densities have been made directly either visually or photographically (Guzman and Marin 1983), or indirectly from catches in commercial trawls or various types of research nets. Underwater photographic estimates have given krill densities of 50,000–60,000 m^{-3} (Ragulin 1969), and up to 550 individuals m^{-3} (Guzman and Marin 1983). Density estimates from commercial catches and net-sampling of visible swarms exceed acoustically derived estimates by at least two orders of magnitude. Miller and Hampton (1985) consider that while no conclusive explanation of

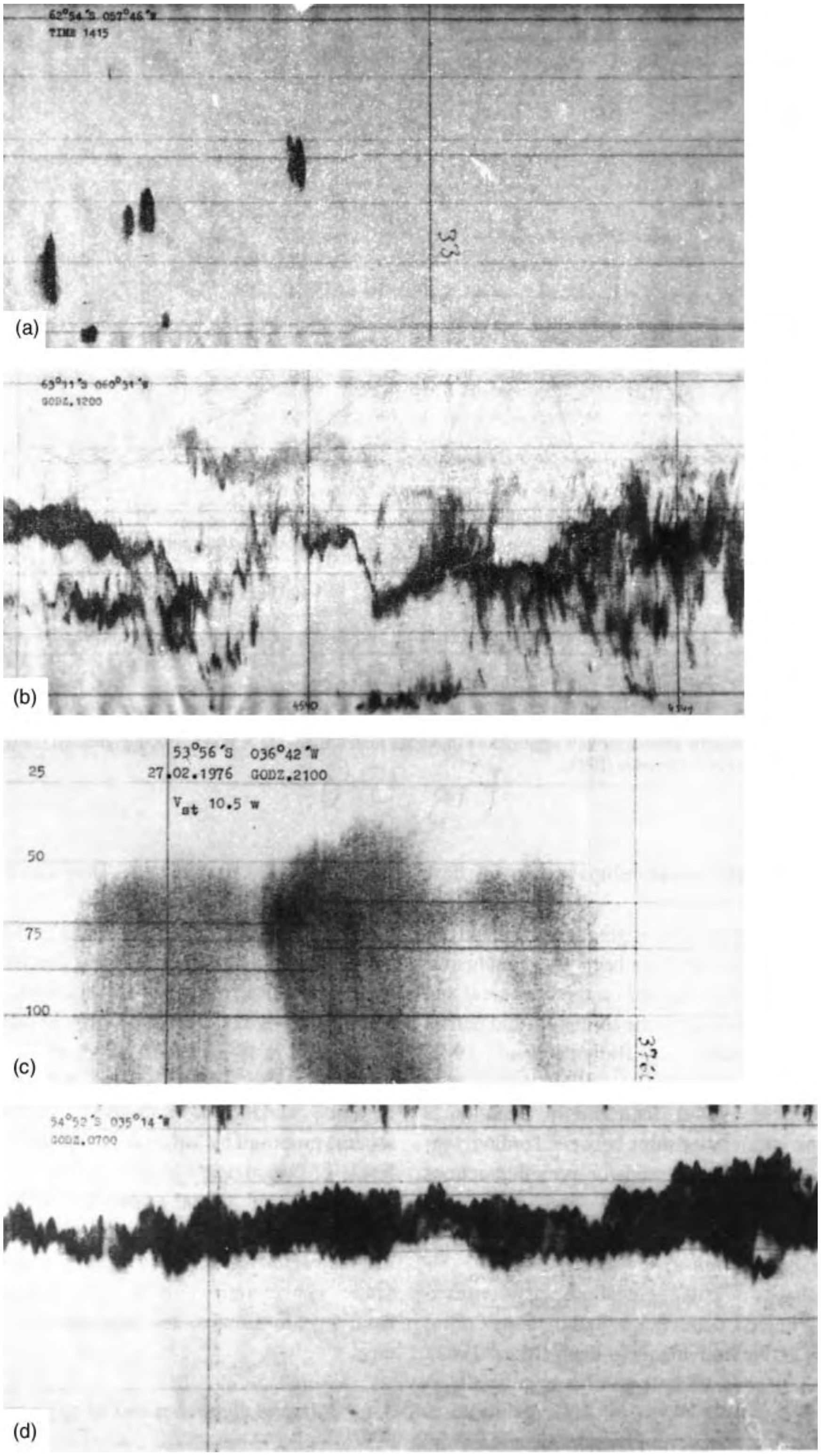


FIGURE 5.9 Echorecordings of different forms of krill aggregations: (a) swarms; (b) irregular forms; (c) scattered forms; (d) layers. (From Kalinowski, J., Witek, Z., *BIOMASS Handbook No. 27*, SCAR/SCOR, Scott Polar Research Institute, Cambridge, 9, 1985.)

this discrepancy could be offered at that time, it should be noted that nonacoustic estimates could be biased towards larger and denser swarms (cf. discussion in Hampton 1985; Nicol et al. 2000).

5.4.3.2 Superswarms

Particular interest in krill aggregation behaviour in recent years has focused on the relatively rare occurrence of

TABLE 5.2
Vertical Migration of Some Southern Ocean Euphausiids

Species	Day Depth Range (m)	Night Depth Range (m)	Total Vertical Range (m)
Euphausia superba	100–10	70–0	900–0
Euphausia frigida	500–250	100–50	750–0
Euohausia tricantha	500–250	250–0	750–0

Source: From Mauchline, J., Fisher, L.R., *Adv. Mar. Biol.*, 7, 1, 1969. With permission.

ultra-large (over 1 km across) aggregations containing very large numbers of animals, which have been termed “superswarms” (Cram et al. 1979). Superswarms have been reported from the Gerlache Strait (Cram et al. 1979), off South Georgia (Kalinowski and Witek 1982), off Enderby Land (Kanda et al. 1982), near Elephant Island (Mathisen and Macaulay 1983; Macauley et al. 1984), and in the Prydz Bay region (Higgenbottom and Hosie 1989). The size of such swarms can be as large as 150 km^2 (Macauley et al. 1984) and extend over 13 km (Higgenbottom and Hosie 1989), or even 21.6 km (Siegel and Kalinowski 1996). Maximum density can reach 1,530 g m^{-3} (Higgenbottom and Hosie 1989), although the average density is generally between 40 and 500 g m^{-3} (Macauley et al. 1984). The biomass of these superswarms can be very high. For example, Macauley et al. (1984) estimated from acoustic measurements that the biomass of a superswarm covering an area of about 450 km near Elephant Island during FIBEX was 2.1 million tons. However, the BIOMASS Working Party (Anonymous 1986) substantially revised the acoustic target strength expression used for the estimate, and the use of this revised estimate would reduce the estimate to about 200,000 tons. Nevertheless this would still be a very high biomass for a single krill aggregation.

5.4.3.3 Layers and Other Scattered Forms

Layers and other scattered forms are diffuse aggregations which may extend many kilometres at least in one direction, and which appear on echo-sounding recordings as thin layers (Figure 5.9d), or at other times as clouds or diffuse smudges of far greater vertical extent (Figure 5.9c). According to Kalinowski and Witek (1982, 1983), their density is generally low in the order of 10 g m^{-3} which distinguished them from the high density superswarms. Thin layers have been found both day and night (Cram et al. 1979; Kalinowski and Witek 1982, 1983), whereas broad layers appear to be formed by the dispersal of day-time swarms (Everson 1982; Kalinowski and Witek 1982, 1983).

Watkins and Murray (1998) have compared the characteristics of layers and swarms near Elephant Island (Figure 5.9d). Krill length, sex and maturity stage, net and acoustic estimates of number density were found to vary significantly with the large layers sampled. The variation occurring in a set of 28 swarms sampled contemporaneously with the layers. Thus unlike a krill swarm, a whole krill layer may account for a substantial amount of the variation in the local krill population. The layers are considered to play an important role in the ecology of the krill within the area. Firstly, these large layers may contain a significant proportion of the biomass within an area. Secondly, the structure of the layers gives some insight into the way in which krill swarm formation and dispersal may be occurring.

5.4.3.4 Irregular Forms

Kalinowski and Witek (1982, 1985) distinguish between swarms with well defined boundaries and larger irregular aggregations with poorly defined boundaries, and also those with variations in density (Figure 5.9b). They reported that such aggregations are typically tens of meters thick, and vary in density between a few and several hundred grams per cubic metre. A distinguishing feature is that they are often multispecific, containing other macroplankton species such as *Thermisto* sp., *Thysanoessa* sp. and salps (cf. Schulenberger et al. 1984; Kalinowski and Witek 1985).

The relative proportions of krill that are present in compact swarms or in dispersed forms is debatable. However, it appears that the major proportion of krill in any one area is concentrated in swarms (Miller 1986a). Cram et al. (1979) found that in the Gerlache Strait, 82% of the krill was concentrated in swarms (particularly in a few superswarms), whereas in the Scotia Sea the proportion was 47%. The corresponding proportions in layers were 5.5% and 51.5% respectively.

5.4.4 BIOLOGICAL CHARACTERISTICS OF AGGREGATION

The biological characteristics of krill may vary between swarms, and even in those swarms close together. The size, maturity stage, moult- and feeding-state of the krill in one swarm may be quite different from that in an adjacent swarm (Buchholz 1985; Watkins 1986; Watkins et al. 1986, 1990; Priddle et al. 1990). In situ observations by divers (Hamner et al. 1983; Hamner 1984; O’Brien 1987) have shown that krill within individual swarms are often positioned in a very organized way, and may show parallel orientation and coordinated behaviour such as seen in fish schools (Shaw 1978). The size distribution of krill within a swarm is often more restricted than that of the local population (Marr 1962). Sometimes the majority of krill are of the same sex or in the same phase of the moult cycle; hypotheses to explain such observations have involved various types of size-dependent sorting mechanisms (Kils 1981; Hamner et al. 1983; Watkins et al. 1992) or behavioral responses such as synchronous moulting (Buchholz 1985).

5.4.4.1 Homogeneity

The available data from research and commercial catches might convey that that most krill aggregations are monospecific (e.g., Marr 1962; Everson 1977b; Lubimova et al. 1980), although as noted above this may not be true for irregular aggregations. Schulenberger et al. (1984) have investigated the composition of a superswarm of krill studied by Brinton and Antezana (1984) and Macauley et al. (1984) near Elephant Island. They found that the large swarm was not composed entirely of euphausiids. Large fractions of many of the samples consisted of copepods, amphipods, and salps. The euphausiid fraction of the superswarm did not consist entirely of *E. superba*. In many samples, *E. superba* were outnumbered by *E. crystallorophias*, and/or *Thysanoessa* spp. co-occurred. There was some evidence for the separation of high concentrations of larvae from high concentration of adults, with the separation occurring both horizontally and vertically.

The age and sex composition of krill swarms are variable. Swarms may consist exclusively of groups restricted in terms of size, age, or sex (e.g., one of two successive larval stages, or of a single sex) in contrast to other swarms of mixed size and age groups and mixed sexes. Watkins (1986) found significant differences in the length distributions of krill taken from adjacent swarms, whereas length distributions in samples taken from the same swarm were not significantly different. In a subsequent study, Watkins et al. (1986) found extensive heterogeneity in length, sex ratio, moulting condition, and gut fullness of krill taken in 28 discrete aggregations.

Several authors have assumed that krill are evenly distributed within the swarms, while others have observed that the density across a swarm can vary by some orders of magnitude (Godlewska and Klusek 1987). Godlewska and Kluseck found that, at least in larger swarms, on average krill tend to concentrate at the centre of the swarms. Thus individuals near the swarm edge are more loosely packed and therefore less connected to the swarm than the centrally situated individuals. It has been suggested that individual krill move from aggregation centre to edge, and vice versa, in response to either feeding conditions and behaviour (Antezana et al. 1982; Antezana and Ray 1983), concentration of excretory products (Strand and Hamner 1990), and/or predation pressure (Antezana and Ray 1983).

5.4.4.2 Swimming

Swimming activity is an integral part of aggregation behaviour. Hamner (1984) estimated that krill in orientated swarms could swim rapidly (with speeds of up to 20 cm s^{-1}) for considerable distances. He suggested that animals in such a swarm maintained communication by rheotactic cues generated by the individuals above and ahead of them. This would ensure coordinated swimming in the dark. The swimming speeds in the wild were consistent with those measured in the laboratory.

Observations made by Kanda et al. (1982) off Enderby Land showed that moving swarms can stay together for long periods while covering considerable distances. They tracked one superswarm for 19 days over a distance of 116 nautical miles, and another for a distance of 45 miles over 8 days. The average speeds were approximately 15 and 12 cm s^{-1} respectively. Both swarms moved south against the prevailing current, as indicated by the drift of nearby icebergs. The swimming speeds are consistent with those reported by Hamner (1984) and are close to the figure of 13 cm s^{-1} which krill can maintain without exceeding their "standard" (i.e., hovering) metabolism.

5.4.4.3 Orientation

With a rare exception, swimming animals observed by Ragulin (1969) and Hamner et al. (1983) were orientated parallel to each other, even at night. Hamner et al. (1983) consider that parallel orientation of swarming krill is indicative of active foraging and is incompatible with intensive feeding, and this is supported by the observation that krill were feeding rapidly in the only nonorientated swarm which they observed. Underwater photography of swarming krill by Guzman and Marin (1983) showed predominantly parallel orientation, except in the early morning and at night when the orientation was more random. They suggested that the latter behaviour might be typical of night time feeding.

5.4.4.4 Feeding

In summer feeding occurs over a wide range of phytoplankton concentrations, suggesting that krill do not have to disperse to find food. Krill in swarms often have full stomachs. Hamner et al. (1983) observed that feeding was more intense when the swarms were small and dense. They concluded that nonorientated swarms were feeding, while parallel orientation by swarming krill was an indication of active foraging. In an analysis of variation in krill feeding between swarms Priddle et al. (1990) could not link gut fullness to animal length, sex and maturity stage, or to the properties of the swarm (swarm size, depth, time, density). Their conclusion was that the observed variability reflected the patchiness of the food source.

A possible advantage of aggregation is to improve foraging efficiency (to search for food resources) as suggested by Kanda et al. (1982). In winter phytoplankton food supply in the water column is minimal, and krill predominantly live directly beneath the ice where they are dispersed (Garrison et al. 1986a, 1986b; O'Brien 1987; Marschall 1988; Siegel et al. 1992). Almost no swarming could be detected in winter in the open water zone of the entire Antarctic Peninsula area (Sahrhage 1989b; Siegel 1989) until the onset of pack ice retreat in the spring when krill switch from the cryopelagic to the pelagic habitat and recommence swarming (Cuzin-Roudy and Schalk 1989; Siegel et al. 1998). This seasonal change in behaviour initiates a strong association between krill feeding and aggregation behaviour.

5.4.4.5 Reproduction

As aforementioned krill swarms are often dominated by one sex or one particular maturity stage (e.g., Marr 1962; Everson 1977b; Anonymous 1981a). It has therefore been suggested that reproductive behaviour may influence aggregation behaviour or, alternatively, that close proximity of individuals in swarms may play an important role in mating and/or spawning (Miller and Hampton 1985). While it has been postulated that certain krill swarms, especially those in specific areas associated with particular topographic features, constitute spawning or breeding aggregations (Marr 1962; Naumov 1962; Makarov 1973, 1979a; Kock and Stein 1978), the relationship between swarming and reproduction are not at all clear. Naito et al. (1986) observed mating in association with swarming and concluded that a single pair of mating krill can stimulate other animals in a swarm to mate. However, the male:female ratio in swarms can vary considerably, e.g., from 1:3 to 4:1 in one study (Watkins et al. 1986) and 1:1.5 to 1:47.1 in another (Siegel 1986a). Quetin and Ross (1984) found that while gravid females were present in most discrete swarms sampled, they were dominant in only a few swarms. They concluded that females do not have to dominate a swarm to produce eggs.

5.4.4.6 Moulting

Krill from the same swarm are often found to be of the same moulting stage (Buchholz 1985). Morris (1985) developed an integrated model of krill swarming, feeding, and moulting behaviour, with the soft, most endangered post-moult stages living in deeper layers during the day and only swarming near the surface at night. Hamner et al. (1983) even observed synchronized moulting within a swarm and concluded that discarded moults may act as a decoy for predators.

5.4.4.7 Interactions with Predators

Although there is much indirect evidence (based on records of diving patterns) to suggest that seals and some penguin species feed on krill swarms mainly at night (e.g., Croxall et al. 1985; Doidge and Croxall 1985), there have been only a limited number of observations of predators feeding on krill in the field.

Some of the models outlined below are based in the assumption that the gregarious behaviour of krill confers greater defence against predators. They assume that predators have greater difficulty in locating patchy prey, that rapid satiation occurs once the patches are located and that they may be distracted or confused, making the capture of prey more difficult (Cerri and Fraser 1983). However, as Antezana and Ray (1983) point out, this would not apply to whales as "mass" predators. Much more information is needed on the strategies used by the various predators (cephalopods, fish, seals, whales, and some benthic invertebrates) and the behaviour of krill in avoiding predators.

5.4.5 FACTORS AFFECTING AGGREGATION

There has been much debate as the factors that involved in the formation of aggregations and the relative importance of the various factors. In considering the causes of swarm formation, it is useful to follow Nicol's proposal (cf. Miller and Hampton 1985) whereby a distinction is made between proximate causes (factors that serve to trigger aggregation) and ultimate effects (adaptive advantages of aggregation). The most important factors are light, physiological stimuli, phytoplankton (i.e., food) concentration, and a range of hydrographic mechanisms. Mauchline (1980a) considers that aggregation is probably achieved by several or all of the following processes rather than any one in isolation: (a) the innate drive towards aggregation, triggered in some populations by the attainment of a physiological condition (e.g., approaching sexual maturity); (b) the physical and chemical discontinuities and gradients in the environment in conjunction with the physiology of the species population, resulting in the population having a restricted distribution (this situation produces populations in which the threshold densities that trigger the formation of shoals and swarms occur); (c) visual cues in the presence of threshold densities; (d) chemical cues in the presence of threshold densities which may be an order of magnitude less than the densities active for visual cues; and (e) mechano-reception by individuals, probably assuming greatest importance in maintaining and structuring shoals and swarms.

5.4.5.1 Light and Diurnal Variation

Euphausiids in general have well developed vision and it might be expected that they would respond actively to light (Mauchline and Fisher 1969; Kalinowski and Witek 1985), and thus exhibit vertical migration patterns. Many observers (e.g., Hardy and Gunther 1936; Marr 1962; Nast 1978; Witek et al. 1981; Everson 1982) have found changes in size density and depth of aggregations with time of day. The most common feature which emerges from these studies is the tendency for euphausiids to migrate towards the surface and disperse at night, although such behaviour is by no means consistent and regular (Table 5.2).

At a site south of Elephant Island, Nast (1978) calculated a mean depth of 20 m for krill concentrations at night, while the species moved down to an average depth of 136 m during the day. At South Georgia, Kalinowski (1978) found that krill swarms were concentrated at about 50 m during the day, whereas at night krill dispersed throughout the upper 159 m. However, Everson (1984a) could not detect any clearly defined vertical migration off South Georgia, although swarms observed during the day dispersed at night time. Several more studies have found no evidence for any detectable vertical migration pattern or dispersal during the night in various parts of the Southern Ocean such as the western Atlantic sector or the Prydz Bay region

(Schulenberger et al. 1984; Higgenbottom and Hosie 1989). Azzali and Kalinowski (1998) did not observe vertical movements of krill aggregations in the Ross Sea during summer, when daylight was almost continuous.

In analysing data on krill vertical migration patterns, Siegel and Kalinowski (1996) came to the following conclusions: "First, the primary dependence of diurnal migrations upon changes in light intensity appears to be an important event, although difference in latitudinal light regimes should be considered. Furthermore feeding activity and food availability appear as primary factors which markedly affect both aggregation and vertical migration. Second, although krill tend to migrate upwards towards the surface and disperse at night, this is by no means a consistent or regular feature of krill swarming. Therefore all the factors involved in the formation of aggregations do not appear to act independently, but may be interlinked."

5.4.5.2 Physiological Stimuli

The question as to whether rhythmic changes in krill aggregation behaviour could be induced by physiological or other intrinsic rhythms, as distinct from behavioral responses to external factors, has yet to be resolved. Miller and Hampton (1985) point out that the results from field and laboratory studies are not consistent with strict physiological or intrinsic control over feeding and aggregation, since they do not show regular periodicity in either of these activities.

5.4.5.3 Phytoplankton Concentrations

Phytoplankton concentrations have been proposed as stimuli for krill swarming, but krill swarms occur in clear as well as phytoplankton rich water. Even inverse relationships between swarming and phytoplankton availability has been observed (e.g., Nast and Gieskes 1986) and it is not clear from the data whether this effect is due to intense grazing or avoidance of phytoplankton-rich areas. In contrast Weber and El-Sayed (1986a) used a detailed spectral analysis to indicate a positive correlation between in vivo flourescence and krill biomass at scales of 2–20 km. In laboratory studies, Antezana et al. (1982) showed that krill can feed over a wide range of phytoplankton densities. Small-scale measurements made by Priddle et al. (1990) suggested that microscale patchiness in food supply seems likely to contribute most to swarm-to-swarm differences. Orientated swimming has been observed in both clear water and in the midst of a dense phytoplankton bloom (Hamner et al. 1983) and this would perhaps indicate the absence of a causal link between aggregation and phytoplankton density.

5.4.5.4 Hydrographic Factors

Rakusa-Suczczewski (1978), Witek et al. (1981), Hampton (1985), and Weber and El-Sayed (1985) have all investigated the influence of various physical and chemical factors (e.g., temperature, salinity, oxygen concentration, and concentrations of various nutrients) on krill horizontal distribution, but all failed to find any direct association between such factors and krill aggregations. There is, however, some evidence to indicate that vertical stratification of water properties (e.g., temperature and oxygen concentration) may influence aggregation by causing krill to concentrate at certain depths. Hampton (1985) found that krill tended to be most abundant near the top of the thermocline (Figure 5.10). Because chlorophyll *a* concentrations were always greatest below the thermocline, it seems likely that this behaviour was directly related to food density.

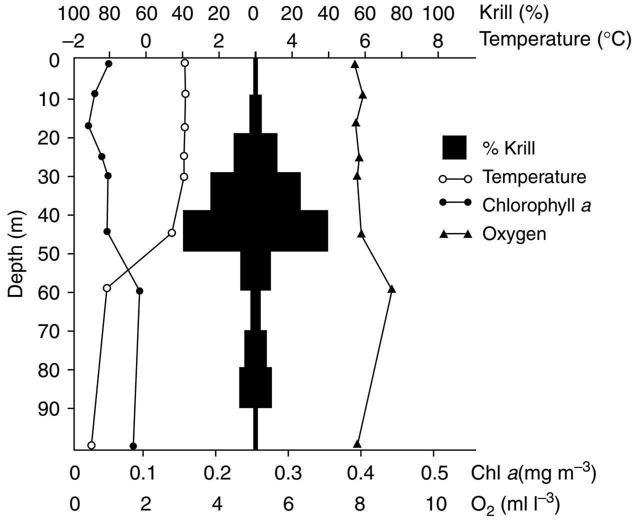


FIGURE 5.10 Vertical profiles of krill abundance, temperature, chlorophyll *a* and dissolved oxygen at a typical station during the M.V.S.A. *Agulhas* krill survey in the Southern Ocean between 15°E and 30°E. Krill abundance profiles constructed from underway echo-sounder data interfaced with a digital echo integrator 50 km on each side of station position. (From Hampton, I., *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 294, 1985.)

Hofmann and Murphy (2004) have stressed the role of advection in structuring the large scale distribution of krill. This is due to the Antarctic Circumpolar Current providing a mechanism for large scale transport of both larval and adult krill. Advective connections occur at circumpolar, regional, and local scales in the Southern Ocean. The dependence of Antarctic krill populations at South Georgia on upstream inputs that come from the west of the Antarctic Peninsula and Weddell Sea regions is one example of these connections. The circum-polar nature of the Antarctic system allows advective transport to develop over large spatial scales and hence be a potentially primary control on productivity in the system.

5.4.5.5 Sea Ice

Seasonal sea ice plays an integral role in the ecology of krill. Ice edge blooms are an important and predictable food supply, particularly for reproducing adults and first-feeding larvae. Daly and Macauley (1991) investigated the distribution and behaviour of krill in the marginal ice zone of the Weddell and Scotia Seas. Their results indicated that juvenile krill were more abundant under the pack ice than in the open water in spring (Daly and Macauley 1991) and that ice biota were an important food source for krill in winter (Daly 1990). Numerous additional reports of krill associated with sea ice (Kawaguchi et al. 1986; Hosie and Stolp 1989) and of krill feeding on ice algae at the ice edge (Hamner et al. 1983; Stretch et al. 1988; Siegel et al. 1990), deep in the pack ice or under the fast ice (Spiridonov et al. 1985; O'Brien 1987; Marschall 1988), indicate that association between krill and sea ice is common in the Southern Ocean.

5.4.6 MODELS OF AGGREGATION

5.4.6.1 Introduction

As detailed below euphausiids, especially *E. superba*, tend to disperse when feeding and to re-aggregate after feeding. Swarms also actively migrate horizontally in search of food. Dispersion and aggregation suggests that communication between individuals is maintained. From the work carried out to date it is clear that the formation and dispersal of swarms in krill is a complex process brought about by patterns of vertical migration, responses to environmental gradients, responses to predation, and by hydrographic features. Most of the models that have been developed have concentrated on the interaction between feeding and aggregation/dispersal. In such models, feeding state is the proximate cause of aggregation or dispersal, while aggregation itself is thought to improve the feeding efficiency of the aggregation and ultimately the survival, growth, and reproduction of the population.

5.4.6.2 Models

Pavlov (1969) was the first to advance a model linking feeding and aggregation. He stated that krill feed in dispersed aggregations near the surface where phytoplankton is abundant. When replete, the animals form into swarms and migrate downwards, remaining in swarms until they ascend to feed again.

Hamner and his co-workers (Hamner et al. 1983; Hamner 1984) proposed that krill actively search for food in compact-orientated swarms (maintained by rheotactic cues). No feeding takes place during the search phase, but when a patch of food is located the animals engage in bouts of rapid feeding during which the swarm structure is disrupted and a slow-moving aggregation develops. Hamner et al. (1983) suggested that this pattern of alternate foraging and intensive feeding when suitable food conditions are found promotes the efficient use of a patchily distributed food resource. This then is the ultimate beneficial effect of swarming. However, such a pattern is by no means universal.

Antezana and Ray (1983, 1984) combined laboratory-based information on feeding behaviour designed to test the hypothesis that feeding and swarming are mutually exclusive events (Antezana et al. 1982; see also Section 5.4.4) with field data to produce a model of feeding and swarming based on the principles of optimal foraging theory (Pyke et al. 1977). The widespread occurrence of swarming in zooplankton (Omori 1978) suggests a variety of adaptive strategies for aggregation behaviour. By analogy with schooling fishes, these include minimized predator detection and rapid predator satiation once schools (or swarms) are encountered (Brock and Riffenberg 1960).

Antezana and Ray (1983) hypothesized that small foraging schools locate feeding groups and assemble into large-scale aggregations, where feeding occurs in semi-stationary swarms until the depletion of the food resource, whereupon the swarm disengages into small schools, where foraging is associated with horizontal migration and diel vertical migration. In Figure 5.11 the dynamics of feeding aggregation in *E. superba* is subdivided into three stages: formation, maintenance, and dispersal.

This is contrary to the model proposed by Pavlov (1969) and discussed above, where it was suggested that krill dispersed to feed and swarmed only on repletion. This has not been supported by recent laboratory experiments (Antezana et al. 1982) and field observations (Antezana and Ray 1983, 1984; Hamner 1984). These authors showed that krill at aggregation densities similar to those encountered in the field (approximately 2,000–5,000 individuals m^{-3}) fed at elevated rates in the laboratory, and had elevated stomach contents and rapid ingestion rates in swarms in the field.

In contrast to the models discussed above, Witek et al. (1982b, 1988) have proposed one that does not involve feeding (Figure 5.12). They point out that there are numerous publications linking the formation of large krill concentrations and the circulation of water masses (e.g., Marr 1962; Makarov et al. 1970; Elizarov 1971; Maslennikov 1972). The connection between the occurrence of commercial krill concentrations and eddies and fronts has been

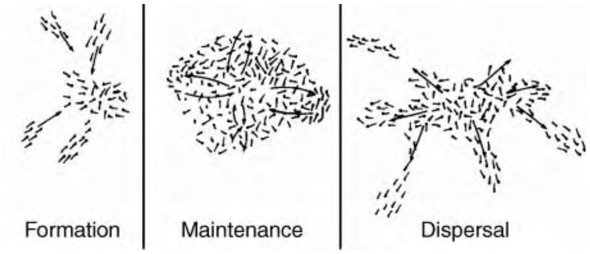


FIGURE 5.11 Dynamics of feeding aggregations of *Euphausia superba*. Formation: (1) detection and encounter of feeding grounds by small schools of solitary individuals; and (2) horizontal migration and assemblage into larger feeding groups. Maintenance: feeding in large semi-stationary swarms until the depletion of the resources. Individuals are randomly orientated with respect to one another and moving to and from the periphery. Dispersal: (1) disbandment of large feeding swarms into small foraging schools composed of individuals with parallel orientation and unidirectional motion; and (2) foraging is associated with horizontal and vertical diel migrations until they encounter of new feeding grounds. (From Antezana, T., Ray, K., *Ber. Polarforsch.*, 4, 199, 1983.)

pointed out by Wolnomiejski et al. (1978) and Witek et al. (1982). These researchers suggested that water circulation patterns cause the inflow of krill into an area, and here specific reactions to turbulent water flow combined with social behaviour serve to maintain and concentrate the swarms in large stabilized currents where the water flow in laminar krill are dispersed. Here swarms of krill, both small and large quantities, are dispersed outside the swarms. In regions of meanders and eddies there is increased turbulence and high gradients of current velocity, and the krill react in such a way that they tend to concentrate in quiescent regions, which are most likely to exist in the centre of localized areas and current meanders and which develop on either side of the strong flow.

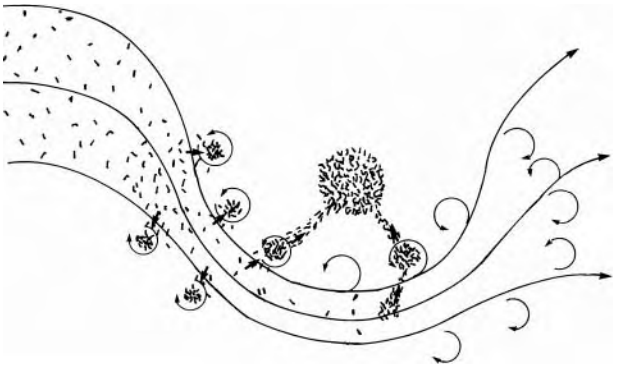


FIGURE 5.12 Schematic representation of the processes whereby krill may accumulate in current meanders: long arrows represent the direction of the prevailing current flow; short arrows represent the direction of krill movement; individual krill. (From Witek, Z., Grelowski, A., Soszka, G.J., *ICES* Cm 1982/L., 59, 1982.)

5.5 DISTRIBUTION AND ABUNDANCE

5.5.1 INTRODUCTION

In this section an attempt is made to summarize recent data on krill distribution and abundance, methods of estimating abundance, factors controlling krill distribution, and the question as to whether the Southern Ocean krill constitute a single stock or a series of stocks. The starting point is Everson's (1977b) review of the living resources of the Southern Ocean, There have been several substantial reviews of krill distribution and behaviour (e.g. Mackintosh 1972, 1973; Everson 1977b; Bengtson 1978, 1985a, 1985b; Lubimova et al. 1980; Daly and Macauley 1991; Quetin and Ross 1991; Everson and Miller 1996; Siegel and Kalinowski 1996; Azzali and Kalinowski 1998; Reid et al. 1999; Nicol et al. 2000; Murphy and Reid 2001); the broadscale oceanography of the krill's habitat (e.g., Deacon 1937; Ostapoff 1965; Treshnikov et al. 1978; Baker 1979; Forster 1981, 1989; Amos 1984; Anonymous 1985a; Hellmer et al. 1986); and correlations between the hydrography and biological productivity of Antarctic waters in general (e.g., Jaragov 1969; Knox 1970, 1983, 1994; Everson 1977b; Deacon 1982, 1984; Tranter 1982; Amos 1984; Hempel 1985a, 1985b).

The determination of the distribution patterns and abundances of Antarctic euphausiids, and in particular krill, is extremely difficult. In the past there have been numerous attempts to estimate the overall biomass of krill in the Southern Ocean, but such estimates have little relevance in an ecological sense. Abundance estimates are complicated by krill's aggregation behaviour. As we have seen krill can on occasions form very large swarms or superswarms, in which a large proportion of the local population may be concentrated. Swarms also vary enormously in size, shape, and density of individuals. This makes it difficult to sample the krill using a series of stations along transect lines. The chance encounter of one or more large swarms may alter biomass estimates for an area by an order of magnitude or more.

While the broad-scale distribution patterns of euphausiids are known as a result of the work of the *Discovery* Expeditions (Marr 1962; Mackintosh 1972) and that of Russian scientists (Lubimova et al. 1984), we still have much to learn about the finer details of krill distribution, especially on a seasonal basis. The situation is further complicated by the year-to-year variations which occur in krill distribution and abundance (see Chapter 15).

5.5.2 STANDING STOCK ESTIMATION

5.5.2.1 Introduction

Various techniques have been used or proposed for estimating the abundance of krill. Attempts have been made to estimate krill standing stocks indirectly from estimates of predator consumption, primary production, and the assumed surplus arising form the large decline in the large baleen whale stocks. Such estimates have been summarized in Knox

(1970, 1983), Everson (1977b), Lubimova et al. (1980), and Lillo and Guzman (1982). Table 5.3 shows some of these estimates. There are large uncertainties surrounding these estimates arising from errors in the various conversion factors used and the fact that the authors have made little attempt to place error limits on their estimates, or to examine the assumptions upon which they are based. While there is a wide range of figures for standing stock given in Table 5.3, even more conservative estimates indicate that the standing stock is very large for a marine invertebrate species. The principal techniques used for estimating the abundance of krill are net surveys and acoustic surveys.

5.5.2.2 Net Sampling

A variety of nets have been used for sampling krill. The desired qualities of these nets have been discussed in several BIOMASS documents (e.g., Mauchline 1980b), and bongo nets and rectangular mid-water trawls (RMTs) have been recommended as standard krill sampling nets. Unfortunately, there are also certain problems, or disadvantages, associated with net sampling (Everson 1983). There is firstly gear selectivity, the mesh size used introducing a bias into the frequency distribution of the catch, and secondly net avoidance. Large krill, being more powerful swimmers than small krill, are more able to avoid sampling nets. The problem of avoidance is a complicated one dependent on the effect of the towing wire and bridle in front of the net mouth, mesh size, color of the net, towing speed, and time of day. One type of net that avoids some of these complications is the free-fall net which samples as it falls down through the water with no towing wire or bridle in front of the net. A messenger activates a closure mechanism when the required depth is reached. I have used this type of net very successfully in McMurdo Sound investigations. However, it has not been widely used. In addition to the bias resulting from the sampling nets used, net-biased estimates of mean density can be expected to be very inexact because of the krill's contiguous distribution. Miller and Hampton (1985) concluded that, "Given the potentially large biases, the high variances and the relatively small area covered we conclude that density estimates from plankton nets are of little real value in estimating global abundance."

5.5.2.3 Acoustic Surveys

Increased sophistication, coupled with reliability, has meant that hydroacoustics became a recognized and standard method for estimating fish abundance. Hence, during the BIOMASS Programme a concerted effort was made to test the suitability of hydroacoustic techniques for estimating krill abundance (Anonymous 1980). The hydroacoustic methods have several distinct advantages (Everson 1983). Firstly, the time delay between the transmission pulse and the return echo can be measured very accurately, thus giving a fine depth discrimination. Secondly, large areas can be surveyed in a relatively short time compared to net sampling, which is very time consuming. Thirdly, because the pulse repetition frequency is quite high, sampling along a transect is effectively complete. Unfortunately, there are also a number of difficulties. Firstly the technique cannot discriminate between euphausiid species, or the life history stages of krill. Hence, this must be determined by net hauls aimed at specific targets. Secondly, the depth range is limited to about 120 m, and due to the use of downward directed transducers there is an unsampled layer from the surface to about 10 m. Thirdly, to convert acoustic data into abundance measures a scaling factor, the target strength (TS), is required (Anonymous 1986). While in principle acoustic techniques can give rapid and direct estimates of density over a wide area, the accuracy of such estimates is determined by sampling variance, systematic errors (particularly from inaccurate calibration and errors in the expression used to estimate target strength for length), and bias arising from failure to detect part of the population (Miller and Hampton 1985).

During FIBEX (1981), SIBEX I (1093), and SIBEX II (1984), (First and Second International BIOMASS Experiments) phases of BIOMASS (Anonymous 1980, 1981a,

TABLE 5.3
Some Indirect Estimate of Total Krill Standing Stock

Estimate ($t \times 10^6$)	Method	Source
750	Estimate of total secondary production: krill taken as 50% of total herbivorous zooplankton	Gulland (1970)
5,000–7,000	As above	Moiseev (1970)
305–1,200	Primary production	Knox (1983)
953–1,350	Primary production	Makarov and Shevtsov (1972)
(14–277)	From estimates (Gulland 1970) of total annual production (109 tonnes) assuming phytoplankton/euphausiid conversion ratios of between 10:1 and 40:1 and that krill comprise between 10% and 50% of total herbivorous zooplankton	
(>111)	Total present-day predator consumption	Everson (1977b)
(>71)	Potential "surplus" from whale decline (estimated at 147 million tonnes)	Laws (1977b)
(>55)	As above (surplus estimated at 100 million tones)	Moiseev (1970)

Source: Adapted from Miller, D.G., Hampton, I., *Biomass Sci. Ser.*, 9, 1, 1985.

1982, 1986) systematic echo-integrator surveys were made in selected areas of the Southern Ocean. The most comprehensive use of these was in FIBEX during which eleven ships from ten nations surveyed four sectors in the West Atlantic and Indian Oceans. From joint analyses of the integrator data (Anonymous 1981a; Hampton 1983; Anonymous 1986), total krill biomass was assessed and the survey variance estimated (Table 5.4). Everson and Miller (1996) have discussed the results and implications of the BIOMASS acoustic surveys. Subsequently it was found that the acoustic target strength to size relationship reported in Anonymous (1984b) was not correct. The CCAMLR Krill Working Group considered the question of krill target strength and the FIBEX standing stock estimates and used a multiplication factor of 5.62 to convert the Anonymous (1984b) results to total standing stock for the Atlantic sector. This gave an estimate of 15,477 kilo tons. While it is difficult to extrapolate the results to the Southern Ocean as a whole two such attempts have given figures of 41 million tons (Miller and Hampton 1985) and 25 million tons, values which are substantially lower than the most conservative indirect estimates from predator consumption.

5.5.2.4 Predator Consumption of Krill

E. superba is the single most important prey species taken by a range of higher predators during the breeding season. The quantity, size distribution, life history stage, and sex ration of the krill eaten by these predator has been extensively studied, especially at South Georgia (Croxall and Prince 1980a, 1980b; Croxall et al. 1999). In order to assess the importance of this predation on the local krill population and in particular on its population dynamic, it is important to know which component of the krill population is exploited by different predators and which proportion of the total krill population of an areas is consumed.

Reid et al. (1996) investigated the krill caught by predators at South Georgia. They found that the length-frequency of krill was broadly similar between those caught by nets and those consumed by the predators, although the krill taken by diving species formed a homogeneous group which showed significant differences from krill taken by other predators and by nets. There were significant differences in the maturity/sex stage composition between nets and predators. In particular all predator species showed a consistent bias towards female krill. Similarities in the krill taken by Macaroni (offshore feeding) and Gentoo (inshore feeding) penguins and differences between krill taken by penguins and albatrosses suggest that foraging techniques were more important than foraging location in influencing the type of krill in predator diets. Most krill taken by predators were adult; most female krill were sexually active. Because female krill are larger, and probably less maneuverable, than males, the biased sex ratio in predator diets may reflect some combination of selectivity by predators and superior escape response of male krill. Overall, adult, sexually active female krill, forming 40% by number of the local krill population, may comprise 60–70% by number and 75–88% by mass of the krill taken by their main seabird and seal predators at South Georgia in February. It is thus clear that the sizes and sex ratios of krill taken by nets and those taken by predators are different.

5.5.2.5 Conclusion

In 1988 Everson posed the question, "Can we satisfactorily estimate variation in krill abundance?" and concluded that the answer must be "no," because although we can estimate variation within each sampling method, there is no information to indicate how these estimates relate to total krill abundance as a whole. However, despite all these uncertainties, attempts to estimate krill standing stock directly have narrowed the possible range of estimates that previously had been inferred (Miller and Hampton 1985). It is unlikely that the mean summer standing stock is either as low as the lowest estimate in Table 5.3 or in excess of 1,000 million tons. It can be concluded that typically the stock size in summer is probably in the order of hundreds of millions of tons—an exceptionally high biomass by global standards.

TABLE 5.4
Data on Krill Aggregation Parameters Determined Acoustically During FIBEX

	Mean	SD Mean	Range
Depth[a] (m)	44	0.3	152
Horizontal dimension[a] (m)	73	6	25,682
Thickness[a] (m)	5	0.1	96
Spacing[a] (km)	2.2	0.01	366
Area[a] (m^2)	1,021	124	51,3640
Density[b] $(g\ m^{-3})^2$	59	3	5612

[a] $N=7{,}623$.
[b] $N=2{,}793$.

5.6 GENERAL DISTRIBUTION PATTERNS

There are many papers which outline in general terms the distribution of krill in the Southern Ocean, in particular those arising from the *Discovery* Expeditions and from studies of the numerous Russian Expeditions. These have been summarized by Marr (1962), Makarov et al. (1970), Mackintosh (1972), Vorinina (1972, 1974), Everson (1976, 1977b), Lubimova et al. (1980), Maslennikov (1980), and Amos (1984). Further information is to be found in the reports of the BIOMASS surveys (Hampton 1985; Everson and Miller 1994; Siegel and Kalinowski 1996) and in an account of Japanese commercial catches (Shimadzu 1984a). Recent accounts of the distribution and ecology of krill include those of Quetin and Ross (1991), Quetin et al. (1996), Nicol et al. (2000), and Murphy and Reid (2001). However, because of the size of the area involved and the problems of sampling krill quantitatively, there is still a great deal of uncertainty about important details.

Around the Antarctic Continent krill postlarval forms are distributed between the Antarctic Continent and the Polar Frontal Zone. There is universal agreement that krill are most abundant in the East Wind Drift, the Scotia Sea, the Weddell Drift, round South Georgia, in the vicinity of the Kerguelen-Gaussberg Ridge, and in the Ross Sea (Marr 1962; Nemoto 1972; Mackintosh 1973; Everson 1977b). Three views of krill distribution are given in Figure 5.13: those of Amos (1984) (Figure 5.13a), Mackintosh (1973) (Figure 5.13b), and Maslennikov (1980) (Figure 5.13c). It should be pointed out that these were all drawn at a time when it was believed that krill were absent from the Ross Sea. All of these show a series of circular, elliptical, or eddy-like patches ringing the Antarctic Continent. Some coincide with major gyres known from hydrographic studies, the one of most importance in krill distribution being those in the Weddell Sea, the east Atlantic, and the Ross Sea. In the Indian and Pacific Oceans, krill seem to be concentrated in the East Wind Drift, particularly in the vicinity of the Antarctic Divergence (Marr 1962; Vorinina 1968; Nasu 1983; Amos 1984; Lubimova et al. 1984). By far the greatest concentration of krill occur in the Scotia Sea-Weddell Drift area, and this is the region which has been the most intensively studied. In the Scotia Sea an important feature is the confluence between the Pacific Water of the Antarctic Circumpolar Current and the Weddell Sea Water in the Weddell Gyre. Bogdanov et al. (1980) described this, and his conclusions have been supported by Gordon and Goldberg (1970) and Mackintosh (1973). Areas of divergence and eddy formation would appear to be important mechanisms in maintaining the observed distribution patterns.

Pakhomov (1995) points out that a common feature of the large-scale distribution of *E. superba* is the increase in density in two different zones of the Southern Ocean designated as the southern and northern zones (Makarov and Spiridonov 1993). The southern circumpolar ring of high krill density is restricted to the zone of the Antarctic Coastal Current (East Wind Drift), north of the shelf edge and above the upper part of the continental slope. The northern zone of high krill density is connected with areas where waters characteristic of high latitudes are mixed with water of the Antarctic Circumpolar Current. This zone is not as continuous as the southern one (Makarov and Spiridonov 1993) but is distinctly identified within the Weddell and Ross Sea gyres (Marr 1962; Mackintosh 1972) and may also be observed in the Bellingshausen, Larazez, Riiser-Larsen, Cosmonaut, Cooperation, and Dumont D'Urville seas around the Antarctic Continent (Makarov and Sysoera 1983; Williams et al. 1983, 1986; Iganake et al. 1984; Hampton 1985; Miller 1986a; Shirakihara et al. 1986; Bibik et al. 1988; Pakhomov 1995). Makarov and Spiridonov (1993) have concluded that some characteristics of the life span are very different in the different regions and vary from year to year in response to environmental conditions.

Recently Siegel (2005) has reviewed data on krill distributuin and biomass. Nicol et al. (2000) used historic krill distribution maps of the *Discovery* studies to delineate the krill distribution range and biomass. Their circum-Antarctic biomass estimates fell between 50 and 150 million tonnes. Siegel (2005) considered that this estimate was too low and considered that more recent data indicated that the potential biomass may range between 67 and 297 million tonnes. He provided a map of the circumpoiar krill distribution and average regional density (Figure 5.14) This shows a pronounced concentration of krill in the Southwest Atlantic sector where 58–71% of the krill are located. In any one place, the abundance of krill is a function of production and survival as well as retention and export. Year-class strength, i.e recruitment, is determined by winter sea ice conditions. This seems to be the proximate cause of krill stock size.

5.6.1 KRILL DISTRIBUTION IN THE ROSS SEA

The *Discovery* Expeditions (1935, 1939, and 1950–1951) gave the first information on krill in this area. On the basis of the results of these expeditions, Marr (1962) concluded that *Euphausia superba* was almost completely absent in the Ross Sea Shelf, where it was replaced by *Euphausis crystallorophias*. Marr's conclusion, conformed later by Mackintosh (1973), Lubimova et al. (1984), and Shimadzu (1984a) effectively directed research on krill to other areas of the Southern Ocean. Despite these early studies, analyses of the stomach contents of Minke Whales in the Ross Sea (Ichii and Kato 1991) which identified that they fed on *E. superba*, and the annual consumption of krill by Minke Whales in the Ross Sea was estimated to be about 3 million tons.

Azzali et al. (1991, 1996) and Azzali and Kalinowski (1998) have summarized the results of extensive investigations of krill distribution and biomass carried out in the Ross Sea by expeditions of the Italian Antarctic Programme. In contrast to the early studies listed above they found very dense concentrations of *E. superba* in the southern part of the Ross Sea, up to 76°S. In these areas, density peaks of krill consumers (Minke Whales, Crabeater Seals, and Adélie Penguins) were found.

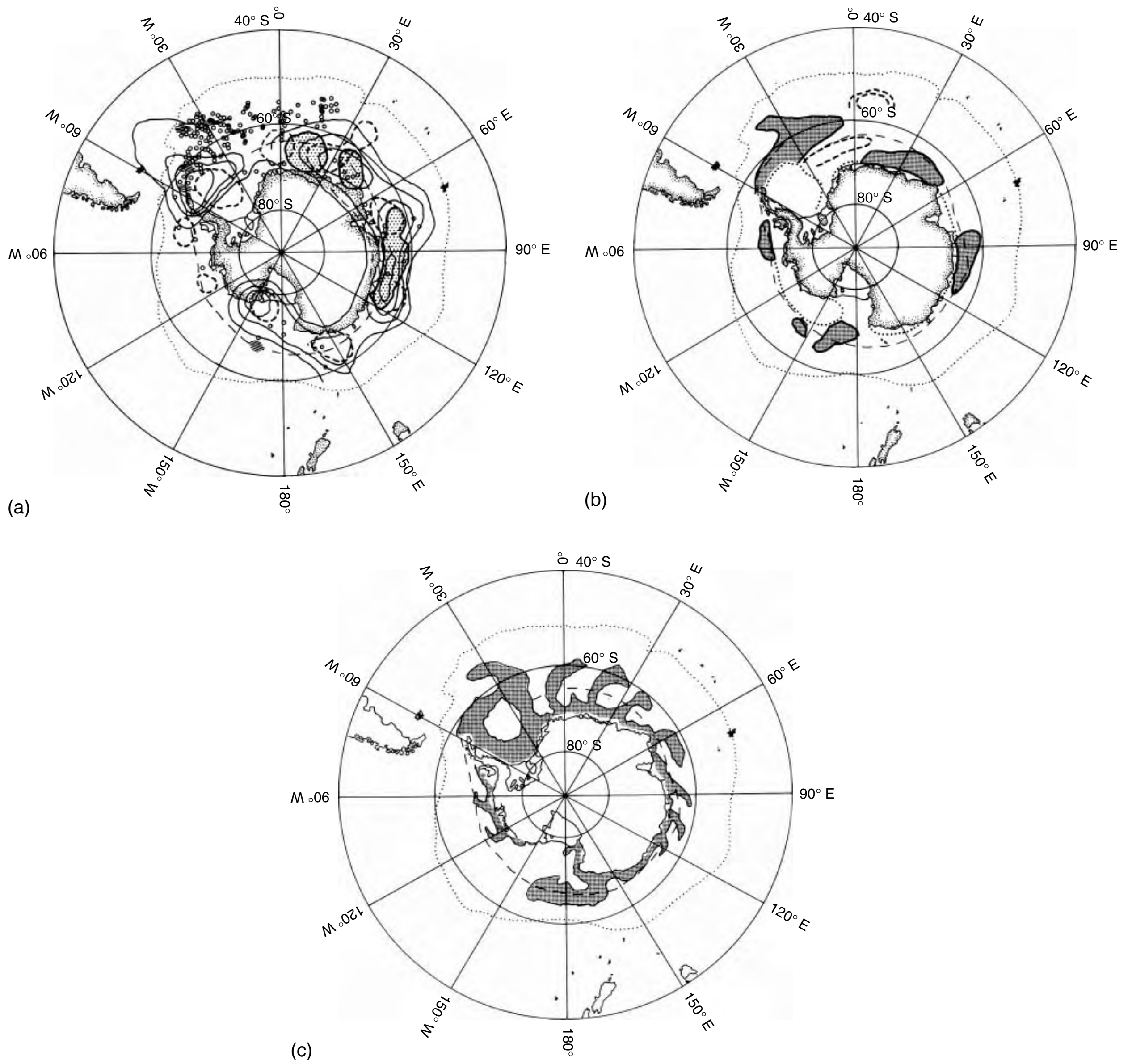


FIGURE 5.13 Large scale concentrations of krill in the Southern Ocean. (a) Based on Amos (1984), after Jarogov (1969). Circles are Marr's (1962) major krill concentrations; stipled areas based on data from Canadian sources; small black areas are krill concentrations as found by Russian expeditions up to 1969; dotted and unbroken contours are overlying "cyclonic activity" (contour values unknown). Location of the Antarctic Convergence (dotted line) and northern limit of the East Wind Drift (dashed line) are shown. (b) According to Mackintosh (1973). Dark areas are "stocks" of krill; determined mainly from pre-1940 *Discovery* observations; heavy dashed lines (**- - -**) enclose low-density regions east of the Weddell Sea; heavy dotted line (· · ·) is the minimum (March) extent of the sea ice. Location of the Antarctic Convergence (light dotted line,…) and the northern limit of the East Wind Drift (light dashed line, - - -) are shown. After Amos (1984). (c) According to Maslennikov (1980). Dark areas are hypothetical patterns of krill and zooplankton concentrations from Soviet data. Location of the Antarctic Convergence (dotted line) and the northern limit of the East Wind Drift (dashed line) are shown. (From Amos, A.F., *J. Crust. Biol.*, 4, Special Issue No. 1, 306, 1984.).

They came to the following conclusions:

1. Contrary to what is generally believed, the Ross Sea is not krill deficient. In particular very high concentrations of krill were found in the southern part of the continental shelf, which is considered to be krill-absent in the literature.
2. A substantial proportion of the *E. superba* population occurred in swarms. In the 1994 surveys, 891 swarms were identified. The average size of the swarms in horizontal extent was 58.2 m and in vertical extent 15.6 m. Mean density was 676 g m^{-3} or 1,121.1 individuals m^{-3}.

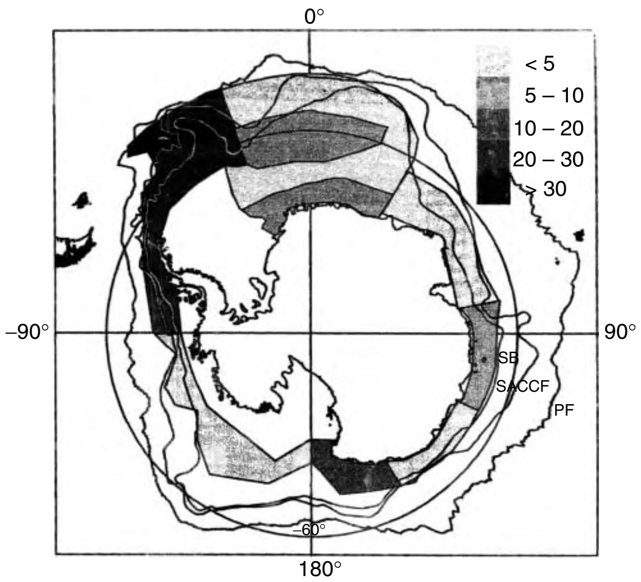


FIGURE 5.14 Circumpolar krill distribution and average regional density from acoustic survey estimates, modified after Nicol et al. (2000). Source: Siegel, V., *Polar Biol.*, 29, 16, 2005. With permission.

3. The biomass of *E. superba* in the Ross Sea, estimated in late spring 1994, was around 3 million tons, and the mean biomass density ranged from 250 to 100 tons nm^{-2}. These values are similar to those given in the literature for the Atlantic sector.
4. When the sea was almost fully covered by ice or when the ice edge was receding northwards, populations of *E. superba* were restricted to narrow ice-free areas enclosed in the ice, where very dense aggregations were formed. Around these areas, density peaks of krill consumers were found.
5. Biomass of *E. superba* was the main part of the zooplankton biomass on the continental slope and the central part of the continental shelf (from lat. 75° up to the Ross Sea Ice Barrier), but westwards (from long. 171°, along lat. 75°, up to Terra Nova Bay) this relationship progressively changed in favor of smaller zooplankton, and *E. superba* became replaced by *E. crystallorophias*.

5.6.2 Krill Distribution in the Weddell-Scotia Sea Region

Siegel (1988, 2005), has discussed in detail the patterns and variability of krill distributions of this region. Siegel (1988) gave a conceptual view of the seasonal, variation of Mil abundance/distribution in the Antarctic Peninsula and adjacent areas (Figure 5.15) Krill abundance is low in the region during winter and krill occur mainly above the continental shelf. From November onwards, krill abundance increases rapidly and krill distribution extends beyond the continental shelf break into oceanic waters as far north as 59° S (Siegel et al. 1990). This very northern distribution limit is reached only during the period of maximum krill occurrence, i.e., in January/February.

Krill spawning occurs over the summer during the time of maximum abundance, mainly within the time window from December to March. During the austral summer, a spatial succession of krill developmental stages has been observed. Juveniles inhabit the coastal waters of the Antarctic Peninsula while large adult, spawning stages occur in oceanic regions along and beyond the continental shelf break. From March onwards, after the end of the apawning season, the krill stock size shows a dramatic decline long before the winter sea ice cover.

The life history strategy of krill places the developing larvae in locations distinct from the adult population which avoids competition for food, but also prevents predation on larval krill by adults. The spatial segregation of developmental stages may be explained by active offshore/onshore migration of the adults (Siegel 1988). Krill are capable of migrating over distances of 50–100 km in a relatively short period over a few weeks (Kanda et al. 1982). Changes in seasonal vertical migration might be another possible explanation of the very low densities observed in the winter due to a bias in routine sampling depth which may have not sampled deep enough during the winter.

5.7 FACTORS AFFECTING DISTRIBUTION

Many theories have been proposed to explain the observed distribution pattern of krill (see Marr 1962; Mackintosh 1972, 1973; Everson 1977b; Amos 1984; Daly and Macaulay 1991; Brieley et al. 1999) and some of these have been discussed in the previous sections. Spatial

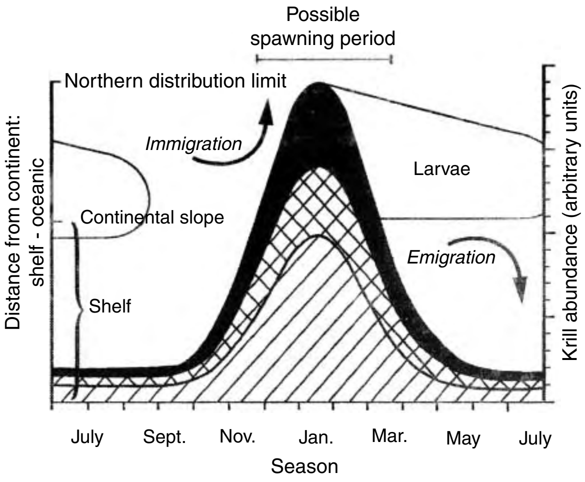


FIGURE 5.15 Conceptual view of the seasonal variation in krill stock density and spatial succession of size classes and maturity stages along the Antarctic Peninsula (modified after Siegel, 1988 and Siegel, 2000). Source: Siegel, V., *Polar Biol.*, 29, 3, 2005.With permission.

heterogeneity, population structure, and abundance variability are all affected by physical factors, such as resource limitation and predation. The question is, "To what extent are adult krill passively carried by the prevailing currents, or to what degree must their behaviour must also be taken into account." The interaction between passive advection and behavioral factors are complex and will vary depending on the particular conditions. Priddle et al. (1988) described the interannual change in krill abundance at key sites and attributed the large fluctuation which were found to occur to mesoscale hydrographic variation, thus leading to the suggestion that the animals act as passive tracers of the circum-Antarctic circulation. In contrast, several descriptions of krill aggregations (Kalinowski and Witek 1985) and breeding (Siegel 1989) suggest behavioral factors are also very important and that krill are capable of altering their geographic position over spatial scales from hundreds of metres to hundreds of kilometres (Kanda et al. 1982). Watkins et al. (1986) studied krill swarms in a restricted area of the Bransfield Strait and found that the composition of individual swarms did not reflect random sampling of the local population. On a larger scale, Siegel (2000, 2005) proposed a pattern of ontogenetic migration in the vicinity of the Antarctic Peninsula based on the spatial and temporal segregation of different life cycle stages.

5.7.1 FLUCTUATIONS IN KRILL DENSITY AND BIOMASS

Surveys of krill distribution, especially in the Atlantic sector (Hewitt and Demer 1993; Brierley et al. 1999) have revealed wide year-to-year variations in krill abundance. Brierley et al. (1999) investigated the interannual fluctuations of krill density at South Georgia and Elephant Island. The South Georgia area is not considered a krill breeding-site (Ward et al. 1995), and the island is not believed to support a self-sustaining krill population. Rather it has been variously proposed that krill at South Georgia have their origins at the Antarctic Peninsula or in the Weddell Sea, and are transported to South Georgia via the prevailing north-easterly flowing ocean currents (reviewed by Murphy et al. 1988, 1998). Similarly there is evidence to suggest that some krill at Elephant Island may originate from further south along the Antarctic Peninsula (Siegel and Loeb 1995).

Table 5.5 compares krill density estimates and gradient change in density between subsequent years. It can be seen that density has varied considerably over the past two decades. Within the framework of this variability, however, abundance at Elephant Island has most often been higher than at South Georgia. There are several possible explanations for this. Firstly, systematic differences may be due to the differences in the survey and data-analysis techniques. This has been discounted. Secondly, the differences in krill density between South Georgia and Elephant Island may be the result of krill dispersal mechanisms operating over the entire Scotia Sea (reviewed by Lubimova et al. 1984; Sahrhage 1988b; Watkins 1999; Murphy et al. 1998). A common and central tenet of the literature on krill distribution is that krill spawned at the Antarctic Peninsula, or in Weddell Sea waters, may become entrained within the north-easterly flowing Antarctic Circumpolar Current and be carried toward South Georgia, possibly via Elephant Island.

Brierley et al. (1999) concluded that known ocean currents and their dispersive effects can be used to explain both systematic differences in absolute biomass and similarities in krill densities at the two locations (South Georgia and Elephant Island), and support the existence of teleconnection processes across the Scotia Sea, which transmit possible environmental-mediated change in density across this basin. In a year characterized by low krill abundance in one location, abundance will be low throughout the Scotia Sea. In such years krill-dependent predators are likely to be impacted with reduced breeding success.

TABLE 5.5
Euphausia superba

	SG		EI	
Year	**Density ($g\ m^{-2}$)**	**Gradient ($g\ m^{-2}\ yr^{-1}$)**	**Density ($g\ m^{-1}$)**	**Gradient ($g\ m^{-2}\ yr^{-1}$)**
1981	50.7	–	68.5	–
1990	53.7	−0.7	58.3	−1.1
1991	6.3	−47.3	26.3	−32.0
1992	95.0	88.6	45.4	19.1
1994	5.9	−44.5	8.7	−18.4
1996	33.5	13.8	75.5	33.4
1997	40.1	6.8	100.5	25.0

Krill-density for South Georgia (SG) and Elephant Island (EI) for years in which data were available for both regions and gradient of change in density between subsequent years. In all instances, there is concordance between sites (agreement between signs of gradient).

Source: From Brierley, A.S. et al., *Mar. Biol.*, 134, 678, 1999. With permission.

5.7.2 KRILL ABUNDANCE AND PREDATOR PERFORMANCE

The interaction between krill population variability and predator performance has been extensively investigated in the South Georgia region (see Murphy and Reid 2001). Krill are a major prey item in the diet of a wide range of predators in the area, including penguin, seals, and whale species (Croxall et al. 1988b; Priddle et al. 1988). Variation in the abundance of krill within the predator foraging regions affect the foraging and breeding performance of the predators and are associated with changes in the plankton community composition and dynamics (Croxall et al. 1988b, 1999; Atkinson et al. 1999).

Interannual fluctuations in krill abundance at South Georgia were first noted in the early part of the twentieth century during the whaling period (Priddle et al. 1988). There appear to be 2–3 years in each decade where the abundance of krill at South Georgia is low, the predator foraging and breeding performance is reduced, and the krill fishery reports reduced catch levels and rates (Croxall et al. 1988a; Priddle et al. 1988; Murphy et al. 1998; Brierley et al. 1999). These fluctuations are well-documented and also highlight that the years of low density (below about 10 $g\ m^{-2}$) tend to be followed by years in which krill abundance recovers back to higher values (greater than about 25 $g\ m^{-2}$) (Brierley et al. 1999; Reid et al. 1999). Acoustic estimates of krill abundance at South Georgia vary widely, for example, from 11.7 $g\ m^{-2}$ (Murphy et al. 1991) to 95 $g\ m^{-2}$ (Goss and Everson 1996). Figure 5.16 depicts various measures of the interaction between krill abundance and the feeding and breeding success of the various krill predators. It can be seen that in years of high krill abundance (e.g., 1984, 1992, and 1996) foraging trip duration for seals was low, meal masses were high, and breeding success was enhanced. In contrast the opposite occurred in years when krill abundance was low (e.g., 1986, 1990, and 1994).

5.7.3 HYDROGRAPHIC FACTORS

Practically all of the early attempts to explain large-scale distributional patterns in krill concentrated on water circulatory effects on the larvae and/or postlarvae. As we have seen the major circulatory features of the eastward flowing Antarctic Circumpolar Current and the cyclonic Weddell Sea gyre to the west of the Antarctic Peninsula are the main features maintaining the observed asymmetrical circumpolar krill distribution (Marr 1962; Mackintosh 1972, 1973; Everson 1977b; Deacon 1977, 1984).

Recent studies have emphasized the importance of gyres and eddies in the region of the divergence between the two major current systems: the Antarctic Circumpolar Current and the Antarctic Coastal Current. Such features, which vary considerably in size and life span, must result in the exchange of krill between the two current systems (Maslennikov 1980; Lubimova et al. 1984). Large-scale, topographically-induced gyres have been identified in the surface waters north and east of the Ross Sea, east of the Kerguelen Plateau, north of Prydz Bay, and in the Lasarev Sea (Makarov and Solyankin 1982; Amos 1984; Anonymous 1984a). These gyres plus the Weddell Gyre coincide to a large degree with the distribution of Mackintosh's proposed krill stocks (Figure 5.14b), and with the general distribution of Soviet commercial krill catches (Lubimova et al. 1984).

Figure 5.17 depicts the distribution of water temperatures at 50 m off Enderby Land along with the Catch Per Unit Effort (CPUE) from Japanese commercial krill trawlers (Nasu 1974). It is clear that krill are concentrated in an area of about 15 miles N/S and 25 miles E/W, where a strong meandering isotherm and evidence of small eddy formation were observed. The location of these krill concentrations corresponds with the southern limit of the Warm Deep Water where the Antarctic Divergence occurs. Here upwelling deep water brings nutrient salts to the surface. According to Nasu (1974) the major krill concentrations are to be found in meandering oceanic fronts and cyclonic or anti-cyclonic circulation south of the Polar Front.

5.7.4 ENVIRONMENTAL FACTORS

Only a limited number of studies have demonstrated a clear relationship between environmental factors and krill. For example, temperature, salinity, and oxygen were not found to influence the distribution of krill swarms (Witek et al. 1981; Weber et al. 1986) and no correlation was found between latitude, seawater density and stability, dissolved organic matter, or nutrient concentrations and krill density (Weber and El-Sayed 1985). *E. superba* is well adapted to the narrow range of sea water temperatures (−1.8–2.0°C) typical of the Southern Ocean; thus temperature may not be a dominant factor controlling the distribution of krill within its geographic range. Temperature, however, does influence growth and development rates (Ikeda and Dixon 1982a; Ross et al. 2001) and thus may affect spatial patterns of biomass and population structure.

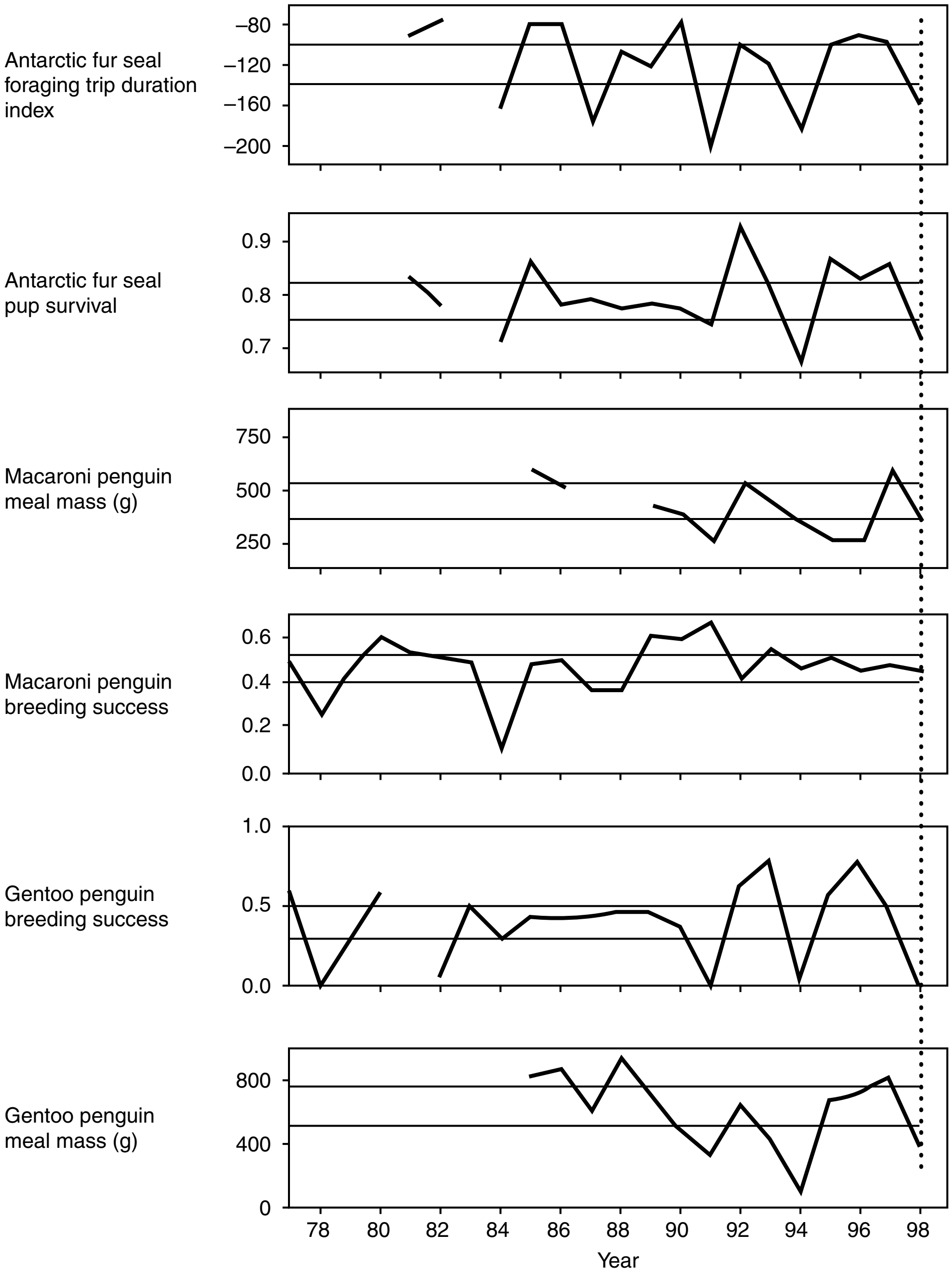


FIGURE 5.16 Antarctic fur seal (*Arctocephalus gazella*), macaroni penguin (*Eudyptes chrysolophus*), and gentoo penguin (*Pygocelis papua*). Foraging and reproductive performance at South Georgia between 1976 and 1998. Upper and lower 95% confidence intervals for long-term mean are shown for each series. (From Reid, K., Barlow, K.E., Croxall, J.P., Taylor, R.I., *Mar. Biol.*, 135, 651, 1999.)

5.7.4.1 Food Availability

The geographic location of food has the potential to affect the spatial patterns and behaviour of krill. Chlorophyll distribution is highly patchy; highest concentrations are found in coastal regions, frontal zones, and the marginal ice zone, while concentrations in the open ocean are similar to those in oligotrophic regions (Sakshaug and Holm-Hansen 1984; Smith and Sakshaug 1990). The primary factor affecting the accumulation of phytoplankton biomass is light intensity, which is a function of seasonal solar radiation, extent of ice cover, and depth of vertical mixing. In addition, low seawater temperatures limit specific growth rates of phytoplankton, while nutrients rarely limit growth.

When phytoplankton concentrations are low all stages of krill feed omnivorously (Hopkins and Torres 1989; Daly 1990); as a result chlorophyll concentrations may not always be the best indicator of food availability. Furthermore, as we have seen, adults can live for up to 7 months without food by utilizing their own lipid and protein and

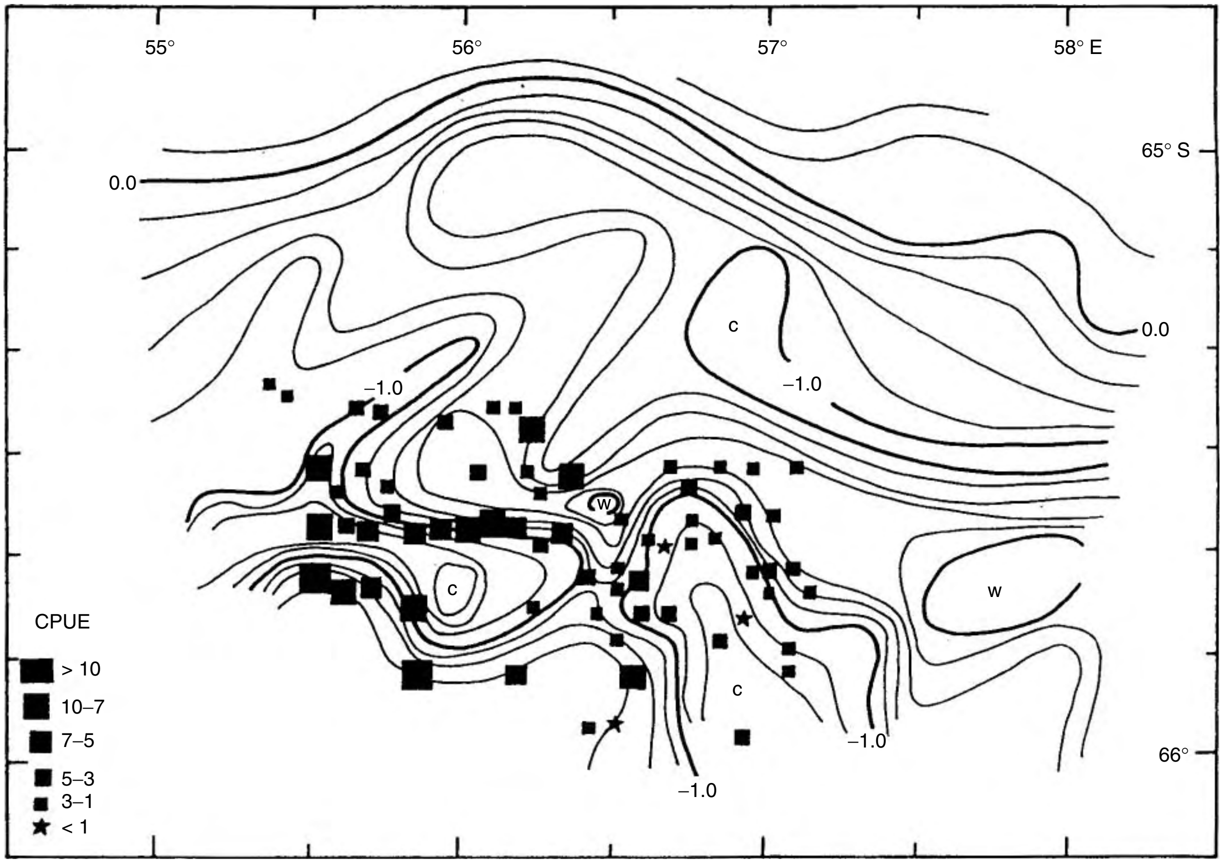


FIGURE 5.17 Distribution of water temperatures at 50 m off Enderby and together with Catch Per Unit Effort (CPUE) from Japanese commercial trawlers. (From Nasu, K., *Ber. Polarforsch.*, 4, 216, 1983.)

shrinking in size (Ikeda and Dixon 1982b). Nevertheless, field data and laboratory experiments suggest that growth of krill may be food-limited, particularly in the open ocean regions (Brinton and Townsend 1984). Experimental evidence also indicates that first-feeding larvae do not survive delayed food availability (Ikeda 1984a) and that food availability affects the timing of reproduction in adults and the number of batches of eggs spawned in a season (Ross and Quetin 1986). Both positive and negative correlations between food availability and krill distribution have been reported (Rakusa-Suszczewski 1982; Brinton and Townsend 1984; Weber and El-Sayed 1985; Nast and Gieskes 1986).

5.7.4.2 Predation

Predation also has the potential to affect the distribution and behaviour of krill since predation is considered to be the main cause of mortality in plankton populations. This has already been considered in Section 5.4.4.7. While the consumption of krill by predators is well known, there is no experimental evidence for krill population control by predation, and krill-predator interactions are not fully known (Croxall et al. 1985).

5.7.4.3 Social Behaviour

This factor may influence the distribution of krill. As we have seen, swarming behaviour is characteristic of krill distribution patterns. Swarming is assumed to be a response to environmental interactions, yet little is known about motivating factors or seasonal patterns in krill behaviour. *E. superba* is sensitive to variation in food availability (Hamner et al. 1983) and changes in risk of predation (Hamner 1984; O'Brien 1987). In one experimental study, the structure of krill swarms did not appear to change in response to water flow but rather to behaviorally-induced mechanisms, such as food and predators In another study krill were induced to swarm in a tank when a model of a predator was introduced (Strand and Hamner 1990). Complex schooling has been observed in all life history stages of *E. superba*, including foraging, feeding, predator avoidance, and mating behaviour (Hamner 1984; Naito et al. 1986; O'Brien 1987). Furthermore a large swarm repeatedly fished by trawlers remained coherent and was observed to migrate over 187 km in 18 days (Kanda et al. 1982). Therefore on a local scale, the formation distribution of individual swarms are not the result of environmental mechanisms such as currents but are behaviorally determined.

5.7.4.4 Sea Ice

The interaction of sea ice with swarming behaviour had been considered in Section 5.4.4.5. As we have seen the distribution of pack ice and the ice edge zone, a region of enhanced phytoplankton production have an impact on krill swarming behaviour. Concentrations of krill have frequently been reported in the ice edge zone (Fraser 1936; Marr 1962; Mackintosh 1972, 1973; Nast 1982). The ice biota provide a food source for both larval and adult krill (Guzman 1983; Hamner et al. 1983). Daly and Macauley (1991) investigated the seasonal distribution and behaviour of *E. superba* in the marginal sea ice zone of the Weddell and Scotia Seas. Their results suggested that juvenile krill were more abundant under pack ice than in open water in the spring (Daly and Macauley 1998) and that the ice biota were an important food source for larval krill in the winter (Daly 1990).

Numerous reports of krill feeding on ice algae at the ice edge (Stretch et al. 1988; Siegel et al. 1990), deep in the pack ice, or under fast ice (Spiridonov et al. 1985; O'Brien 1987; Marschall 1988; Ikeda and Kirkwood 1989) indicate that the association between krill and sea ice is common in the Southern Ocean. Yet not a great amount is known about the physical, chemical, and biological dynamics that generate structure and spatial patterns in krill populations in the ice edge ecosystem.

Daly and Macauley (1991) investigated the relationships between the spatial distributions of ice cover, temperature, salinity, food availability, and life history stages of *E. superba* in the marginal ice edge zone of the Weddell and Scotia Seas. They found that while physical processes control the extent of ice cover, the magnitude and location food, and the distribution of pack ice predators, physical processes did not appear to directly affect krill. Instead, the seasonal distribution and behaviour of krill was interpreted to be a function of the need to acquire food and avoid predators. These two factors were also hypothesized to be the proximate cause of swarming behaviour. Seasonal sea ice played a major role in the ecology of krill (Figure 5.18). Ice edge blooms were an important and predictable food supply, particularly for reproducing adults and first-feeding larvae. Ice floes provided protection for larvae, juveniles, and sea ice biota, a widespread food source. This is important to the survival of larvae during the winter. In the marginal ice zone, overwintering strategies of adults included regression to an immature (sub-adult) stage, reduction of metabolic rate, and omnivorous feeding in the water column. Adult krill may migrate deep into the pack ice in the winter where they feed on the ice biota. They concluded that the sea ice biota act as a stabilizing mechanism against extreme seasonal oscillations of food supply for overwintering krill, thus contribution to the persistence of populations of *E. supernba*.

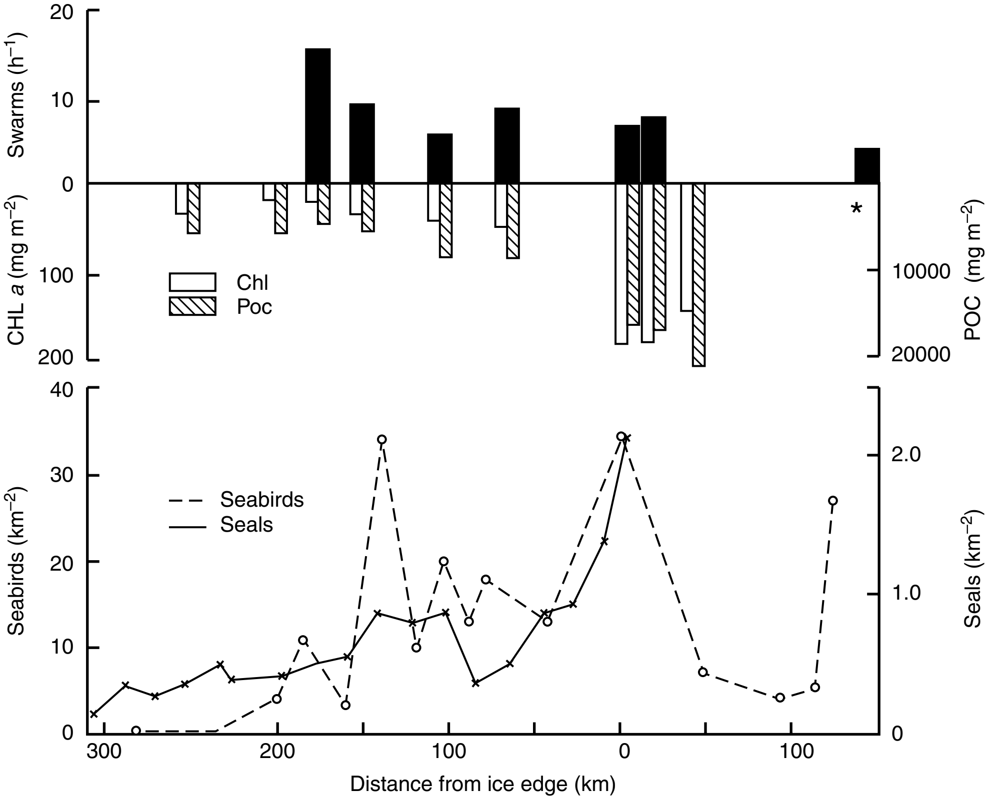


FIGURE 5.18 *Euphausia superba*. Spring horizontal distribution of swarms in relation to distance from the ice edge n the Weddell and Scotia Seas, food availability and predator density. Chlorophyll *a* (chl *a*) and particulate organic carbon (POC) are integrated to 100 m (* denotes chl and POC concentrations are unknown), and densities of swarms, seals and seabirds are from the eastern transect. (From Daly, K.L., Mcauley, M.C., *Mar. Ecol. Prog. Ser.*, 79, 56,1991.)

5.7.5 CONCLUSIONS

The location of the Polar Front was thought to strongly influence meso- to large-scale abundance and distribution (Quetin et al. 1996). While this may apply to the South Georgia region in other areas krill occur well south of the Polar Front. Other large-scale phenomena which have become apparent included sea ice coverage, as discussed above, and ENSO effects which impact on circulation patterns and sea ice extent.

Fluctuations in population parameters are often caused by food availability and quality. Changes in primary and secondary productivity create a potential for fluctuatio krill survival, probably causing reduced spawning success, increased larval mortality, and finally lower recruitment success. Ultimately, changes krill productivity are caused by a combination of factors (climate effects, oceanography, food and prey availability, composition, competition, predator pressure, etc.).

According to Nicol (2006) krill have evolved a life history that is obviously highly successful at exploiting their seasonally variable environment. In the model that he presents the various history traits that krill possess are part of an overall system that allows them to survive in a highly seasonal fluid environment. For the purposes of the model, krill are divided into development stages: larvae, juveniles and adults. A secondary division separates gravid females from the rest of the adult population. These groupings are thought to remain geographically separate (Siegel 2000). A simple seasonal representation of these life history stages is shown in Figure 5.19 and Figure 5.20. In summer, the adult krill population is centered close to the shelf break, which allows access to pelagic food supplies but also places the population within a counter-current circulation system with the ACC to the north and the Coastal Current to the south. Small movements within this region can have major effects on the horizontal distribution of individuals and populations. Krill females that move offshore to spawn place their young into the eastward-flowing waters of the ACC, but the developing stages are not lost to the system, because of the gyral circulation patterns that link the ACC or the Coastal Current and because of the vertical circulation pattern near the shelf break (Figure 5.19a). These currents will also bring the larvae back inshore to the shelf region where juveniles are encountered the following summer. Sea ice microbial communities are essential for larval krill in winter, and their movement is linked to that of the ice (Figure 5.19b). Adult krill are robust and can utilize other food resources and thus they would not need to compete with the larvae that must feed, develop, and grow over the winter-months. Adult krill can thus be found deeper in the winter, and may also move inshore in deep tpoughs.

5.8 OVERWINTERING MECHANISMS

Until comparatively recently, *E. superba*, unlike other euphausiids that are characterized by versatile feeding behaviour, was widely regarded as being totally dependent on phytoplankton food (Mauchline and Fisher 1969). The generally accepted picture of *E. superba* as an active (Kils 1981), swarm-forming (Hamner et al. 1983), filter-feeding herbivore (Mauchline and Fisher 1969; Boyd et al. 1984), with a high respiration rate (Kils 1981), restricted in its adult phase to the upper 200 m water layer (Mauchline and Fisher 1969), is in reality true only in the summer ice free habitats (Smetacek et al. 1990). In the past there had been much speculation, without hard evidence, as to how *E. superba* survived during the winter when phytoplankton stocks were severely depleted.

Huntly et al. (1994) in discussing the over-wintering of *Euphausia superba*, suggested that the feeding behaviour of this species allows for year-round growth. In spring and summer krill are predominantly herbivorous, though even then occasional animal food may be ingested (Hopkins 1987). As the period of high primary production draws to a close in autumn and phytoplankton food becomes scarce, the krill diet becomes predominantly carnivorous. During the winter krill remain in the upper 200 m of the water column, approximately where they were in the summer, and feed on the relatively high abundance of zooplankton from the productive summer. This mode of feeding continues until the late winter, when daylight increases and primary production in the sea ice (Kottmeier and Sullivan 1987) gives rise to high abundances of microalgae (Daly 1990). As the season progresses, krill move toward regions such as the marginal ice zone where the food-laden sea ice has begun to disintegrate, and then taking advantage of the large concentrations of microalgae that form when the sea ice melts (Marschall 1988), thus completing the annual cycle. Growth continues throughout the year.

Quetin and Ross (1991) reviewed the mechanisms employed by krill to survive the winter period when planktonic food supplies are low. Four major hypotheses, shrinkage, lipid utilization, switching of food sources, and “hibernation” (Figure 5.21) have been proposed to explain how krill survive the six-month winter period of low food, low light, and often extreme ice cover. To test these hypotheses and to estimate their relative importance for populations of adult *E. superba* west of the Antarctic Peninsula, Quetin and Ross compared the physiological condition of krill in the field at different times of the year.

5.8.1 SHRINKAGE

This phenomenon was discussed previously in Section 5.3.7. Ikeda and Dixon (1982b) found that when starved for long periods individual krill shrink 1–2% during each intermoult period of about a month. However, Stepnik (1982), in an analysis of length frequencies of *E. superba* from Admiralty Bay, found positive growth in late winter and early spring, suggesting that shrinkage may not occur in some field populations.

In their investigation Quetin and Ross (1991) found that in the late summer and early autumn growth was positive

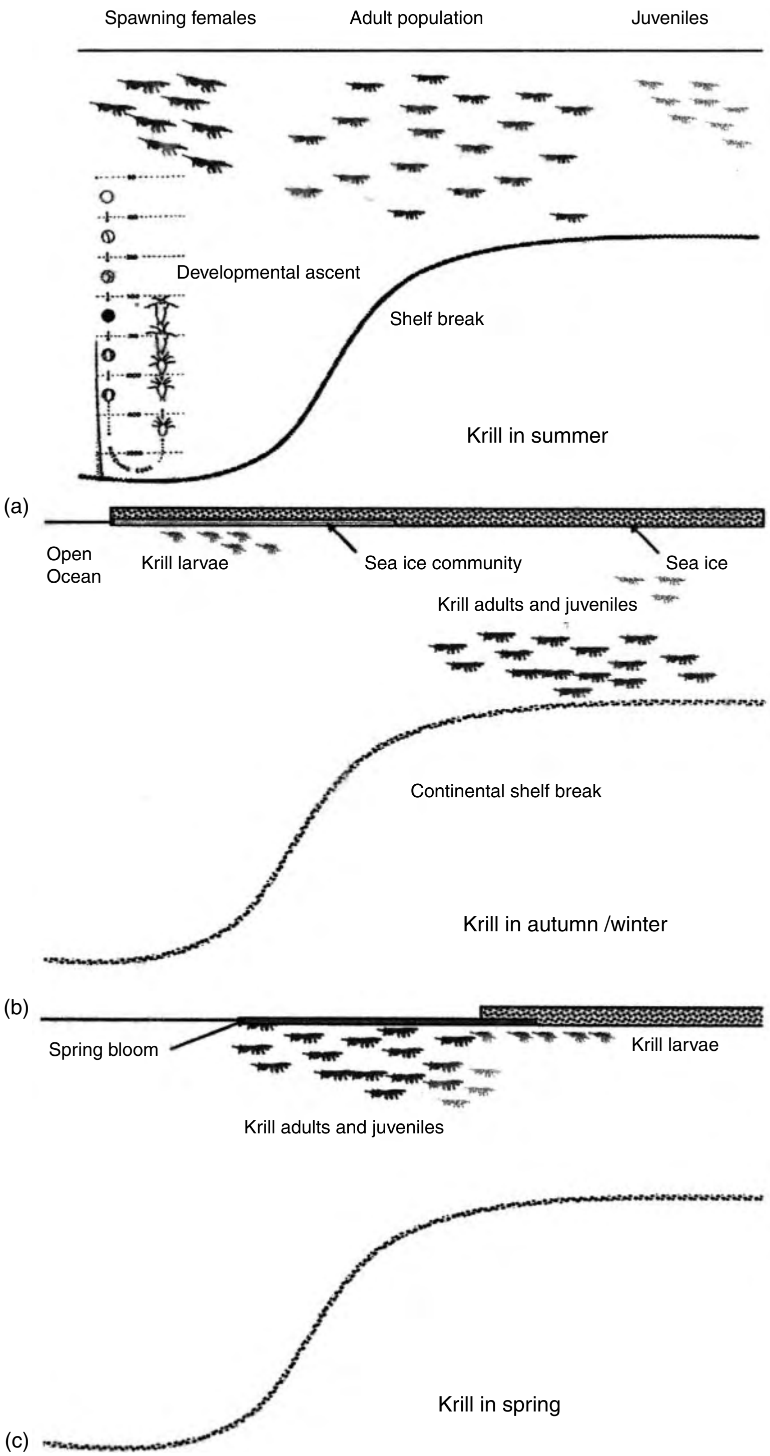


FIGURE 5.19 Simplified seasonal representation of the vertical and horizontal distribution of krill from offshore (left) to onshore (right): (a) summer, (b) autumn-winter, and (c) spring. Source: Nicol, S., Bioscience, 56, 117, 2006. With permission.

(1.75–4.40%). Growth in the winter was negative (-0.16 to -2.03) per intermoult period, and intermoult periods were twice as long. Krill not only shrank in linear dimension but they also lost volume. The wet weight of a krill 42 mm long decreased from 667 to 542 mg, a loss of 125 mg.

5.8.2 LIPID UTILIZATION

Stored lipids may be used as an energy source during the winter. In contrast to the other dominant Antarctic euphausiids such as *E. crystallorophias* and *Thysanoessa macrura*,

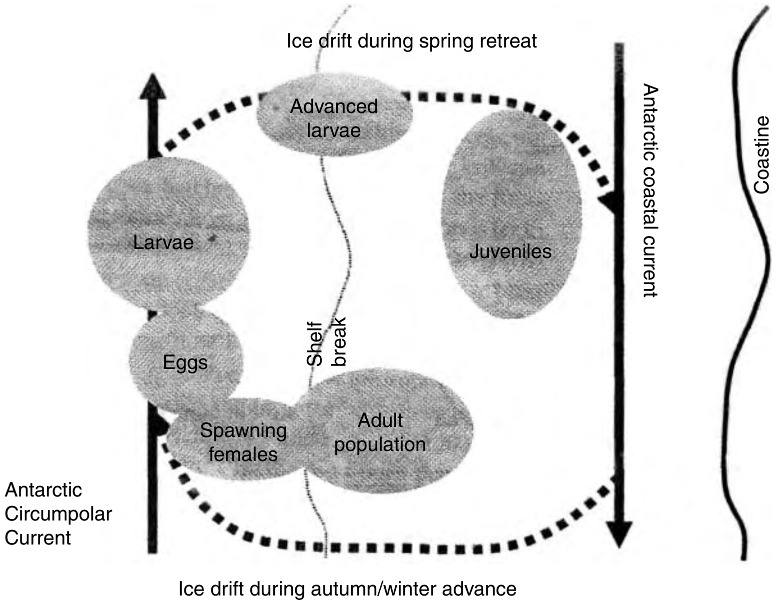


FIGURE 5.20 Seasonal ontogenetic migration pattern of Antarctic krill, showing how krill utilize the gyral circulation patterns that link the two major current systems. Source: Nicol, S., *Bioscience*, 56,118, 2006. With permission.

which store lipids in the form of wax esters *E. superba*, relies on triacylglycerol and phosphatidylecholine. Quetin and Ross (1991) analysed samples in the late summer early autumn and late winter for total lipid content. The average lipid content was 7.8% in the autumn, dropping to 3.86% in the late winter, indicating that lipid reserves were used during the winter for energy. Hagen et al. (2001) investigated lipid storage as an overwintering strategy in krill. They found a mean total lipid content of 28.2% of dry mass at the end of summer with levels peaking at 39.2% in the autumn. After the overwintering period mean lipid content decreased to a minimum of 10.5% of dry mass, indicating extensive utilization of lipid reserves during the winter period. It is thus clear that lipid reserves play an important role in krill overwintering.

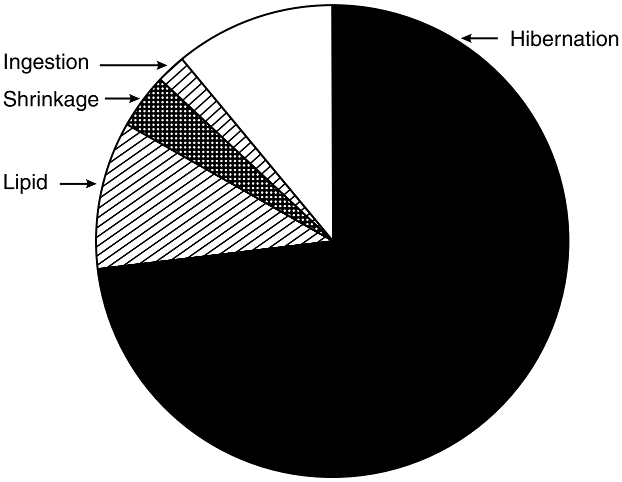


FIGURE 5.21 Relative importance of the four major winter-over mechanisms proposed for a nonhibernating *Euphausia superba* in the waters west of the Antarctic Peninsula. The entire circle represents the energy requirement for the six months of low food availability as predicted from summer metabolic rates. The hibernation segment shows how much the energy requirement would be reduced by hibernation. The white segment is the proportion of the energy requirement that remains unexplained. (From Quetin, L.B., Ross, R.M., *Amer. Zool.*, 31, 702, 1991.)

5.8.3 SWITCH OF FOOD SOURCES

Food resources available to krill during the winter period could include copepods, the invertebrates of the sea ice microbial communities, invertebrates associated with the under-ice water layer, the sea ice microalgae, detritus, or, in shallow water, the benthic microalgae.

As discussed in Section 5.10.7, krill are omnivorous and potentially can feed on other zooplankton species, especially copepods. While Price et al. (1988) found in their experimental work that krill could feed very efficiently on copepods, they concluded that such feeding would meet less than 10% of their minimum metabolic requirements at the "typical" copepod densities reported from Antarctic waters. However, it is possible that the large concentrations of copepod development stages which have been reported as being associated with the bottom layer of the sea ice and the platelet ice layer (Fukuchi and Tanimura 1981; Fukuchi et al. 1985b; Hoshiai et al. 1987; Waghorn and Knox 1988) could provide a substantially greater potential prey resource.

A number of studies (Garrison et al. 1986b; Marschall 1988; Stretch et al. 1988) have documented widespread feeding by krill on sea ice microalgae. Marschall (1988) found that in the winter in the Weddell Sea krill were scarce in the water column with densities of 2–4 individuals m^{-3}. This contrasted with remote operated vehicle surveys which indicated densities under the ice of 40–400 individuals m^{-3}. It is now clear that krill undertake seasonal migrations to the north in the summer and to the south in the winter. During the winter when the water column phytoplankton stocks are low the sea ice microalgae are a major food resource. This may be supplemented by carnivory, detritivory, and cannibalism.

In an investigation of the marginal ice edge zone during the winter in the Scotia-Weddell Sea Confluence area, Daly (1990) found that krill larvae were abundant at the ice edge and on the undersurface of the ice floes. Larval development and growth, which are dependent on food supply, progressed steadily from June to August. The krill larvae moulted about every 30 days and growth rates (0.7 mm day^{-1}) were similar to reported summer rates. Gut fullness indicated that 98% of the larvae were feeding both day and night. Examination of gut contents revealed that typical sea ice diatoms, such as *Nitzschia cylindrus*, *N. curta*, *N. pseudonana*, and *Pinnularia* sp., as well as the archaeomonad *Archaeomonas aereolata*, were common. In addition to the diatoms dinoflagellates, scales of prasinophytes and chrysophytes were present. Thus, if heterotrophic carbon (protozoans and possibly detritus) is taken into account larval krill feeding on sea ice biota could ingest enough carbon to support the observed growth.

Little is known of the predators of larval krill. Hamner et al. (1983b) observed predation by a ctenophore and the ice amphipod *Eusirus antarcticus*. In the marginal ice zone in autumn larval krill were found in the guts of two species of copepods *Euchirella rostromanga* and *Heterorhabdus austrinus*, the euphausiid *Thysanoessa macrura*, the ice amphipod *E. antarcticus*, the chaetognath *Sagitta marri*, the salp *Salpa thompsoni* and the fishes *Bathylagus antarcticus*, *Electrona antarctica*, *Gymnoscopelus braueri*, and *G. opisthopterus* (Hopkins and Torres 1989). Also, furcilia are occasionally found in the guts of adult *E. superba*. Refuge from these predators is provided by the undersurface of the pack ice with the rafting of ice floes providing numerous caverns and crevices.

In their experiments on krill feeding, Quetin and Ross (1991) found that ingestion rates decreased from 5 μg chl *a* wet wt^{-1} h^{-1} in late February to near zero in early autumn and remained very low throughout the winter. Winter rates of phytoplankton ingestion were less than 2% of the summer rates. Fecal pellet production rates decreased from 185 μg C day^{-1} in late summer to less than 3% of the summer rate during the late winter. They concluded that since both the rates of fecal pellet production and ingestion of phytoplankton in winter were less than 3% of the summer rates, adult krill do not derive a large proportion of their energy from carnivory in winter.

5.8.4 HIBERNATION

The final hypothesis is that krill "hibernates" or enters a state of severely reduced metabolism and only swims enough to remain in the water column during the winter. Evidence suggests that there is a reduction in respiration (Kawaguchi et al. 1986) and digestive enzyme activity (Mumm 1987) in the late autumn and early winter. In laboratory experiments Boyd et al. (1984) found that under winter environmental conditions the respiration rate of krill was half that of krill maintained under summer conditions, while Quetin and Ross (1991) found that the rates of oxygen consumption were only 33% of those in the summer. In the autumn a large proportion of the krill may migrate south and reduce their metabolism. Respiration rates increase again in the spring. Kawaguchi et al. (1986) found that they increased twofold from August to September. There is also evidence that growth rates derived from length frequency measurements start to increase again in the early spring well before the onset of phytoplankton primary production (Mackintosh 1972).

Figure 5.21 from Quetin and Ross (1991) depicts their evaluation of the relative importance of the four major overwintering mechanisms for krill west of the Antarctic Peninsula. It appears that in contrast to the multi-year pack ice of the Weddell Sea where the ice cover is predictable and extensive with complex undersurface providing hiding places and ample food, the ice cover west of the Antarctic Peninsula is unpredictable and its smooth undersurface provides the krill with little refuge from predation and the krill remain in the water column and feeding is reduced. From Figure 5.21 it can be seen that "hibernation," or lowered metabolic rate, was by far the most important mechanism for successfully surviving the winter. Over 71% of the anticipated energy requirements was saved by this lowering of metabolic rates. Direct lipid utilization provided almost 11% of the energy, and utilization of protein and lipid in the body from shrinkage in both total length and in volume provided another 4% of the predicted energy requirements. However, the balance may be quite different in other regions of the Southern Ocean. For instance, in areas of lower productivity, lipid reserves may not be as high, so either additional shrinkage or weight loss may occur. As we have seen, krill can feed on the sea ice microalgae and its availability may differ in different areas. The predictability, extent, and morphology of the ice cover will play an important role in determining the relative importance of the various overwintering mechanisms.

5.9 STOCK SEPARATION

Over the years there has been much speculation as to whether local krill concentrations represent discrete krill stocks, or whether substantial intermixing occurs (Mackintosh 1972; Makarov 1973; Lubimova et al. 1984). However, recent research has not been able to confirm the existence of separate stocks of krill.

Siegel (1986a, 1986b), in an analysis of morphometric variability in krill populations around the Antarctic Peninsula, was unable to distinguish any differences in krill from the northern Bellingshausen Sea, the Drake Passage, the Bransfield Strait, and the northern and southern Weddell

Sea. Because of the inherent difficulties associated with morphometric studies an alternative approach, the electrophoretic analysis of variations in the structure of enzyme proteins, has been developed. While early electrophoretic analyses (Ayala et al. 1975; Fevolden and Ayala 1987) suggested the existence of at least distinct krill populations in the Antarctic Peninsula region, this has not been confirmed by subsequent studies. Analyses of krill samples from locations in the Weddell Sea, the Scotia Sea, and around the Antarctic Peninsula and Prydz Bay (MacDonald and Schneppenheim 1983; Schneppenheim and MacDonald 1984; Fevolden 1986; Scheppenheim 1990; Fevolden and Scheppenheim 1988) have shown that all of the samples were from a single population.

5.10 FEEDING AND ENERGY EXPENDITURE

5.10.1 INTRODUCTION

Because of the abundance of *E. superba* and its pivotal position in the food web between the primary producers and secondary consumers, its feeding activities have consequences of great importance to the structure, function, and management of the Antarctic marine ecosystem (Quetin and Ross 1985). The Peruvian anchovy is one of the few comparable examples of a single species whose abundance is so crucial to the structure of a large marine ecosystem (Idyll 1973). Field studies have indicated that feeding in krill is one element of a complex interaction between nutritional requirements, swimming, swarming behaviour, and vertical and horizontal migration (Pavlov 1969; Nemoto 1972; Gubsch 1979; Kalinowski and Witek 1982; Kils 1981; Morris et al. 1983, 1984; Boyd et al. 1984; Morris and Priddle 1984; Morris and Ricketts 1984; Morris 1984, 1985). Field and laboratory studies on the feeding of krill have provided much information on potential feeding mechanisms, filtration, ingestion and egestion, effects of chlorophyll levels, and swarming behaviour in relation to feeding.

5.10.2 SWIMMING BEHAVIOUR

Swimming behaviour, which is intimately related to feeding, has been investigated in detail by Kils (1979b, 1981, 1983) utilizing experimental aquaria and in situ underwater observations. Krill use two methods to produce propulsion for active forward movement: swimming by beating the abdominal pleopods (the normal method of forward propulsion) and tail swimming characterized by jerky driving of the tail (generally used as a flight reaction). Figure 5.22 depicts the maximum swimming velocities of pleopod and tail swimming. Roughly it can be seen that krill can reach eight times its body length per second with pleopod swimming and eleven times its body length per second with tail swimming. In Kil's experiments on swimming activity, krill maintained swimming speeds of 1.5–3.5 body lengths s^{-1} for more than a week.

The density of krill at 1,070 g cm^{-3} is extraordinarily high for a pelagic animal. According to Aleyev (1977), most pelagic animals have densities similar to that of seawater; of 67 investigated pelagic species from different animal groups, all values were under 1.055 g cm^{-3}. Where the density of the body tissue exceeded this value, the animals possessed other diverse buoyancy aids which are lacking in krill. Thus krill must constantly swim to maintain position in the water column, otherwise they would sink within three hours to a depth of 500 m.

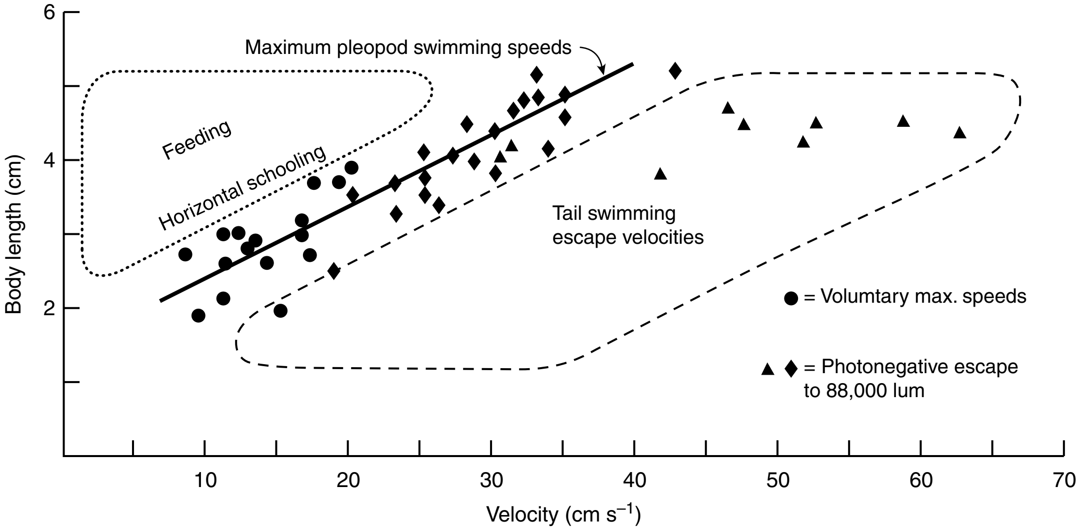


FIGURE 5.22 Swimming speeds versus body lengths of *Euphausia superba*. Voluntary maximum pleopod swimming speeds of disturbed individuals in a 751 l aquarium at Palmer Station were measured via a stopframe analysis of video tapes. Dotted lines encompass the presumed ranges of feeding and schooling speeds maintained by pleopod swimming and of backward escape velocity generated by tailswimming. (From Hamner, W.M., *J. Crust. Biol.*, 4, Special Issue 1, 67, 1984.)

5.10.3 The Feeding Mechanism

It is clear that in the summer when phytoplankton is high *E. superba* feeds predominantly on phytoplankton (Barkley 1940; Hart 1942; Hustedt 1958; Marr 1962; Nemoto 1972; Clarke 1980a; Boyd et al. 1984). Studies of feeding behaviour (Hamner et al. 1983; Kils 1983; Boyd et al. 1984; Morris 1984; Quetin and Ross 1985) have provided detailed descriptions of the feeding mechanism of krill. Descriptions of the feeding apparatus have been provided by Berkes (1975), Kils (1979a, 1983), Alberti and Kils (1990), Antezana et al. (1982), Clarke and Morris (1983a), McClatchie and Boyd (1983), and Marschall (1985). A V-shaped filtering basket is formed by the six periopods (thoracic appendages or thoracopods). The first two segments of the periopods bear primary setae, each of which have two rows of secondary setae arranged along their length. Tertiary setae on the latter result in a filter net mesh size smaller than 1.0 μm. The terminal appendages of the periopods bear comb setae which have a comb-like device at their ends. The two basic types of setal arrangement form two different kinds of filter nets: (1) a very fine net with a relatively large net area formed by the filter setae (mesh size 1–4 μm), and (2) a coarse net with comparatively small net area formed by the basal parts of the comb setae (mesh size 25–40 μm) (Figure 5.23).

When not feeding *E. superba* swims rapidly, pressing its six pairs of thoracic legs (periopods) together to form a keel. Two principal feeding methods have been proposed (Kils 1981, 1983). In the first, "pumping filtering," the filtering basket formed by the thoracopods is periodically opened and closed directing food towards the mouth. This type of feeding has been observed by several workers, both in the laboratory (Antezana et al. 1982; Kils 1983; Boyd et al. 1984) and in the field (Hamner 1984).

The second method of feeding is termed "compression feeding." In this method the periopods are extended to push a pocket of water through the feeding basket which is rapidly collapsed. Food particles are retained by the setae as the water is extruded (Antezana et al. 1982; Hamner et al. 1983). The feeding basket is filled and compressed with a frequency that varies from 1 to 5 Hz. The relationship between the filtering net and the potential food organisms is shown in Figure 5.23. These filter-feeding mechanisms can reject particles greater than 30 μm and potentially retain particles greater than 1 μm, including bacteria.

Kils (1983) notes that the dactylopodes (terminal segments) of the thoracopods (thoracic appendages) have rake-like structures which have a quite different morphology to that of the normal setae; they are much stronger and increase in diameter from the tip to the base. They are thus well suited to grazing diatoms from the ice or other surfaces. As discussed in Section 5.10.3, this has been confirmed by observations of krill actively feeding on sea ice microalgae and by laboratory experiments. In laboratory experiments, Hamner et al. (1983) concentrated and refroze sea ice

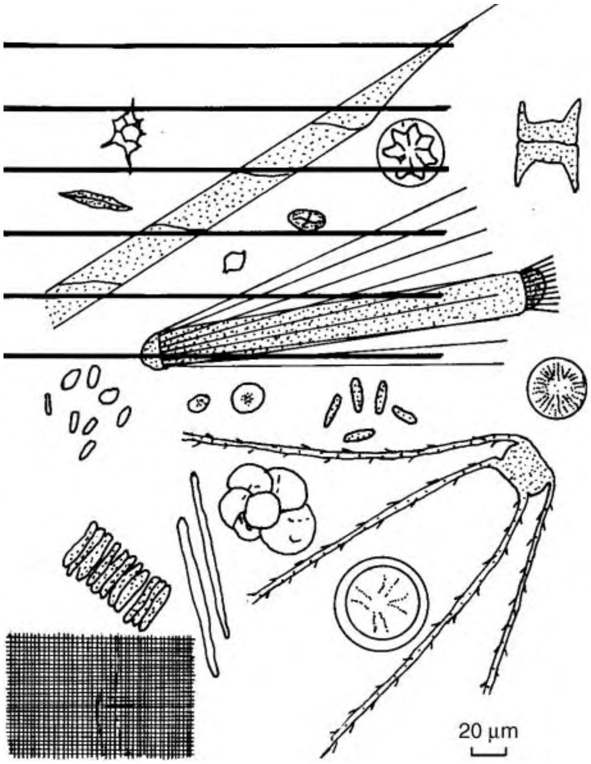


FIGURE 5.23 Size relationship between ambient food organisms and the filtering nets of *Euphausia superba*. Top solid bars represent comb setae net; Lower left corner represent filter-setae net. (From Kils, U., *Ber. Polarforsch.*, 4, 130, 1983.)

microalgae into small blocks which were then floated in an aquarium containing krill. As the blocks softened, the *E. superba* located the food by area-intensive search. They then extended their dactylopods and raked the ice algae into the feeding basket, moving along the submerged surfaces of the blocks or holding them in place at sites of high algal concentration.

The observations of Hamner et al. (1983) have been confirmed by O'Brien (1987), Spiridonov et al. (1985), Marschall (1988), and Stretch et al. (1988). Stretch et al. (1988) found that when *E. superba* foraged near ice floes, they exhibited two distinct behaviour patterns. When stimulated by algae released from the melting ice they show area-intensive foraging behaviour. This behaviour is characterized by high speed swimming and rapid turning, accompanied by rapid opening and closing of the feeding basket. This is often followed by ice grazing behaviour during which the euphausiids orient themselves towards the undersurface of the ice to rake algal cells off the ice by their dactylopodites.

Observations by Marschall (1988) used a remotely operated vehicle which enabled assessment of krill abundance and behaviour in relation to ice conditions. The highest concentration occurred in rugged ice caused by the piled up floes of pressure ridges and/or melting. Individuals located close to the ice were mostly feeding and had dark green guts. They moved along the ice at approximately 0.1–0.5 body length s^{-1}, continuously scraping the surface with the tips of their thoracopods and opening and closing their feeding baskets at a frequency of 2–3 Hz. These observations were confirmed by laboratory experiments in which the krill left clearly visible feeding tracts of glass plates covered with sea ice microalgae.

Krill are also capable of raptorially capturing and holding large particles, including moulted cuticles of crustaceans, in their feeding basket (Hamner et al. 1983; Boyd et al. 1984). Boyd et al. (1984) carried out a series of experiments in which furcilia larvae were fed to adult krill. Filtration rates and ingestion rates of these adults feeding on furcilia, when normalized to mg dry wt of adult predator, were surprisingly close to that obtained when adults were fed algal cells. McWhinnie and Denys (1979) noted that in krill kept in aquaria cannibalism was relatively common and they were also observed to feed on other zooplankton. Thus, under certain circumstances krill may be carnivorous or cannibalistic (Miller 1982).

5.10.4 Studies on Feeding and Filtration Rates

A number of feeding studies have investigated the clearance (filtration) rate and the apparent selectivity of food particles. Clearance rates have been determined in a variety of ways from the rate of chlorophyll *a* depletion in closed vessels containing euphausiids and natural phytoplankton (Kato et al. 1979; Meyer and El-Sayed 1983); from the difference in chlorophyll *a* in the seawater from the inlet and outlet of an aquarium containing thousands of animals (Antezana et al. 1982); and from changes in cell numbers of natural phytoplankton consumed by krill in flow-through (Morris 1984) or closed systems (Boyd et al. 1984; Quetin and Ross 1985). The clearance rates obtained with the flow-through systems used by Morris were several orders of magnitude higher than those reported by other investigators using closed vessels (see Table 5.6).

The apparent filtration rate derived from the particle size analysis in Morris's 1984 experiment is plotted for each size channel in Figure 5.24. The shape of this curve indicates that not all particles are filtered with equal efficiency (Kils 1981; Boyd et al.1984; Hamner 1984). The maximum filtration rate occurred in the 24 μm size range and was 42.8 l h^{-1}. The highest rate measured in any experiment was 66.8 l h^{-1}. Kils (1981) estimated that the retention efficiency of *E. superba* at approximately 50%, while McClatchie and Boyd (1983) suggested a maximum efficiency of 30–40%. These estimates indicate that the actual filtration rates are in the range of 80–100 l h^{-1}. If, however, some degree of particle selection occurs then these high filtration rates will be overestimates.

In a series of closed experiments, Quetin and Ross (1985) found that the maximum clearance rates were closely linked to size but, not the species, of phytoplankton being ingested (Table 5.7). The physical dimensions—not the chemical composition—of the cells are probably the most important parameters affecting maximum clearance rates. Several other studies indicate that *E. superba* does not feed equally well on all sizes of phytoplankton (Clarke and Morris 1983a; Meyer and El-Sayed 1983; Boyd et al. 1984; Morris 1984). Morris (1984) found that particles of 30 μm were maximally retained, and that particles of greater than 30 μm in diameter were apparently rejected (Figure 5.24). Boyd et al. (1984) found that phytoplankton with diameters of greater than 12 μm were retained maximally, and that cells of only 6 μm in diameter were retained with a 50% efficiency (Figure 5.25). The maximum clearance rate of 357 ml h^{-1} found by Quetin and Ross (1985) generally agrees with that found by Boyd et al. (1984) who obtained a clearance rate of 500 ml h^{-1} for euphausiids of 45 mm total length, and the value of 210 ml h^{-1} measured by Antezana et al. (1982). The differences between the three studies are probably due to the different sizes of the animals used. Morris (1984), on the other hand, reported a maximum clearance rate for *E. superba* of 66,816 ml h^{-1}, more than 130 times the maximum rate found by other workers. Such a rate is considered on theoretical grounds to be much too high.

In their flow-through experiments on the omnivorous feeding behaviour of *E. superba*, Price et al. (1988) found that the clearance rate for phytoplankton increased linearly with phytoplankton concentrations. Clearance rates increased from approximately 300 ml $krill^{-1}$ h^{-1} at an initial concentration of 0.1 μg chl *a* l^{-1} to over 800 ml $krill^{-1}$ h^{-1} at the highest concentration of 13 μg chl *a* h^{-1}. Other authors have reported conflicting results. The discrepancies may be due to differences in the types and sizes of the cells and the range of concentrations used. However, it seems that krill do not become saturated under most field conditions, since algal concentrations, except under bloom conditions, seldom exceed 13 μg chl $a\ \mathrm{l}^{-1}$ and generally are much lower, in the order of 0.6 μg chl $a\ \mathrm{l}^{-1}$ (Holm-Hansen and Huntley 1984).

The complex interaction of krill filtration mechanism, particle size distribution in the water, and experimental conditions have produced varied data for the actual filtration rates. These are summarized for a 50 mg dry wt animal in Table 5.7. It can be seen that there is wide variation in the data. However, it is clear that the filtration rates are high, on the order of hundreds and in some cases thousands of ml h^{-1}. Flow-through particle size analysis data are more likely to be representative than data obtained from constant volume exchange.

TABLE 5.6
Estimates of Krill Filtration Rates

Method	Filtration Rate (ml h^{-1})	Source
Constant volume		
Chlorophyll *a*	20.3 ± 15.2	Kato et al. (1979)
	21.2 ± 14.8	Kato et al. (1982)
	257.6 ± 50.5	Meyer (1981)
	43.6	Antezana et al. (1982)
	210.0	Boyd et al. (1984)
	1,411**	Price et al. (1988)
Particle counter		
> 3 μm particles	175.0	Boyd et al. (1984)
	24.6 ± 9.5	Morris (1984)
$F_{\max}$	210*	Antezana et al. (1982)
	754.7	Morris (1984)
	430*	Boyd et al. (1984)
	357	Quetin and Ross (1985)
Flagellate *Isochrysis galbana* (= 4 μm sphere)	130	Quetin and Ross (1985)
Pennate diatom *Phaeodactylum tricornutum* (EDS = 4 μm)	167	Quetin and Ross (1985)
Centric diatom *Ditylum brightwellii* (EDS = 30 μm)	281	Quetin and Ross (1985)
Centric diatom *Thallasiosira eccentrica* (EDS = 40 μm)	371	Quetin and Ross (1985)
Flow-through		
> 3 μm particles	947 ± 524.9	Morris (1984)
$F_{\max}$	66,816	Morris (1984)
Extrapolations		
Filter basket	169–777	Antezana et al. (1982)
Chlorophyll *a* required	320–5,120	Morris (1984)
	700–13,400*	Morris (1984)
	1,000–20,000	Ikeda and Bruce (1986)
Energy equivalents	1,800–4,700	Kils (1979b, 1979c)
Oxygen consumption	1,893	Rakusa-Suszczewski and Opalinski (1978)

Calculated for an animal of about 50 mg dry weight, except: $F_{\max}$ and other values for animals of unknown weights *. Very large (50 l) experimental container used.

Source: From Morris, D.J., *J. Crust. Biol.*, 4, Special Issue 1, 185, 1984; Miller, D.G., Hampton, I., *Biomass Sci. Ser.*, No. 9, 1, 1985. With permission.

5.10.5 FEEDING BEHAVIOUR

The data discussed in the previous section, together with the information on the great numbers, biomass, and production of *E. superba* (e.g., Hempel 1985a, 1987) and, on the other hand, the rather moderate phytoplankton resources of the Southern Ocean, suggest that in order to fulfil its energy requirements *E. superba* must act as a "vacuum cleaner" which sucks in and filters everything in its way (Kils 1983; Morris 1984). This supposition about the *E. superba* mode of feeding seems to be corroborated by laboratory experiments, the food gut contents, the set of digestive enzymes in krill (Kawamura 1981; Buchholz 1985; Turkiewicz et al. 1989), the value of the metabolic coefficient O:N, and the energy expenditures for locomotion and filtration (Kils 1983). However, a number of investigators have suggested selective feeding by *E. superba* (see Tanoue 1985; Maciejewaka and Opalinski 1993).

Krzysztof et al. (1997) compared the gut contents of *E. superba* with the water column phytoplankton. It was found that the distom *Thalassiosira* was preferred as a food item, and small pennate diatoms, *Nitzschia*, and *Navicula* were only tolerated as food. Other algal taxa, such as *Tropidoneris*, *Dactyliosolen*, *Chaetoceros*, and *Gyrodinium* were clearly avoided. With respect to phytoplankton cell size, *E. superba* preferred cells with a length of 20–40 μm, and cells larger than 70 μm were rejected. It is thus clear that *E. superba* prefers certain sizes and qualitative groups of food particles and avoids others.

Hernandez-Leon et al. (2001) investigated the abundance, gut fluorescence and gut contents of juvenile krill over a diel cycle in the Gerlache Strait. Krill remained in the upper layers (0–100 m) during the day and migrated downwards below this depth during the night, coinciding with the vertical ascent of the copepod *Metridia gerlachei* to shallower layers. Krill fed on phytoplankton during the day, whereas they switched to carnivory during the night. Other studies (e.g., Price et al. 1988; Hopkins and Torres 1989; Graneli et al. 1993; Nishino and Kawamura 1996; Atkinson and Snyder 1997), have documented the feeding

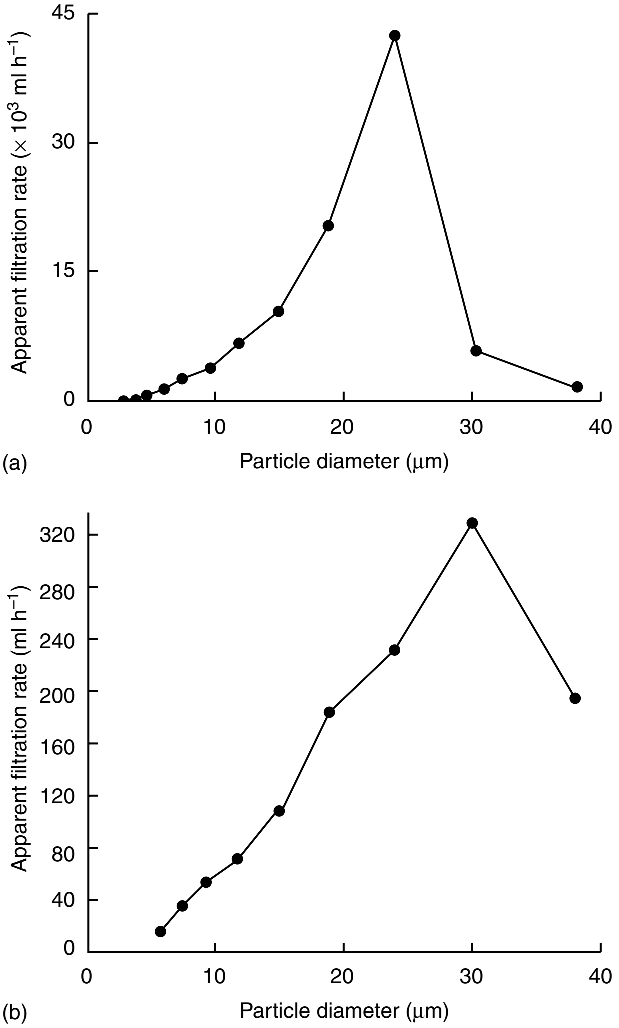


FIGURE 5.24 (a) Apparent filtration rate (R_f) for Euphausia superba as a function of mean particle size from constant volume experiments; krill wet weight = 226.0 mg. (b) As for (a) but for flow through experiments; krill wet weight = 255.5mg. (Form Morris, D. J., *J. Crust. Biol.*, 4, 185, 1984.)

of krill on copepods. Atkinson and Snyder (1997) found that krill preyed on copepods in the range of 1–3 mm (the most common of the large copepods in Antarctic waters). Perissinotto et al. (2000) found that the heterotrophic component of the diet in krill guts accounted for an average value of 79%.

Atkinson and Snyder (1997) investigated feeding by juvenile krill near South Georgia. Krill consumption was estimated by incubations in natural seawater and seawater moderately and highly enriched with phytoplankton and zooplankton. Phytoplankton dominated carbon in the natural incubation water, but dinoflagellates and small calanoid copepods dominated the carbon intake of krill in the enriched water. Maximum clearance rates were on 1–3 mm calanoid copepods. Copepods larger than this (e.g., late copepodite stages of *Calanoides acutus* and *Rhincalanus gigas*) were cleared more slowly. *Oithona* spp. were cleared more slowly than calanoids of similar size, despite their greater abundance. Established clearance rates gave estimates of krill removing daily 0.2% of phytoplankton stocks, 0.6% of protozoans and 1.6% of small calanoid copepods. It is thus clear that krill have a varied diet and that on occasions copepods dominate their diet.

In inshore waters a further algal food resource is the benthic microalgae. Ligowski (2000) investigated benthic feeding by krill in Admiralty Bay. Benthic diatoms in Admiralty Bay grow down to a depth of 150 m (Ligowski 1992). Krill usually occur at a depth of 100–200 m (Siegel 1985; Godlewska 1996), but have been recorded at depths of even 400–450 m in Bransfield Strait and 100 m in the Drake Passage (Marin et al. 1991). Benthic diatoms in the Antarctic coastal sublittoral develop all year round, and their biomass rapidly increases in spring before the phytoplankton bloom (Dayton et al. 1986; Gilbert 1991a, 1991b). At similar geographical latitudes to Admiralty Bay (60–64°S) the bloom of benthic diatoms after winter occurred in early October (Krebs 1983; Ligowski 1992), while the

TABLE 5.7
Percentage of Cell Retained by *Euphausia superba* Feeding on Four Species of Phytoplankton

Species	CDS (μm)	*A*	*B*	*C*
Thalassiosira eccentrica	49.7	48	45	78
Ditylum brightwelli	40.9	38	35	58
Phaeodactylum tricornutum	7.5	18 (22)	14 (18)	35
Isochrysis galbana	5.3	18 (14)	14 (10)	17

A, estimates using the regression on the single highest clearance rate; B, estimates using the regression on the average of the highest clearance rates for each animal; and C, estimates based on a 95% retention efficiency for an 80 μm particle (McClatchie and Boyd 1983) and computed using the calculated spherical diameter (CDS) for each phytoplankton species.

Source: From Quetin, L.B., Ross, R.M., in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 372, 1985. With permission.

phytoplankton bloom was as late as November or even December (Clarke and Leakey 1996). Epiphytic diatoms reach a density of 200,000 cells cm^{-2} (Thomas and Jiang 1986), or even 2,000,000 cells cm^{-2} of macroalgae (Ligowski 2000). In Admiralty Bay, macroalgae occur down to a depth of 90–100 m and cover 35% of the bay bottom (Zielinski 1990). They are a substrate of huge surface area which is colonized by diatoms all year round (Ligowski 1992).

Ligowski (2000) found that in Admiralty Bay in the summer while phytoplankton was consumed so also were benthic diatoms. In the winter benthic species, such as *Paralia sol* and *Trachyneis aspersa* and the epiphyte *Cocconeis costata* accounted for many of the diatoms in the diet. In the krill winter food, large amounts of detritus, mineral particles, and sponges occurred, along with benthic diatoms. Thus benthic food, including diatoms, proved to be an important element for krill both in the summer and winter, particularly in the winter.

5.10.6 FEEDING AND SWARMING

Early conceptual models of the relationship between feeding and swarming in *E. superba* (Pavlov 1969, 1977; Nakamura 1974; Mezykowski and Rakusa-Susczewski 1979; Everson and Ward 1980) assumed that krill did not feed in swarms, particularly in dense swarms, because food was limiting. However, Antezana et al. (1982) challenged this model and suggested that feeding and swarming were co-occurring events. They listed three lines of evidence suggesting that feeding and swarming may neither be exclusive or diel events: (1) in their experiments *E. superba* fed at maximum rates at relatively high densities (2,400–8,900 individuals m^{-3}) which fall within various estimated ranges for krill in swarming conditions (Mauchline 1979; Nemoto et al. 1981; Brinton and Antezana 1984; Macauley et al. 1984); (2) *E. superba* in laboratory swarm densities fed actively within a wide range of chlorophyll concentrations (0.6–11.5 μg chl *a* l^{-1}), which fall within those encountered in the Southern Ocean, including oceanic, coastal, and blooming conditions (El-Sayed 1967; Holm-Hansen et al. 1977; Holm-Hansen and Huntley 1984); and (3) in the experiments ingestion and egestion rates were sustained throughout the day showing no significant diel rhythm.

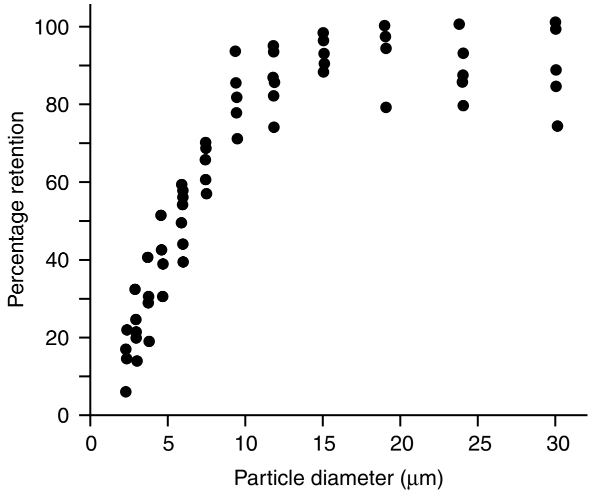


FIGURE 5.25 Efficiency of retention of algal particles by *Euphausia superba*. Data based on filtration rates are normalized to allow the highest efficiency in each experiment to be 100%. (From Boyd, C.M., Heyraud, M., Boyd, C.N., *J. Crust. Biol.*, 4, Special Issue 1, 4, 123, 1984.)

5.10.7 Food Resources and Feeding Requirement

Considerable evidence has accumulated to substantiate the view that krill are essentially herbivorous (Hart 1934; Barkley 1948; Marr 1962; Nemoto 1972; Kawamura 1981; Ligowski 1992), especially during the austral spring and summer when phytoplankton blooms occur. Analysis of krill storage lipids (Clarke 1980b, 1984) and high N ratios confirm the view that they feed predominantly on phytoplankton during the summer.

Unlike other Antarctic zooplankton species, krill are not known to lay down substantial seasonal lipid reserves (Clarke 1983, 1984; Hagen 1988) as a food reserve for the winter when phytoplankton stocks are low. Tanoue (1985) found that the composition of the faecal lipid in small krill (mean body length 21–29 mm) suggested that diatoms constituted the main food consumed, whereas larger krill (mean length 51.2 mm) ingest a mixture of diatoms, choanoflagellates, and other phytoplankton. Tanoue and Hara (1986), through an analysis of essential amino acids, confirmed Tanoue's findings and suggested that choanoflaagellates, which are abundant in Antarctic waters (Silver et al. 1980; Buck 1981; Buck and Garrison 1983; Marchant 1985), could be an important dietary item.

As we have seen there is increasing evidence that in addition to choanoflagellates krill are able to exploit food resources other than phytoplankton. Stomach analyses from field and laboratory studies (e.g., Barkley 1940; Marr 1962; Pavlov 1969, 1977; Price et al. 1988) indicate ingestion of other zooplankton species, especially copepods (see Section 5.10.7). In addition, as we have seen cannibalism has been observed in captive animals (McWhinnie et al. 1979; Miller 1982), and digestive enzyme activity indicates a capacity to assimilate a variety of foods (Mayzand et al. 1985). Krill may also consume heteroflagellates and planktonic protozoa such as the tintinnids, which are often common, but which are extremely difficult to detect in stomach contents.

In their study of krill and their food resources in the Scotia Sea, Holm-Hansen and Huntley (1984) found an inverse relationship between phytoplankton biomass and zooplankton, which was first noted by Hardy and Gunther (1936). They also found a marked difference between the composition of the phytoplankton standing crops in January, when zooplankton biomass was low, and March when krill furcilia were abundant (Table 5.8). In March the relatively large diatoms were reduced in concentration (by 98%), as were the dinoflagellates (by 91%). However, the nanoplankton (monads and flagellates) were reduced only 50% in biomass. These data and laboratory feeding studies have demonstrated that krill swarms can change the size composition of the phytoplankton in the water column, shifting it towards the smaller sizes. The effect of selectively reducing the abundance of certain species could have a profound effect on the structure of the phytoplankton community.

TABLE 5.8
Apparent Effect of Grazing by Krill (furcillia) on the Composition of the Phytoplankton Crop

	Biomass (μg C l^{-1})	
	January	March
Diatoms		
Pennate	30	2.0
Centric	221	1.2
Dinoflagellates		
Thecate	12.1	0.1
Non-thecate	5.8	1.5
Monads and flagellates (> 10 μm)	29.3	14.7

Note: Data are from 5-m depths at a station north of Elephant Island sampled January 27–28 and March 16–18, 1981. Plant carbon has been estimated by floristic analysis of preserved samples, in which all cells are counted, sized and cellular organic carbon calculated by applying data equating cell size to organic carbon.

Source: From Holm-Hansen, O., Huntley, M., *J. Crust. Biol.*, 4, Special Issue 1, 156, 1984. With permission.

Holm-Hansen and Huntley (1984) also assessed the food requirements of the krill in the above study area. The mean krill biomass in the upper 200 m of the water column was estimated at 10.6 mg dry wt m^{-3} and this was calculated to require a food ration of 0.105–0.322 mg C m^{-3} day^{-1}. The corresponding value for the krill in a superswarm off Elephant Island was 2.4–5.4 mg C m^{-3} day^{-1}. On the other hand, the phytoplankton productivity for the upper 200 m in the Scotia Sea and the superswarm area was estimated to be 4.8 and 4.2 mg C m^{-3} day^{-1} respectively. On this basis it would appear that there was ample phytoplankton to provide for the food requirements of the krill. They estimated that the krill in the superswarm were consuming between 58% and 81% of the daily production and that the mean *E. superba* populations in the Scotia Sea consumed only between 2.5% and 3.5% of the daily primary production. They point out that there are several reasons why the consumption of *E. superba* should be substantially lower than the total primary production. First, though *E. superba* may dominate the zooplankton, it makes up no more than half of the total zooplankton standing stock (Holdgate 1967; Knox 1970), and thus could be expected to consume about half of the total zooplankton composition of the phytoplankton. Second, a large proportion of the primary production occurs in the particle sizes less than 10 μm, which are filtered at relatively low efficiencies (McClatchie and Boyd 1983; Morris 1984; Quetin and Ross 1985). If it is assumed that the production of particles large enough to be effectively filtered by *E. superba* is approximately 10% of the total primary production (Von Brockel 1981) and that approximately half of this must be shared with the noneuphausiid zooplankton, then about 5% of the total primary production would be available for consumption by *E. superba*. This compares well with Holm-Hansen and Huntley's (1984) estimate of 2.5–5%.

Miller et al. (1985) used acoustic measurements of krill standing stock, together with concurrent primary productivity measurements and recently published data on krill energy requirements, to assess the importance of *E. superba* as an herbivore in a sector of the Indian Ocean surveyed during FIBEX. The mean phytoplankton production measured during the survey was 188 mg C m^{-3} day^{-1}, or 1.88 g (wet wt) phytoplankton m^{-3} day^{-1}, assuming a phytoplankton:C ratio of 10:1 (Holm-Hansen et al. 1977). Expanding this over the survey area gave a daily phytoplankton production of approximately 1.2×10^6 tons. The acoustically derived estimate of krill density was 1.46 g m^{-3} (Hampton 1985), giving a standing stock of 9.1×10^5 tons at the time of the survey. Miller estimated that the krill consumed 3.66×10^4 of phytoplankton day^{-1}, or 3.05% of the estimated daily phytoplankton production. This agrees well with the estimate arrived at by Holm-Hansen and Huntley (1984) for the Scotia Sea.

The question arises whether there is competition between krill and other consumers, especially copepods, for planktonic food resources. This has been investigated by Schnack (1985b). In constant volume feeding experiments he found no great differences between the feeding patterns of *E. superba* and five copepod species. Schnack points out that the very similar feeding behaviour implies that severe competition for food might occur. However, he notes that there is a great difference between the distributional patterns of copepods and krill with few copepods being found in regions where large swarms of krill occur. In addition, niche separation on the basis of differences in distribution during the life histories of krill and copepods could be a mechanism for reducing potential competition.

Meyer et al. (2003) investigated the feeding ecology of larval krill in the vicinity of Adélie Island. They found that the daily ration (DR) increased with food concentration and reached mean values of 28% body C in CIII, 25% body C in FI, and 15% body C in FII. Huntley and Brinton (1991) reported for larval krill from the Gerlache Strait with a mean food concentration of 2 μg chl $a\,l^{-1}$, a DR of 17.8% body C for CIII to FI, and 8.5% body C for FI to FII. However, Meyer et al. (2003) demonstrated, for FII larvae from the Lazarev Sea in autumn, an increase in DR with increasing food concentration. Meyer et al. (2003) found that the maximum DR and the minimum carbon ration (CR) was reached at food concentrations in the range of 100–200 μg C l^{-1}. This corresponds to 3 μg chl $a\,l^{-1}$, assuming a C:chl *a* ratio of 50. A similar value, 3.5 μg chl $a\,l^{-1}$ was reported by Ross et al. (2000) as a critical concentration for maximum growth of larval/postlarval krill near the end of their first year of life.

Across the size spectrum of diatoms (8–79 μm in size), Meyer et al. (2003) found that CIII cleared small cells most efficiently, as did FI to a lesser degree. FII, however, showed no clear tendency for a specific cell size. Across the measured size spectrum of motile taxa, all larval stages showed a clear preference towards the larger cells. Estimates C assimilation efficiencies were high, from 70% to 92% (mean 84%). It was concluded that krill larvae would not grow well in the less-than-1-mg m^{-3} chl *a* that typify large areas of the Southern Ocean. A dependence on high phytoplankton concentration for a large part of the season, whether in ice or open water, may be prerequisites for successful recruitment of krill.

5.10.8 ENERGY BUDGETS

As yet the problem of balancing the energy budget and daily carbon requirements of krill *E. superba* has not been satisfactorily resolved (Quetin et al. 1985; Daly 1990; Perissinotto et al. 2000). There have been a number of attempts to develop energy budgets for individual krill (e.g., Chekunova and Rhynkova 1974; Clarke and Morris 1983a, 1983b; Ikeda 1984b; Quetin et al. 1994). Data from these studies can be combined with information on population biomass and structure to produce a population energy budget (e.g., Everson 1977b; Nemoto and Harrison 1981) and thus estimate krill production. Energy budgets based on the consumption of autotrophic material during laboratory incubations have shown that ingestion rates are generally insufficient to meet the daily metabolic requirements of krill (Antezana et al. 1982; Holm-Hansen and Huntley 1984; Morris 1984; Priddle et al. 1990; Pond et al. 1995). More recently, in situ measurements of krill ingestion rates have demonstrated that *E. superba* is capable of much higher ingestion rates (1.5–6 times) than those obtained in the laboratory (Quetin et al. 1994; Perissinotto et al. 2000). In many areas, however, phytoplankton stocks are not adequate to support the entire carbon requirements of the local krill population and are below the level of its grazing potential. If the daily carbon ration of krill were to be met from an entirely autotrophic carbon source, high chlorophyll concentrations similar to those observed in phytoplankton blooms would be required to sustain its metabolism. As we have seen krill can consume nonalgal carbon, especially copepods to meet its metabolic requirements (Perissinotto et al. 2000).

We are still a long way from being able to produce population energy budgets and to estimate production due to the scarcity of data on important parameters and the comparative lack of data on winter energy budgets. Because of the strong seasonality in primary production, the availability of food is likely to be the major factor influencing krill's growth, reproduction, and life history (Clarke 1980a, 1983), and hence population energy budgets. Thus, at present, we do not have sufficient information to estimate accurately the annual energy consumption and expenditure.

5.10.8.1 Energy Budgets for Individual Krill

In estimating the energy budget of individuals, the traditional formulation (Ricker 1968) is

$$C = P + R + U + F,$$

where C is the total energy consumed (also termed *ingestion*); P is production (i.e., growth and gonad development), R is the energy used in respiration (energy metabolism), U is the energy lost through excretion, and F is the energy egested as faeces. However, as discussed by Clarke and Morris (1983a), this equation is inappropriate for krill since this species must expend significant amounts of energy merely maintaining its position in the water column. Clarke and Morris (1983a) partitioned respiration into three separate physiological processes—basal metabolism, metabolic cost of feeding, and metabolic cost of swimming. Thus a better formulation of the above equation is:

$$C(\text{or } I) = (P_s + P_g) + (R_b + R_a + R_s + R_g) + U + F,$$

where P_s and P_g represent somatic growth (including exuviae) and gamete synthesis, respectively, and the respiration term is subdivided into R_b (basal or maintenance costs), R_a (the costs of all activity, including locomotion and feeding) and R_s and R_g are the energy lost as heat during the synthesis of new tissue because according to current best estimates synthesis is only 70–80% efficient (Parry 1983), R_s and R_g are now believed to account for most of the so-called specific dynamic action (SDA, the increase in metabolic rate due to the ingestion of some foods) observed following feeding (Jobling 1983).

The various components of the energy budget will vary with age, season, and factors such as food availability and temperature. A complete understanding of the energetics of krill will therefore necessarily involve knowledge of the physiology of all the life stages, and how this responds to environmental variables.

Clarke and Morris (1983a) have given an estimated energy budget for an adult male and female *E. superba* during a 190-day summer growing period (Table 5.9). It can be seen that the information at that time was not available for many of the items in the energy budget. Basic metabolism (R_b) cannot be determined directly, and Clarke and Morris (1983b) made the assumption that the oxygen consumption of krill at −1.0°C approximates the true basal metabolism. It is important that this be more accurately determined. The metabolic cost of swimming (R_s) is most likely to be a function of krill size, but this is as yet unknown. As we have seen swimming activity is intimately related to feeding, and the as yet undetermined metabolic cost of feeding (R_f) must be added to that of the metabolic basic rate. Feeding behaviour is complex and the proportion spent on filter-feeding and compression-feeding and raking (grazing on sea ice microalgae) will need to be taken into account. Clarke and Morris (1983a, 1983b) assumed that total respiratory losses were 80% of the assimilated energy in males. There does not appear to be any agreement as to the metabolic cost of moulting (M). Clarke and Morris (1983a, 1983b) calculated this to be at 0.837 kJ for a male krill over the 190 days of the spring–summer period, i.e., 2.2% of the assimilated energy. M has been determined as 38% in a similar species, *E. pacifica* (Paranjape 1967). Ikeda and Dixon (1982a) assumed M to be 40% of the daily O_2 uptake on the day of moulting. There is a need to determine more accurately not only the energetic cost of the actual moulting process, but also the energy loss in the discarded exoskeleton.

TABLE 5.9
An Estimated Energy Budget for Adult Male and Female *Euphausia superba* during the Summer at South Georgia

	Total Energy Intake in 190 Days (kJ)	
	Male	**Female**
Basal metabolic rate (R_b)	7.637	8.742
Metabolic cost of activity (R_s) (including swarming and vertical migration)	Unknown	Unknown
Metabolic cost of feeding (R_f)	Unknown	Unknown
Somatic growth (P_g)	6.754	6.754
Moults (M)	0.837	0.837
Testis (P_t)	Unknown	–
Ovary (P_r)	–	6.390
Total	15.228	22.723
	37.955[a]	

[a] Assuming total respiratory losses (basal + swimming + feeding) are 80% of assimilated energy in males. If mean weight of a male krill in summer is taken to be 1.08 g (=3.94 kJ), then daily energy intake is 0.0506 $\text{J J}^{-1}\,\text{day}^{-1}$ (=5.1% body weight per day). Daily energy intake for females is higher due to large amount of energy involved in reproduction.

Source: From Clarke, A., Morris, D.J., *Polar Biol.*, 2, 69, 1983b. With permission.

Using the relationships discussed above, Clarke and Morris (1983a) calculated that the total energy intake during the spring-summer season (~190 days) is about 5% (6% or more for females) of the body weight. This is very similar to the value calculated by Chekunova and Rynkova (1974) from estimates of oxygen consumption and food intake but ignoring swimming activity. Chekunova and Rynkova also calculated the metabolic carbon loss by an individual krill during its life from calorific equivalents. Their estimate of 74% is very similar to Ikeda's (1984b) range of 71.5–85% of the total carbon assimilated from egg to adult.

From laboratory data on the ingestion rates of chlorophyll *a* (Antezana et al. 1982; Kato et al. 1979) it has been calculated that krill's daily energy requirements are equivalent to between 1.0% and 1.7% body carbon. The maximum clearance rates in the experiments of these authors were between 150 and 210 ml individual^{-1} h^{-1} for krill weighing approximately 250 mg, with maximum ingestion rates of 1.8–2.0 g chl *a* individual^{-1} h^{-1} being found at average concentrations of 8–12 μg chl *a* h^{-1}. On the other hand, experiments by Price et al. (1988) at similar average concentrations of chlorophyll *a* gave ingestion rates of 10 μg chl *a* individual^{-1} h^{-1}. If these higher ingestion rates are used in calculations of energy intake a value of 8.5% of body carbon day^{-1} is obtained, a value which compares favorably with estimated metabolic requirements.

The bulk of the work on the energy budgets of krill have been carried out on adult krill and there are only a limited number of studies of the energy budgets of larval krill (e.g., Quetin and Ross 1985; Fraser et al. 2002a; Meyer et al. 2003). In addition, the majority of energy budget estimates have been based on krill feeding on phytoplankton as the sole food resource. As previously discussed (see Section 5.10.7), there has been increasing evidence that krill can consume substantial amounts of nonalgal food (crustaceans, protozoans, and detrital material).

Perissinotto et al. (2000) investigated the contribution of heterotrophic material to the diet and energy budget of krill in the Lazarev Sea, at the Antarctic Polar Front and around South Georgia. Energy budgets based on the consumption of autotrophic material during laboratory incubations have shown that ingestion rates are generally insufficient to meet the daily metabolic requirements of the krill (Antezana et al. 1982; Holm-Hansen and Huntley 1984; Morris 1984; Priddle et al. 1990; Pond et al. 1995). If the daily ration of krill were to be met from an entirely autotrophic resource, high chlorophyll concentrations, similar to those observed during phytoplankton blooms, would be required to sustain its metabolism. Previous estimates of the energy budgets of krill during its reproductive season have not allowed for sufficient energy input, except at unrealistically high chlorophyll concentrations.

Perissinotto et al. (2000) found that at all the stations sampled the heterotrophic component of the krill diet was substantial and often much larger than the autotrophic component, ranging from 17.4% to 98.9%. Their findings have important implications for the elucidation of the energy budget of krill and its daily carbon ration. The high consumption rates of heterotrophic organisms by krill suggests that this large microphage may be more important than previously believed in re-packaging micro- and mesozooplankton to form large and fast-sinking fecal pellets to the carbon transport to the ocean floor (Fortier et al. 1994; Gonzales 1995).

Meyer et al. (2003) investigated the feeding and energy budgets of larval krill off Rothera Station, while Frazer et al. (2002) studied the energetic demands of larval krill in the winter in waters to the west of the Antarctic Peninsula. Meyer et al. (2003) found that the mean daily carbon rations were 28% body carbon for calyptopus stage III (CIII), 25% for furcilia stage (FI), and 15% for FII. For the phytoplankton size range of 8–79 m CIII cleared small cells most efficiently, as did FI to a lesser degree. FII, however showed no clear tendency for a specific cell size. Estimated C assimilation efficiencies were high, from 70% to 92% (mean 84%). Respiration rates of freshly caught larvae were 0.7–1.1 l O_2 mg DM^{-1} h^{-1}. The calculated respiratory C loss showed a significant increase with increasing food concentration in all larval stages, ranging from 0.9% to 2.4% body carbon day^{-1}. These respiratory losses, combined with the high assimilation efficiencies, showed that the larvae have ample capacity for growth at these food concentrations. Critical concentrations of food to achieve maximum daily rations were in the range of 100–200 μg C l^{-1} (2–4 μg chl *a* l^{-1}). It is thus clear that food concentration are critical for larval growth.

Fraser et al. (2002a) investigated the energetic demands of larval krill in the winter. The average O:N ratio of 3.1 for larvae and juveniles collected beneath the pack ice indicated that they were primarily herbivorous feeding on ice microalgae. This conclusion is supported by studies which document O:N ratios greater than 30 in larger krill from under the pack ice in November (Ikeda and Kirkwood 1989). A comparison of field and laboratory studies conducted at −1.5°C to −1.8°C showed that the larvae from ice-covered waters and fed larvae in the laboratory had oxygen consumption rates significantly higher than those of the larvae collected from open, ice-free water and those starved in the laboratory. These results lend support to the concept that in winter, larval, and juvenile krill are better fed in ice-covered waters than in open water, and to the hypothesis that sea ice biota in the pack ice are an important food source in the winter for larval and juvenile krill.

The difference between the net energy gain from the assimilated energy and the energy losses from respiration can be regarded as the "scope for growth" (Newell 1979). An attempt has been made to depict this for *E. superba* in Figure 5.26. In this diagram the halving of the respiration rate during winter and the two-fold increase that occurs in the spring is depicted. The approximate proportions of assimilated energy from sea ice microalgae and phytoplankton is also shown. A hypothetical growth curve is also depicted. The proportion of assimilated energy from other sources (zooplankton, choanoflagellates, protozoa, detrital organic matter) cannot be estimated from the available data at present.

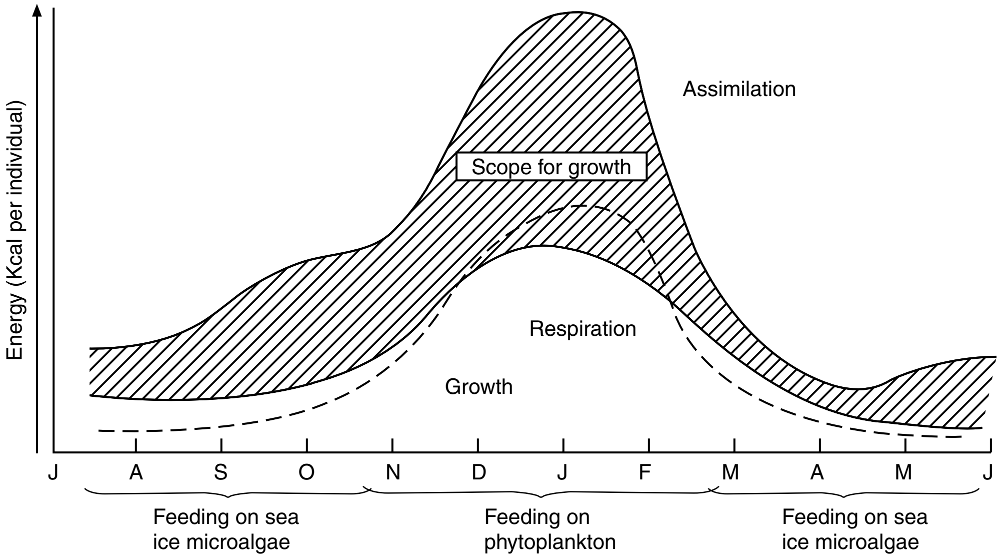


FIGURE 5.26 Scope for growth in *Euphausia superba*.

5.11 KRILL PRODUCTION

5.11.1 INTRODUCTION

For an understanding of the ecological role of krill in the Southern Ocean pelagic ecosystem, it is necessary to know the rate at which new krill biomass is being produced, i.e., the productivity rate of krill production. This is a function of the growth rate of each individual krill, which varies according to the age of the individual. It is a dynamic function that rarely, if ever, can be measured directly, but it is essential if we are to understand the rates of the transfer of energy and materials through the large stocks of krill in the Southern Ocean, and if we can be in a position to undertake sustained rational exploitation of these stocks.

The actual estimation of production requires information on the stock biomass at the beginning and end of some period of time, usually one year. This will give the production per unit time, which is balanced against losses resulting from catabolism, death from natural causes or predation (mortality), and emigration. However, mortality and emigration are difficult parameters to measure (Allen 1971). Consequently, production has to be estimated indirectly. Three indirect methods have been used: (1) estimates from animal size and number over time (Allen 1971), (2) estimates based on energy budgets (Omori and Ikeda 1984), and (3) estimates based on the amount and proportion of the population consumed by its principal predators (Miller and Hampton 1985). An alternative approach, developed below, is to use predator consumption rates.

5.11.2 PRODUCTION ESTIMATES FROM ANIMAL SIZE AND NUMBER

Growth rates and age of krill have been discussed in Section 5.3.7. Such data forms the basis for estimation of production over a given time span, taking into account mortality rates. However, growth and mortality vary throughout the animal's life span. Taking this into account, Allen (1971) has shown that the ratio of production to biomass (i.e., the standing stock *P*:*B* ratio) is equal to the ratio of the total production by any particular cohort to its total biomass over time. Assuming linear growth in length over four time periods with different rates in each, Allen estimated a *P*:*B* ratio for krill of between 1.8 and 2.3. Other investigator have obtained ratios much closer to unity (e.g., Gulland 1970; Hempel 1970; Horwood 1981), indicating that krill's annual production is equal to its biomass. Yamanaka (1983) using data from Kawakami and Doi (1979) calculated *P*:*B* rations of 1.19 and 2.77 for krill surveyed in a sector of the Indian Ocean during FIBEX, while Siegel (1986b) found values of between 0.8 and 1.1 (mean 0.95, excluding 0-year olds) for animals from the Bransfield Strait.

A number of studies (e.g., Waters 1969; Robertson 1979) have shown that there is a general relationship between *P:B* ratios and the life span, the shorter the life span the higher the ratio. Animals with a life span of 4–6 years would be expected to have a *P*:*B* ratio of between 1.0 and 2.0. To obtain a reasonable estimate of the *P*:*B* ratio in krill, one must have good data on growth and mortality. As Miller and Hampton (1985) point out, there are three serious shortcomings that hinder the estimation of krill production from individual mass data. These include (1) a lack of reliable mortality estimates; (2) inadequate knowledge of growth rates and functions; and (3) incomplete data on age, length-at-age, and longevity. Estimates of mortality vary widely, e.g., 5.50 (Kawakami and Doi 1979), 2.31, and 0.60 for 1–2 and 2–3 year old krill, respectively (Brinton and Townsend 1984), and 1.0 (Siegel 1986a). This would seem to imply significant variations in the composition of the population from different areas.

It is clear that we are still far from being able to estimate krill production with any degree of confidence from individual mass data alone. More accurate information is required on natural mortality at all ages, and on life span, growth, age structure, and rematuration cycles. In addition, we as yet know little of the effects of the austral winter on these parameters.

5.11.3 Prodution Estimtes from Energy Budgets

Energy budgets for individual krill have been discussed in Section 5.10.8. Various attempts have been made to use calculations of the metabolic requirements of individuals to develop energy budgets for populations with varying success (e.g., Holm-Hansen and Huntley 1984; Miller et al. 1985). Given the available information on krill population dynamics, size and age structure, and generation time, and the comparative lack of information on krill energetics during the winter, the development of population estimates from energy budgets is not possible at this time.

5.11.4 Production Estimtes from Predator Consumption

Historically, krill production was largely estimated from assumed relationships between krill and primary production (e.g., Gulland 1970; Hempel 1970; Everson 1977b; Knox 1983). These calculations assessed the annual krill production at between 75 and 700 million tons (Gulland 1970; Makarov 1972; Lubimova 1983). The calculation of these estimates assumed different levels of phytoplankton production, various efficiencies for the conversion of phytoplankton to krill (e.g., 10% by Gulland 1970, and 2.5% by Chekunova and Rynkova 1974), and various values for the ratio of krill to other herbivorous zooplankton (usually 50%, Vinogradov and Naumov 1958; Holdgate 1970; Knox 1970, 1983). Knox (1983) using a range of estimates for annual primary production and conversion efficiencies arrived at krill production estimates from 450 to 1,900 tons per annum. In view of the uncertainties of these estimates they are of little real value for estimating krill production. As a consequence, attention has been focussed on attempts to estimate production from data on predator consumption.

5.11.4.1 Consumption by Whales

Southern Ocean whale stocks, once abundant and diverse, supported the world's largest whale fishery, eventually leading to their marked decline. There is a great deal known about the great whales because of their commercial importance; several reviews have been published (e.g., Mackintosh 1942, 1965; Gaskin 1976, 1982; Gulland 1976; Laws 1977a, 1977b; Nishiwaki 1977; Allen 1980; Brown and Lockyer 1984). The more recent data have been reviewed by Laws (1977a), Bengtson (1985b), Miller and Hampton (1985), Armstrong and Siegfried (1991), and Ichi and Kato (1991) (see Table 5.10). Laws's (1977b) figures indicate that before exploitation, the Antarctic whales removed about 190 million tons of krill annually which gives an ecological efficiency (i.e., the ratio of energy absorbed by the predator to the food energy absorbed by the prey) of about 1%. This is a much lower efficiency than the 10% usually typical of conversions in natural fish populations (Everson 1984c), but is probably due to the slow growth of whales older than four years (Everson 1984c).

Armstrong and Siegfried (1991) and Ichi and Kato (1991) have recently estimated the consumption of krill by Minke Whales in the Southern Ocean. Ichi and Kato (1991) found that *E. superba* was the dominant food species, comprising 100% and 94% by weight in stomachs in the ice edge and offshore zones respectively. The total food consumption per day was estimated to be 1,170 and 596 tons in the ice edge and offshore zones respectively. Armstrong and Siegfried (1991), based on estimates obtained from stomach capacity, ingestion rates and respiratory allometry methods, estimated that an "average sized" female minke whale consumed 56.2 tons of krill during a 120-day stay in Antarctic waters. Their data suggested that the Minke Whale population (760, 396, 132, 230, SHMIREP 1980) in the Southern Ocean (60° and higher) consumes 35.5×10^6 tons of krill annually. Previous estimates for Minke Whale krill consumption gave values between 8×10^6 and 20×10^6 for population estimates smaller than the SHMIREP estimates (Miller and Hampton 1985).

Present consumption of the reduced whale stocks is in the order of 34–42 million tons (Bengtson 1984; Laws 1985; Armstrong and Siegfried 1991), and the difference

TABLE 5.10
Estimated Annual Consumption by Different Species of Whale

	Whale Stock Size ($\times 10^3$)		Krill Consumption ($\times10^6$ t y^{-1})	
Whale Species	Bengtson[a]	Laws[b]	Bengtson[a]	Laws[b]
Blue	4.5	10	1.3	3.38
Pygmy	7.4	–	1.93	–
Fin	126	84	21.21	16.43
Sei	16	40.5	1.01	2.88
Humpback	3.5	3	0.41	0.32
Minke	258.5	200	8.42	19.82
Total	415.7	337.5	34.28	42.83

Based on data in Bengtson (1984) and compared with figures from Laws (1977b, 1985).

[a] Laws (1977b) assumed that minke whales feed all year round.

[b] Bengtson (1984) assumed feeding for only 120 days a year and considered only mature animals.

Source: From Miller, D.G., Hampton, I., *Biomass Sci. Ser.*, 9, 1, 1985. With permission.

(approximately 150 million tons) between this and the pre-exploitation estimate has often been referred to as the "krill surplus" (Lubimova et al. 1984) (Table 5.11). The fate of this "surplus" that is no longer consumed by the whales has been the subject of much conjecture, especially the proportion utilized by other predator groups (see Chapter 9), and thus resulting in increases in their populations (Beddington and de la Mare 1984; Bengtson and Laws 1984).

5.11.4.2 Consumption by Seals

Seal consumption is discussed in Chapter 8. The principal krill consumers are Crabeater Seala (*Lobodon carcinophagus*) and Leopard Seals (*Hydrurga leptonyx*), with smaller amounts being consumed by Fur Seals (*Arctocephalus gazella*) and Ross Seals (*Ommatophoca rossii*) (see Table 5.12). The gross conversion efficiency of krill to Crabeater Seal has been estimated at 1%, the same as Everson (1984c).

5.11.4.3 Consumption by Squid

While it is known that several species of Antarctic squid feed on krill (Marr 1962; Dell 1965; Nemoto et al. 1985), there has been little available information either on the standing stocks of squid krill consumers, or on their krill consumption rates (Okutani and Clarke 1985) (see Chapter 6). Everson (1984a) estimated that the annual consumption of krill by squid could be as high as 30–40 million tons. While there is a great deal of uncertainty concerning the actual consumption, it is potentially important and cannot be ignored.

TABLE 5.11
Estimated Annual Consumption of Krill by Whales Before and after Exploitation

	Whale Stock Size $(\times 10^3)$		Krill Consumption $(\times 10^6\ t\ y^{-1})$	
Whale Species	**Bengtson[a]**	**Laws[b]**	**Bengtson[a]**	**Laws[b]**
Blue	4.5	10	1.3	3.38
Pygmy	7.4	—	1.93	—
Fin	126	84	21.21	16.43
Sei	16	40.5	1.01	2.88
Humpback	3.5	3	0.41	0.32
Minke	258.5	200	8.42	19.82
Total	415.7	337.5	34.28	42.83

Based on data in Bengtson (1985a) and compared with figures from Laws (1977b, 1985).

[a] Laws (1977b) assumed that minke whales feed all year round.

[b] Bengtson (1985a) assumed feeding for only 120 days a year and considered only mature animals.

Source: From Miller, D.G., Hampton, I., *Biomass Sci. Ser.*, 9, 1, 1985. With permission.

TABLE 5.12
Estimated Annual Consumption of Krill by Seals

	Seal Stock Size $(\times 10^6)$		Krill Consumption $(\times 10^6\ t\ y^{-1})$	
Seal Species	**Bengtson**	**Laws**	**Bengtson**	**Laws**
Crabeater	30	14.8	127.62	63.2
Leopard	0.4	0.22	1.15	0.52
Ross	0.22	0.73	0.04	—
Antarctic Fur	1.10	0.20	0.04	0.12
Total	32.45	16.17	129.33	63.92

Based on data in Bengtson (1985a) and Laws (1977b, 1985).

Source: From Miller, D.G.M., Hampton, I., *Biomass Ser.*, 9, 1, 1985.

5.11.4.4 Consumption by Fish

The importance of krill in the diet of fish is discussed in Chapter 7, and the available data indicate that while fish are substantial krill consumers it is not possible at present to determine the exact amount that they consume. Everson (1977b, 1984b) estimated that the fish stocks of the Southern Ocean could potentially consume approximately 300 million tons of food and concluded that the total amount of krill consumed was in the order of several tens of million tons.

Nototheniid and channichtyid consumption of krill in the Scotia Arc regions has been estimated at between 5.4 and 6.6 million tons annually (Lubimova and Shust 1980). Kock (1985) calculated that, in the same region, the total annual consumption of krill by demersal fish prior to the heavy recent commercial exploitation of the fish stocks is in the order of 10 million tons. In addition to the krill consuming demersal species, pelagic species (notably *Pleurogramma antrcticum* and a number of Myctophid species) also consume significant quantities of krill (Rowedder 1979a, 1979b; Lubimova et al. 1984; Hopkins 1985b; Williams 1985a, 1985b), and this added to the consumption by demersal fishes would support the view that a figure of between 10 and 20 million tons for the annual consumption of krill by fish is a reasonable estimate.

5.11.4.5 Consumption by Birds

Birds, especially penguins, and in particular the Adélie Penguin (*Pygoscelis adeliae*), are major euphausiid consumers (see Chapter 10). From a detailed study of food consumption of some 22 bird species in the Scotia Sea Croxall et al. (1984) estimated that they consumed 11 million tons of krill per year. Croxall (1984) estimated that the total sum of direct and indirect (via fish and squid) predation of krill by seabirds at 115 million tons per year. Everson's (1977b) estimate of direct consumption was 25 million tons per year, and a figure of 50 million tons for the annual direct consumption of krill by seabirds seems not unreasonable.

5.11.5 PRODUCTION: BIOMASS RATIOS

Due to the difficulties in the determination of absolute krill abundance and biomass, the estimation of total production (*P*) is subject to similar problems. Several attempts have been made to estimate production to biomass (*P*/*B*) ratios for krill. These were summarized by Miller and Hampton (1985). For E. Superba the ratios range from 0.8 to 2.77. In contrast to some temperate euphausiid species, *E. superba* has a multiyear life cycle, a long larval and juvenile phase, and a relatively low production rate. These temperate species have much higher *P*:*B* ratios, e.g., *Euphausia pacifica* (8.7), *E. krolina* (6.0), and *Nyctiphanes australis* (13.3–14.5).

6 Nekton

CONTENTS

6.1 INTRODUCTION

There is no sharp dividing line between the pelagic animals that are regarded as plankton and those that constitute the nekton. The distinguishing feature is that zooplankton drift with the current systems whereas nekton are active swimmers, and are thus not at the mercy of the currents. Some species that are regarded as part of the zooplankton, such as some crustaceans, chaetognaths, and others, may have considerable swimming speeds, equal to some that are usually treated as part of the nekton. In the previous chapter we have seen that krill have the ability to swim for considerable distances. Many members of the nekton (e.g., larval fish) also exist as plankton during the early stages of their life cycle. There is considerable size overlap between the zooplankton and the nekton. Some species that are regarded as megazooplankton, (e.g., siphonophores, scyphozoans [jellyfish] and colonial salps) can be very large, greatly exceeding in size many nektonic species. Such species, however, generally drift with the currents and do not actively swim.

6.2 SPECIES COMPOSITION AND DISTRIBUTION

In contrast to the zooplankton, larger animals that can control the direction and speed of their own movements rather than drift with water currents constitute the *nekton*. Two groups of marine species—the cephalopod molluscs and the fish—have evolved numerous large, actively swimming species that constitute the bulk of the nekton as generally understood. The fish will be considered in the next chapter, while in this chapter an account will be given of the cephalopods.

Generally, apart from taxonomic accounts, there is a paucity of information available on the Southern Ocean invertebrate nekton fauna, especially those that inhabit the mesopelagic zone of 100–1,000 m (Lancraft, Torres, and Hopkins 1989; Lancraft et al. 1991). In most areas of the ocean a substantial fraction of the mesopelagic fauna migrates from daytime depths (200–500 m) to, or near, the surface at dusk and returns to depth at dawn. At night these vertical migrants can make up greater than 70% of the nektonic biomass in the top 100 m (Foxton and Roe 1974; Hopkins and Lancraft 1984). In the Antarctic the diel light-dark regimes differ markedly between winter and summer. This could have a profound influence on vertical migration patterns. In addition, the shading of the ocean by pack ice could further complicate the vertical migration pattern.

In their study of Antarctic mesopelagic micronekton in the austral spring of 1983, Ainley, O'Connor, and Borkelheide (1984) found that representatives of the classical mid-water crustacean fauna (e.g., Pasiphaeidae, Opolophoridae, Mysidacea, Penaeidae, and Ostracoda) which are common in boreal, temperate, and tropical systems, were not captured with any regularity until north of 58°S. The myctophid fish *Electrona antarctica* and *Gymnocephalus braueri* were the main nektonic prey species of seabirds in open water. However, deep into the pack ice, crustaceans of the genera *Pasiphaea* and *Eurythenes* replaced myctophids in the seabird (principally Snow and Antarctic Petrels) diet. The presence of these species at the surface indicated that the under-ice environment was strongly reminiscent of that of the mesopelagic zone, influencing such species to remain at the surface.

Abundance and biomass data on macrozooplankton and micronekton species in the Southern Ocean, apart from krill and other euphausiids, are fragmentary. While *Euphausia superba* may dominate in the upper 200 m, other species, particularly *Salpa thompsoni*, squid, and mesopelagic fish, can be very important, especially when depths as low as 1,000 m are considered. *S. thompsoni* (Piakowski 1985a, 1985b) can exceed *E. superba* in numerical abundance, and stocks of mesopelagic fish (Rowedder 1979a, 1979b; Asencio and Moreno 1984; Hopkins 1985a, 1985b; Williams 1985a, 1985b) are also considerable. Lancraft, Torres, and Hopkins (1989) have sampled the micronekton and macrozooplankton assemblages in the vicinity of the marginal ice edge zone in the southern Scotia and western Weddell Sea. Forty-nine species, including 17 fish and 19 crustaceans, were collected. Decapod shrimps, which are typically abundant in other oceanic systems, were uncommon, being represented by only three rare species. Most species exhibited broad vertical ranges with no distinct pattern of vertical migration. However, many mesopelagic fish and *S. thompsoni* undertook diel vertical migration.

Biomass was high (2.4–3.2 g dry wgt m^{-2}), four to five times more than that found by Hopkins and Lancraft (1984) in the Gulf of Mexico (0.573 g dry wgt m^{-2}), but was similar to that found by Pearcy (1976) in the sub-Arctic water off Oregon. In terms of biomass, euphausiids were the most important group at shallow depths (0–200 m) but were surpassed by salps in the Scotia Sea and by mesopelagic fish in the Weddell Sea. Mesopelagic fish biomass for the entire Southern Ocean was computed at $133\text{–}191 \times 10^6$ tons, a value close to that estimated by Russian surveys, $140\text{–}190 \times 10^6$ tons (Kock 1992). It is also ten times that calculated for all Antarctic bottom fish (Kock 1987). The estimate of mesopelagic fish biomass (3.3–4.4 g wet wgt m^{-2}) greatly exceeds that for Antarctic birds (0.025–0.070 g wet wgt m^{-2}), seals (0.068–0.089 g wet wgt m^{-2}) and whales (0.167–0.339 g wet wgt m^{-2}) as estimated by Laws (1977b) and Ainley et al. (1985). Thus, on the basis of biomass alone, mesopelagic fish are probably the most prevalent predators on krill in the Southern Ocean.

Piakowski et al. (1994) investigated the nekton community in the Scotia Sea and near South Georgia in summer. Crustaceans were the most important group in terms of species numbers (28 species) followed by mesopelagic fish (24), molluscs (15), and coelenterates (11). Species diversity increased with depth and was higher at South Georgia (76 species) than in the Scotia Sea (62 species). Biomass in the upper 1,000 m was considerably higher in the Scotia Sea (94.6 g wet wgt m^{-2} during daytime, 87 g wet wgt m^{-2} during night) than at South Georgia (10.2 and 13.7 g, respectively), mostly due to dense concentrations of *S. thompsoni* (41.6 g wet wgt m^{-2} during night). The other main contributors to the high biomass in the Scotia Sea were coelenterates (28.3 g wet wgt m^{-2} during night) and mesopelagic fish (4.9 g wet wgt m^{-2} during night). Euphausiids (*Euphausia tricantha* and *E. superba*) accounted for 1.5 g wet wgt m^{-2} at South Georgia during night, with *E. tricantha* the more important of the two (1.4 g wet wgt m^{-2}). Except for *Bathylagus antarcticus* all common mesopelagic fish showed a marked diurnal migration (e.g., *E. antarctica*, *G. braueri*, *Kreffichthys anderssoni*, *Protomyctophum bolini*). During the daylight they stayed in the core of the Circumpolar Deep Water (CWD, 400–500 m) and at night they were mainly distributed in the Antarctic Surface Water (ASW, 0–400 m). Other species with pronounced vertical migration were the hydromedusa *Calycopis borchgrevinki*, the squid *Brachioteuthis picta* and the euphausiid *E. tricantha*. The scyphomedusae *Atolla wyvillei* and *Periphylla periphylla* and the crustaceans *Cyphocaris richardi*, *Gigantocypris mulleri*, and *Pasiphaea scotiae* did not appear to migrate and remained concentrated in the CDW. Four main nektonic communities were identified: (1) a lower mesopelagic nekton community from the deeper layers of the CWD; (2) an upper mesopelagic nekton community from the core of the CWD; (3) an epipelagic nekton community from the ASW over the South Georgia slope; and (4) an epipelagic nekton community from the ASW of the Scotia Sea.

6.3 CEPHALOPODS

6.3.1 INTRODUCTION

The principal group of cephalopods found in the waters of the Southern Ocean are the squids, with their shell reduced to thin, non-buoyant, chitinous stiffening pens. Their ecological role in the Antarctic marine pelagic ecosystem is not yet fully elucidated due to the lack of data on their abundance and relationships. Potentially they represent one of the most important components of the ecosystem. They are major predators on krill and are themselves important prey of a range of vertebrate predators, including fish, birds, seals, and toothed whales. Squid are fast-swimming predators with well-developed nervous systems and are thus able to avoid being caught in ordinary nets. According to Clarke (1977), no net currently available effectively samples any of the species of squid forming the main food of sperm whales. Figure 6.1 makes a comparison between squid caught in research net hauls, commercial trawl nets, and those eaten by predators (Clarke 1977, 1983). Whereas squid in the family Histioteuthidae are dominant in the whale samples, enoploteuthids are dominant in trawl hauls and various other families are important in 9 m^2 net hauls.

The sizes of squid caught in research nets are also very different from those eaten by sperm whales and there is little overlap in the size distributions (Clarke 1985). Nemoto, Okiyama, and Takahashi (1985) have compared the size distribution of the squid *Kondakovia longimana* collected by trawling operations with those found in the stomach contents of sperm whales (Clarke 1980b). The size range (dorsal mantle length) of the former sample was 200–300 mm, whereas that of the latter sample was 340–820 mm.

6.3.2 SPECIES COMPOSITION AND DISTRIBUTION

Approximately 72 cephalopod species are known or thought to occur south of the Polar Front. Of these, 55% are

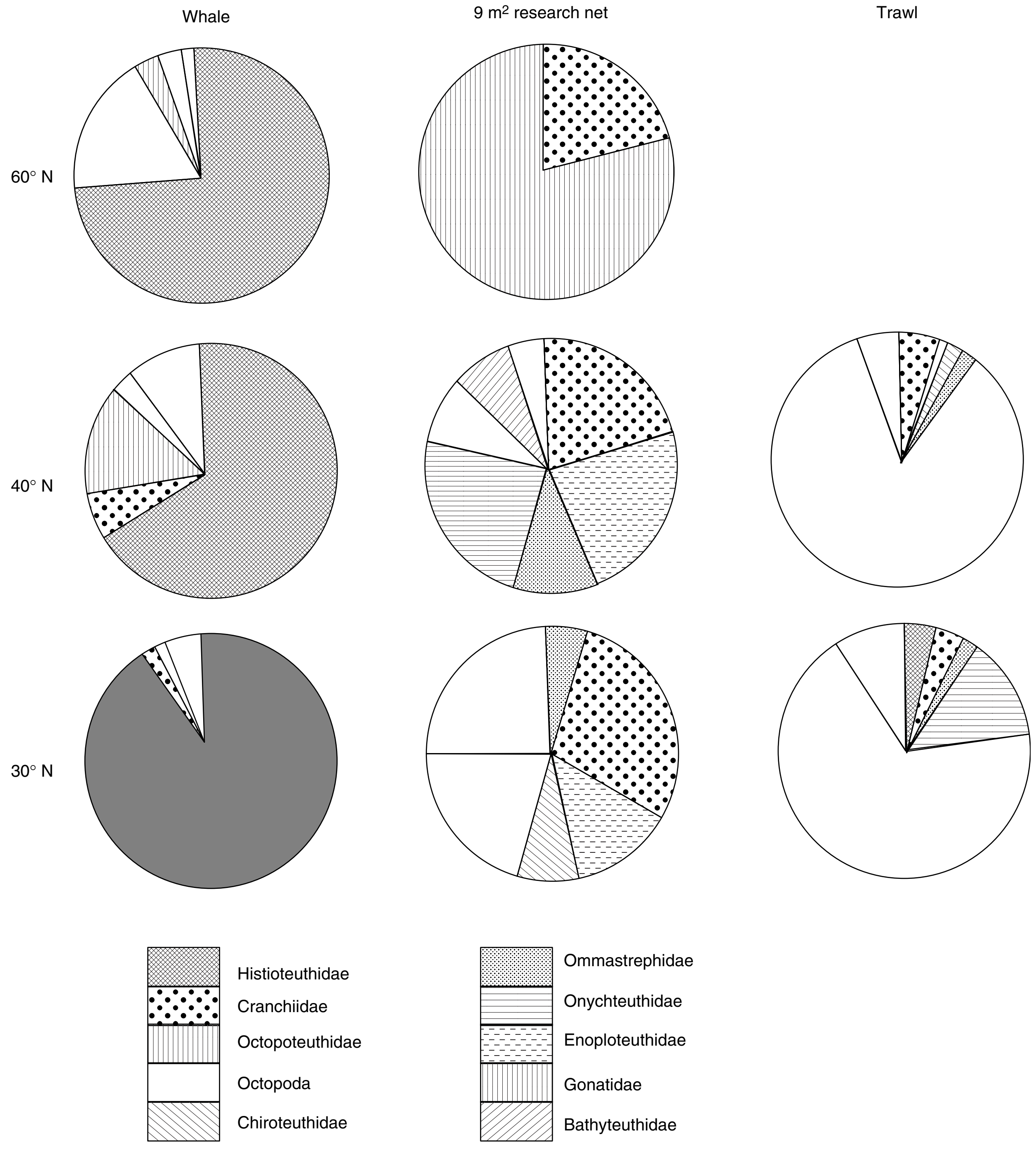


FIGURE 6.1 The families of oceanic cephalopods (mainly squid) caught by sperm whales, research nets (9 m^2 mouth) and commercial trawls in three areas of the North Atlantic. The whales eat mainly histoteuthids, cranchiids, and octopoteuthids, while nets catch mainly squids from other families. (From Clarke, M.R., *Mem. Natl. Mus. of Victoria*, 44, 95, 1983. With permission.)

considered endemic (Filipova 1972). New species are being described over the years (Roper 1969, 1981; SCAR/SCOR 1983b).

The most prominent species is the ommastrephid *Martialia hyadesi* (Rodhouse and Yeatman 1990; Rodhouse 1991). This species forms the principal prey item for a number of vertebrate predators (Rodhouse et al. 1990, 1993; Rodhouse and Prince 1993) that are together estimated to consume 340,000 tons of *M. hyadesi* per year in the Scotia Sea (Rodhouse, Croxall, and Prince 1993). In turn, *M. hyadesi* feeds on other members of the nekton community, for example, myctophids and euphausiids (Rodhouse et al. 1993). Other squid that occur include *Galiteuthis glacialis*, *Gonatus antarcticus*, *Histioteuthis* *eltaninae*, and *Monoteuthis ingens*, a prominent subantarctic species.

6.3.3 REPRODUCTION AND GROWTH

Little is known about reproductive activity growth rates and longevity of Antarctic cephalopods. It seems that many species lay egg masses on continental slopes deeper than 1,000 m (Clarke 1985), as speculated for *G. glacialis* by McSweeny (1978). Large numbers of eggs are produced, followed by rapid growth, spawning, deterioration, and death. Voss (1973) considered that many squid are short-lived, maturing at one year and dying after a single spawning. Some may, however, live for several years (Kristensen 1980).

6.3.4 FOOD AND FEEDING

Although it is known that several species of krill feed on krill (Marr 1962; Dell 1965; Nemoto, Okiyama, and Takahashi 1985), the feeding behaviour is poorly known. Filipova (1972) has noted that some species such as *K. longimana* have not been found outside areas where krill are present and suggested that it and many similar species are specialist predators on krill. Everson (1981) estimated that the annual consumption of krill by cephalopods may be as high as 100 million tons per year.

Nemoto, Okiyama, and Takahashi (1985) have examined the food contents of the stomachs of squid caught by mid-water trawling in depths between 10 and 300 m off the South Shetland Islands. The squid species collected were all considered to be young juveniles distributed at shallower depths than adults. Two species—*K. longimana* and *Moroteuthis knipovitchi*—were dominant. Other species included in the collections were *Pholidoteuthis boschmai*, *B. picta*, and *G. glacialis*. These squid were found to consume various kinds of food, predominantly macrozooplankton and micronekton. The amphipod *Parathemisto gaudichaudii* was a major component of the food of *K. longimana*, which also preyed on small euphausiids (*Thysanoessa macrura*), the large chaetognath *Sagitta gazellae*, fish, and other squid. Fish, together with krill, were the predominant food of *M. knipovitchi*. Nemoto, Okiyama, and Takahashi (1985) concluded that *K. longimana* was predominantly a fish feeder which took myctophids and other fish in the mesopelagic layer. In contrast to the findings of this study, Clarke (1980a, 1980b) found the remains of teleost fish, crustaceans, squid, and sponges in the stomachs and caecae of specimens of *K. longimana* taken by sperm whales. Teleosts were the most common. The larger adult specimens examined by Clarke would have been feeding in deeper water.

Cherel and Duhamel (2003) investigated the diet of the squid *M. ingens* in the upper slope waters of the Kerguelen Islands. They found that *M. ingens* was mainly piscivorous (67% by number and 87% by reconstituted mass), although the diet also included squids (12% and 12%, respectively) and crustaceans (21% and 1%, respectively). The main fish consumed were the paralepidid *Arctozenus risso* (28% by reconstituted mass), the gempytid *Paradiplospinus gracilis* (24%) and various myctophids. *M. ingens* also preyed on conspecifics (cannibalism, 6%), and the euphausiid *Euphausis tricantha* was the main crustacean item. Most of the prey were pelagic organisms performing diurnal migration, suggesting the benthopelagic *M. ingens* catch them when they are near the bottom during the day. *M. ingens* is prey for several species of top predators, including *D. eleginoides* and air-breathing vertebrates. These findings were similar to those of Phillips et al. (2001) who found that around Macquarie and Heard Islands myctophids were the major prey item occurring in 96% of the stomachs.

The work of Karpov and Cailliet (1978), studying *Logilo opalescens* in California, can provide information on some of the factors which could influence the feeding behavior of squid in the Southern Ocean. They found that in California prey composition: (1) is dependent on squid size—large squid feed mainly on euphausiids, cephalopods, and small fish, while small squid feed mainly on crustacea such as megalops larvae, mysids, and cumaceans; (2) is dependent on the depth of feeding; (3) is largely independent of predator sex; and (4) differs between spawning grounds and shallow water areas.

6.3.5 ECOLOGICAL RELATIONSHIPS

The impact of cephalopods as predators in the Southern Ocean ecosystem is considerable but has not been fully quantified. It depends not only on their feeding habits but their depth distribution and abundance. Many of the commercial fisheries of squid are carried out on continental shelves for species which either live near the land, such as the cuttlefish and liligos, or move inshore seasonally, such as the ommastrephids, especially on spawning migrations. In the Southern Ocean cuttlefish, liliogos, and with one exception, the ommastrephids, are absent or unimportant (Clarke 1985).

Squid constitute a significant proportion of the diets of many Antarctic vertebrate predators such as the sperm whale, Commerson's dolphin, killer whales, Weddell seals, Ross seals, elephant seals, penguins, albatrosses, and larger cephalopods (Clarke 1983). Some of these predators at times feed entirely on krill, while others include krill as a substantial component of their diet (SCAR/SCOR 1983a, 1983b).

If the stomachs of sperm whales caught by commercial fisheries in the Southern Ocean are examined, large numbers of squid beaks are found, and as many as 18,000 have been collected from a single stomach (Clarke 1985). These sperm whales catch many species of squid that have rarely been caught in nets. The predominant species in the sperm whale diets (75%) is the cranchid squid *Mesonychoteuthis hamiltoni* which grows to a length of 10 m. This species has been caught in nets only once (Clarke 1983). Second in importance are the oncyhoteuthids *K. longimana* and *M. knipovitchi*. These species are illustrated in Figure 6.2.

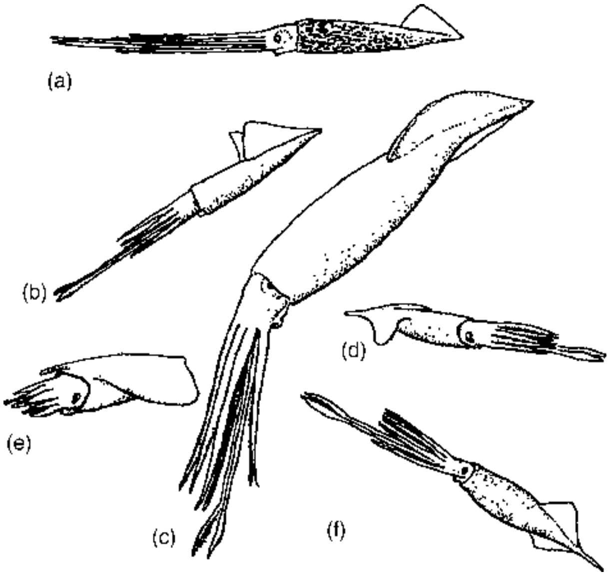


FIGURE 6.2 The three squids of greatest importance in the diets of Southern Ocean squid predators, (a) *K. longimana* (ML > 80 cm); (b) *M. knipovitchi* (ML > 40 cm); (c) *M. hamiltoni* (ML > 200 cm); and three squids which extend into the Southern Ocean from the north; (d) *Todarodes* sp. (ML < 75 cm); (e) *Taningia danae* (ML > 140 cm); (f) *M. robsoni* (ML < 9 cm). (From Clarke, M.R., *Mem. Natl. Mus. Victoria*, 44, 95, 1983. With permission.)

Goodall and Galeazzi (1985) have reviewed the food habits of small cetaceans in the Antarctic. From the scant information that is available the beaked whales (Ziphidae), especially the Southern Bottlenosed Whale (*Hyperioodon planifrons*), all include squid in their diets. Squid appear to form a minor component of the diet of killer whales (*Orcinus orca*) (Shevchenco 1975). Other delphids known to feed on squid include the pilot whale (*Globicephalus obscurus*), the dusky dolphin (*Lagenorhynchus obscurus*), bottlenosed dolphin (*Tursiops truncatus*), and Commerson's dolphin (*Cephalorhynchus commersonii*). The quantitative importance of squid in the diet of these species is unknown.

Cephalopods are also an important prey item for elephant seals, which feed on fish and squid almost exclusively (King 1964; Laws 1960a, 1977b; Clarke and MacLeod 1982a). Clarke and MacLeod (1982a) have reported on the stomach contents of elephant seals at Signy Island. Eight species of cephalopods from four to five families were identified. By number a gonatid *G. antarcticus*, an unidentified teuthoid, an onchoteuthid *M. knipovitchi*, and an octopod comprises 42%, 20%, 14%, and 10% respectively of the total prey taken. By weight the octopod *G. antarcticus* and the squid *K. knipovitchi* comprised 60% and 15% of the cephalopods present.

Ross seals also feed on squid (King 1969; Oritzland 1977). Siniff and Stone (1985) found that in the Antarctic Peninsula area cephalopods were taken in small quantities (10–20%) throughout the year by leopard seals, but that in January squid comprised over 40% of the diet as determined by frequency of occurrence percentage of food items in the stomachs.

Doidge and Croxall (1985) found that at South Georgia in the summer squid comprised 3% by weight of the food taken by female, juvenile, and weaner fur seals and 10% of that taken by males. For juvenile and adult males in the winter they estimated that squid comprised 30% by weight of food consumption. Four taxa of squid were identified from the beaks present in the stomachs: *K. longimana*, *M. knipovitchi*, *G. glacialis*, and an unidentified ommastrephid, with *K. longimana* estimated to form nearly half of the squid diet by weight and the ommastrephid one-third. Further north on Gough Island, the related fur seal *Arctocephalus tropicalis* was found to consume mainly pelagic squid (Bester and Laycock 1985). A surprising find was the presence of the Antarctic species *M. knipovitchi*.

Many species of Antarctic birds take cephalopods in their diet. Abrams (1985a, 1985b) recorded the following species from the African sector of the Southern Ocean as having squid as their principal food: wandering albatross, black-browed albatross, grey-headed albatross, sooty albatross, light-mantled sooty albatross, Antarctic fulmar, Pintado petrel, great-winged petrel, white-headed Petrel, Atlantic petrel, white-chinned petrel, grey petrel, and great shearwater. Prince (1980a, 1980b, 1985) has investigated the feeding ecology of the black-browed and grey-headed albatrosses at South Georgia. He found that 50% of the diet of the grey-headed albatross was squid. Of the squid taken, two species—*Todarodes sagittatus* and *Mesonychoteuthis* sp.—comprised 88% and 8% by number and 91% and 4% by weight respectively. The black-browed albatross, on the other hand, took a lesser quantity of squid (21%). Wandering albatrosses at South Georgia are known to feed on larger squid than they would normally have access to. These larger squid, such as *Taninigia* sp. and *Kondakovia* sp. are probably obtained by feeding on the vomit of sperm whales.

Clarke (1985) has summarized the then available data on consumption of squid by predators in the Southern Ocean (Table 6.1). He estimated the weight, or "biomass," of the cephalopod stocks which must be consumed to sustain the populations of their predators. Croxall, Prince, and Ricketts (1985) have estimated cephalopod consumption for the Scotia Sea. Of the estimated 3.7 million tons of squid taken by seabird and seal predation in the Scotia Sea, 76% is consumed by elephant seals largely around South Georgia. Other species that take more than 1% of all squid eaten are white-chinned petrels (10%), Antarctic fulmars and crabeater seals (2.5% each), and King Penguins (1%). Sperm Whales are considered not to be important in this sector, and are estimated to take 162,000 tons of squid, or about 4% of the consumption of seabirds and seals. About 94% of all squid consumed are taken by species breeding at South Georgia, with seals accounting for 88% and seabirds only 12%. In the rest of the Scotia Sea, crabeater seals and Weddell seals account for 48% and seabirds (mainly Antarctic Fulmars) 52%.

Figure 6.3 depicts the composition by weight of the principal species—by analysis of beak collections and estimation of squid mass from standard relationships (Clarke 1980b)—by the seven predator species that have

TABLE 6.1
The Percentage by Number of the Species of Antarctic Cephalopods in the Diet of Some Predators in the Southern Ocean

	Sperm Whales		Seals				Albatrosses		
	Antarctic	South Georgia	Elephant	Weddell	Fur	Leopard	Wandering	Grey-Headed	Black-Browed
Cranchiidae									
M. hamiltoni	16	30							
G. glacialis			2		44		4	8	25
Taonius							17		
Onychoteuthidae									
K. longimana	18	28	4	<1	14	4	40	<1	1
M. knipovitchi	51	23	14	31	14	92	2		
M. robsoni									
Gonatidae									
Gonatus	4	<1	42	1			6		1
Octopoteuthidae									
T. danae	—	14					1		
Ommastrephidae									
T. sagittatus	—	3			28			88	68
Brachioteuthidae									
B. picta				1					
Histioteuthidae									
Histioteuthis spp.	11	2				15	<1		
Mastigoteuthidae									
Mastigateuthis							3	<1	
Psychroteuthidue									
Psychroteathis glacialis			6	29					
Neoteuthidae									
Allurotenthis sp.			2	2			4		
Octopoda			10	35			2		1

Source: From Clark, M.R., *Key Environments Antarctica*, Bonner, W.N., Ed., Pergamon Press, Oxford, 193, 1985. With permission.

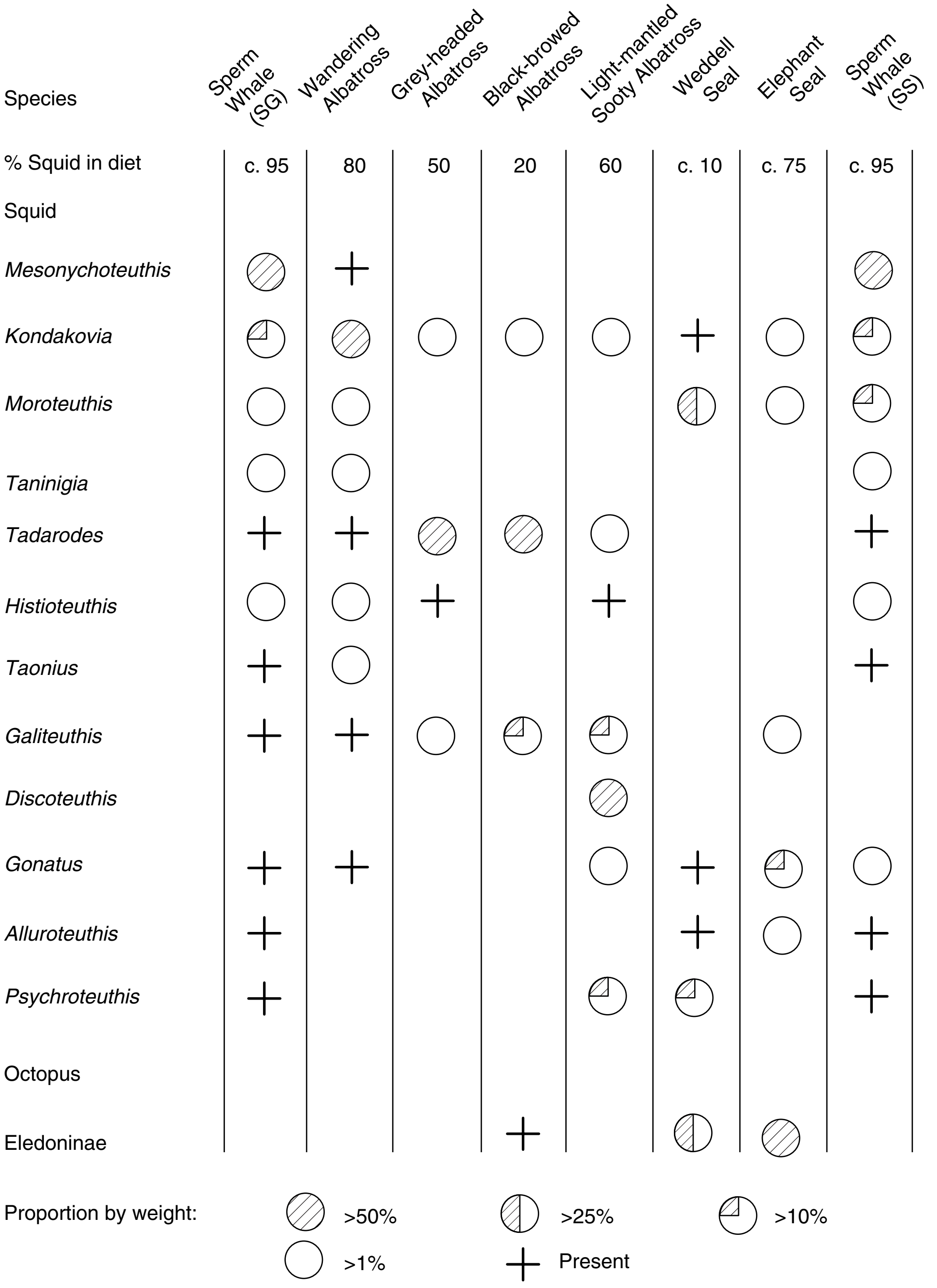
been studied quantitatively (Croxall, Prince, and Ricketts 1985). Although most species of squid are taken by several predators, the main prey of each (apart from the grey-headed and black-browed albatrosses) is usually different.

An estimate of the total consumption of cephalopods in the Southern Ocean can only be extremely rough and of necessity a minimal estimate. One such estimate is that of Clarke (1985), who suggested that the total consumption of cephalopods by whales, seals, and birds is in the order of 30 million tons per year. Clarke also estimated the stock of squid necessary to support predation in excess of 30 million tons a year, and it may well be over 100 million tons, a very large biomass.

The research outlined above has shown that squid are a major element in a food web involving crustaceans (mainly copepods)-myctophids-squid-vertebrate predators as first proposed by Rodhouse et al. (1993). This food web is largely independent of the keystone species *E. superba*. In the past this food web has been largely overlooked and it must be taken into account when assessing carbon flow in the Southern Ocean marine ecosystem.

6.3.6 COMMERCIAL EXPLOITATION

Rodhouse (1990) has reviewed the cephalopod fauna of the Scotia Sea and the South Georgia area and their potential for commercial exploitation. Although no cephalopod fishery existed in the Scotia Sea or other areas of the Southern Ocean, the potential for their commercial exploitation has long been recognized (Voss 1973; Everson 1977a), and the major cephalopod fisheries already exist in adjacent cool temperate waters around the Falkland Islands (Clarke 1987) and in the New Zealand region (Sato and Hatanaka 1983). It has been suggested that the Antarctic stocks of cephalopods have increased this century as a direct result of the decrease in the numbers of their principal consumer, the sperm whale, through overexploitation and as a direct result of the overexploitation of baleen whales. This has resulted in the



Species	Sperm Whale (SG)	Wandering Albatross	Grey-headed Albatross	Black-browed Albatross	Light-mantled Sooty Albatross	Weddell Seal	Elephant Seal	Sperm Whale (SS)
% Squid in diet	c. 95	80	50	20	60	c. 10	c. 75	c. 95
Squid								
Mesonychoteuthis	▨	+						▨
Kondakovia	◔	▨	○	○	○	+	○	◔
Moroteuthis	○	○				◐	○	◔
Taninigia	○	○						○
Tadarodes	+	+	▨	▨	○			+
Histioteuthis	○	○	+		+			○
Taonius	+	○						+
Galiteuthis	+	+	○	◔	◔		○	
Discoteuthis					▨			
Gonatus	+	+			○	+	◔	○
Alluroteuthis	+					+	○	+
Psychroteuthis	+				◔	◔		+
Octopus								
Eledoninae				+		◐	▨	

Proportion by weight: ▨ >50% ◐ >25% ◔ >10% ○ >1% + Present

FIGURE 6.3 Composition by weight of squid in the diet of albatrosses, seals, and Sperm Whales in the Scotia Sea. Only squid comprising more than 1% by weight of the diet of any species are included SS = Scotia Sea; SG = South Georgia. (From Croxall, J.P., Prince, P.A., Ricketts, C., *Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 515, 1985a. With permission.)

presumed greater availability of their common food resource *E. superba*.

Of the twelve common species of squid around South Georgia, the ommastrephid *M. hyadesi*, appears to have the most potential for exploitation. In 1986, 12,000 tons of this species from the Patagonian shelf landed in Japan, and in February 1989 two Japanese squid jigging vessels caught commercial quantities in the Sub-Antarctic Front near South Georgia (Rodhouse 1990). Other candidates for commercial exploitation are the onychoteuthids, *K. longimana*, *M. ingens*, *M. knipovitch* and *M. robsoni*, and the gonatid *G. antarcticus*. All are members of families that are the subject of directed fisheries elsewhere, or are caught as a by-catch and have commercial value.

Cephalopods fished commercially are fast-growing, short-lived, and semelparous. Most species live for approximately one year, spawn once, and die soon after. This life history differs from that of most exploited fish species and poses special problems for stock management (Amaratunga 1987). Because cephalopods are generally semelparous and have a short generation time they are prone to extreme fluctuations in population size and are particularly susceptible to over-fishing because recruitment is dependent on the breeding success of a single exploited generation. Populations are also liable to expand rapidly under favorable conditions and cephalopods may have to be increased to fill the vacant niches created by the over-fishing of fish stocks.

Since a number of predators (especially in the Scotia Sea and South Georgia areas) rely on the cephalopod stocks for a major proportion of their breeding season diet, they would be severely affected by any overexploitation of the cephalopod populations. Adverse impacts on seabird populations by fisheries for their prey species are well documented (Furness 1982; Nettleship, Sanger, and Springer 1984).

7 Fish

CONTENTS

7.1 INTRODUCTION

Investigations into Antarctic fish date back to the mid-nineteenth century when James Clark Ross's expedition to the Southern Ocean (1839–1843) collected the first fish specimens from Antarctic waters. Early studies were principally taxonomic and Antarctic ichthyology did not begin to broaden to include physiological and ecological studies until the 1950s. In most of the world's seas, fish have been the subject of special study because of their economic importance. However, the lack of an indigenous population, the harsh climate, and the opportunity to exploit stocks closer to the markets of the world delayed the exploitation of fish resources of the Southern Ocean. As fish stocks declined in other parts of the world's oceans, the possibility of the existence of substantial exploitable stocks in the Southern Ocean attracted the attention of fishing nations. Exploratory fishing commenced in the early 1960s and developed into large-scale fishing around South Georgia in the late 1960s. It has since spread to other parts of the Southern Ocean.

Studies of Antarctic fish were boosted by the SCAR/SCOR BIOMASS (Biological Investigation of Southern Ocean Systems and Stocks) that was launched in 1976 and ended in 1991. In 1979, a specialized subgroup—the Working Party on Fish Ecology—was established to carry out research on fish stocks. During the course of this program, the first attempts were made to estimate the krill consumption of Antarctic coastal fish, together with an evaluation of the role of mesopelagic fish as predators and prey. Simultaneously, or slightly later, several national

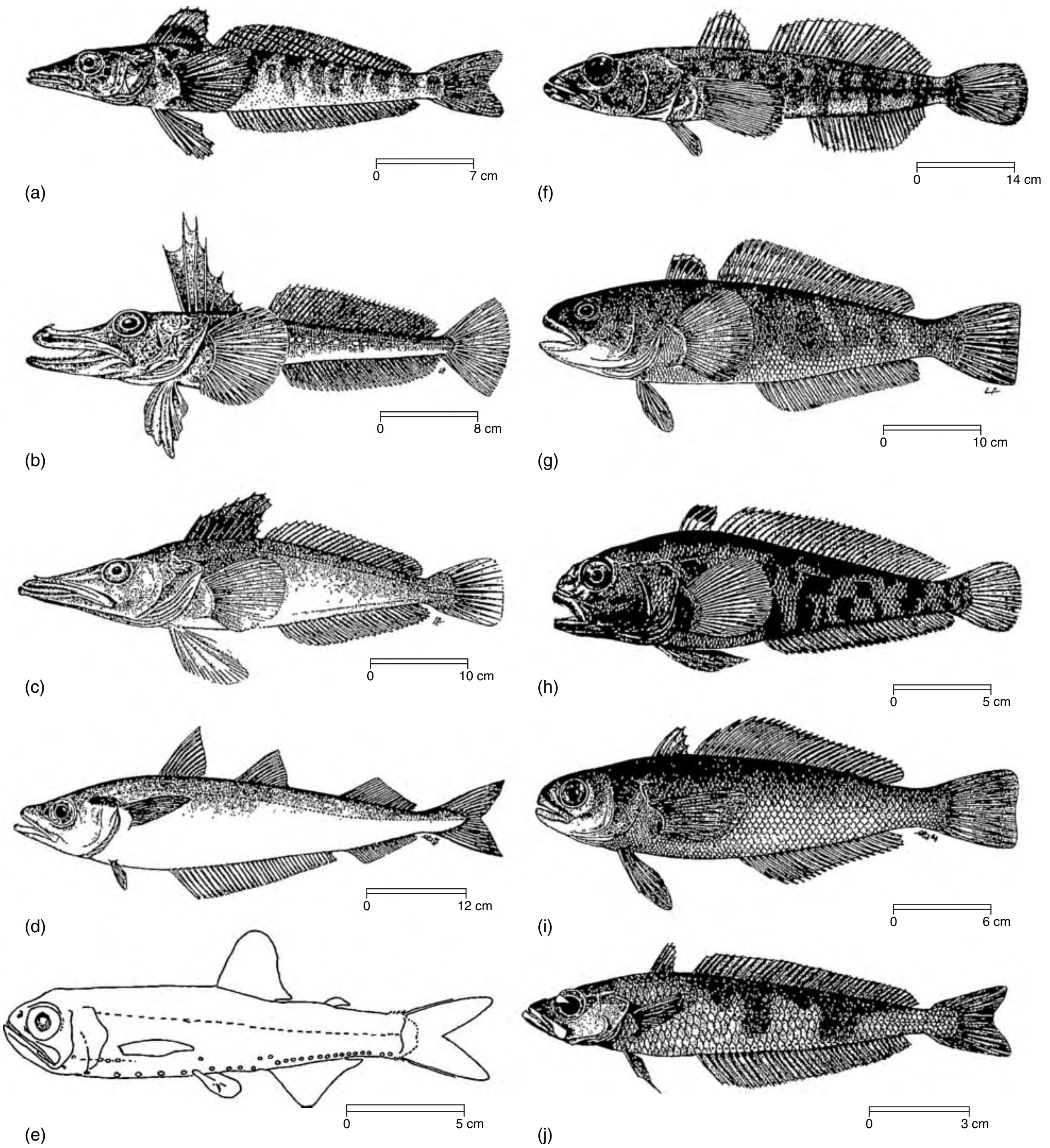


FIGURE 7.1 Illustrations of some common Antarctic fish. (a) *Champsocephalus gunnari* (Fam. Channichthyidae); (b) *Channichthys rhinoceratus* (Fam. Channichthyidae); (c) *Pseudochaenichthys georgianus* (Fam. Channichthyidae); (d) *Micromesistius australis* (Fam. Gadidae); (e) *Krefftichys* (Fam. Myctophidae); (f) *Dissostichus eleginoides* (Fam. Nototheniidae); (g) *Notothenia* (*Notothenia*) *rossii* (Fam. Nototheniidae); (h) *Pagothenia bernacchii* (Fam. Nototheniidae); (i) *Pagothenia magellanica* (Fam. Nototheniidae); (j) *Pleurogramma antarcticum* (Fam. Notothgeniidae). (From FAO, *FAO Species Identification Sheets for Fishery Purposes*, Vol. II, FAO CCAMLR, Rome, 283, 1985. With permission.)

(e.g., the Offshore Biological Programme (OBP) in the United Kingdom or the Coastal Ecological Programme (ECOKER) in France) and international programs, European Polarstern Study (EPOS), developed investigations into the relationships between fish and other components of the Southern Ocean ecosystem.

Because of their physiological adaptation to extreme cold, Antarctic fish have been of considerable interest to physiologists (DeVries 1974, 1977a, 1977b, 1978, 1980, 1983, 1988, 1997; Clarke 1983; MacDonald et al. 1987; di Prisco 1997; Somero et al. 1998). Major reviews of the literature on Antarctic fish and fisheries include those of Marshall (1964), Andriashev (1965), DeWitt (1971), Kock (1975, 1984, 1987, 1992), Permitin (1977), Everson (1978, 1984b), Bengston (1984), Gon and Heemstra (1990), Eastman (1993), Hureau (1994), Kellerman and North (1996), and Eastman and Hubold (1999) Figure 7.1.

7.2 SPECIES COMPOSITION AND DISTRIBUTION

Of the 20,000 or more modern fish species, only approximately 120 species are found south of the Polar Front. This frontal zone has had a marked effect on the evolution and composition of the shallow-water or coastal living species. In general, as discussed in Chapter 1, the depth of the water over the continental shelf is significantly greater than other oceans (Adie 1964) and there is no shallow-water connection from this shelf to the northern continents. For this reason, many of the shelf species have aspects of deep-water fish. A direct consequence of this isolation is the high degree of endemism in the shelf species. The deep-water fish fauna, on the other hand, does not show the same endemism, with only half the species being restricted to the Antarctic (Table 7.1). The two fauna appear to overlap about the continent proper, on the edge and upper part of the continental shelf.

The coastal bottom, or demersal, fish form a diverse group including representatives from fifteen families. The dominant group is the suborder Notothenioidei whose four families, the Nototheniidae (Antarctic cod), Harpagiferidae (plunder fish), Bathydraconidae (dragon fish), and Channichthyidae (ice or white fish), include more than 60% of the species and over 90% of the individuals. The Notothenioidei form a group of approximately 127 species (Balushkin 1988) with a wide variety of ecomorphological types adapted for nearly all habitats from shallow tidal pools to the upper continental slope down to 2,000 m (Kock 1985). With the relatively few nonnotothenoid fish in Antarctic

TABLE 7.1
The Number of Genera and Species of Each Family of Fish Found in the Southern Ocean, Showing the Number Restricted to the Area and the Number Found Farther North

	Antarctic Only		Antarctic and Farther North		Totals	
Family	**Genera**	**Species**	**Genera**	**Species**	**Genera**	**Species**
Geotriidae (lampreys)	0	0	1	1	1	1
Myxiidae (hag fish)	0	0	1	1	1	1
Rajidae (skates)	0	3	2	1	2	4
Synaphobranchidae[a]	0	0	1	1	1	1
Halosauridae[a]	0	0	1	1	1	1
Muraenolepidae (eel cod)	0	2	1	1	1	3
Moridae	0	0	2	2	2	2
Gadidae (true cod)	0	0	1	1	1	1
Macrouridae[a]	0	4	5	3	5	7
Brotulidae[a]	0	1	1	0	1	1
Zoarcidae (eel pouts)	3	8	3	3	6	11
Nototheniidae (Antarctic cod)	4	31	2	3	6	34
Harpagiferidae (plunder fish)	4	14	1	1	5	15
Bathydraconidae (dragon fish)	8	15	0	0	8	15
Channichthyidae (ice fish)	9	15	1	0	10	15
Congiopodidae (horse fish)	1	1	0	0	1	1
Liparidae (snai fish)	0	5	3	0	3	5
Bothidae (flounders)	0	1	1	1	1	2
Totals						
All families	29	100	27	20	56	120
All but abyssal families	29	95	19	15	48	110

[a] Denotes a bathyal or abyssal family (De Witt 1971).

Source: From Everson, I., In *Antarctic Ecology*, Law, R. M., Ed., Academic Press, London, 452–491, 1984b. With permission.

waters, notothenoids fill ecological niches normally occupied by taxonomically diverse fish in temperate waters. The Nototheniidae and Channichthyidae include the major Antarctic fish species currently or potentially of commercial importance (Table 7.2).

In contrast to other oceans, the Southern Ocean does not contain obligate, shoaling, pelagic species. With the exception of the opah, *Lampris gattatus*, and the port-beagle, *Lamma nasus*, that are occasional invaders from the north (Svetlov 1978; Prurtkto 1979; Kock et al. 1992), there are no true epipelagic families (i.e., families which are predominantly confined to surface waters throughout their life cycle). The pelagic families that occur in Antarctic waters are descendants of faunal groups of different origins: bathypelagic species, mesopelagic species and species originating from demersal families that are secondarily adapted to permanent or temporary midwater life.

The mesopelagic fauna living in waters below the euphotic zone, down to a depth of 1000 m, is composed of two groups of species. One group, apparently long-adapted to cold water, gave rise to a number of Subantarctic–Antarctic species (Kock 1984). The most numerous group, by far, consists of the myctophids (*Electrona antarctica*, *Gymnoscephalus braueri*, *Bathylagus antarcticus*, *Cyclothone microdon*, *Protomyctophum antarcticus*, *Protomyctophum* and *Kreffichys*), and the lepid, or ionah, fish *Notolepis coatsi* and *N. annualta*. The second group consists of fish with a more northerly distribution that regularly undertake feeding migrations to the peripheral waters of the Southern Ocean; Notosuridae, Trichiuridae (hairtails), Oreosomatidae (dories), Anotopteridae (daggertooths), and some of the Mtctophidae and Paraleoidae.

The secondarily pelagic species comprise members of the families Nototheniidae, Channichthyidae, Bathydraconidae, and even Harpagiferidae, that either spend the first one or more years in midwater and are often associated with drifting or fast ice, or krill aggregations, or are temporarily or pelagic species during most of their life. Included in the latter group are the widespread and abundant Antarctic herring *Pleurogramma antarcticum* and the epipelagic *Pagothenia* borchgrevinki, the latter associated with the underside of the sea ice in inshore waters (DeVries 1978).

In his review of the significance of fish in the Antarctic marine ecosystem, Hureau (1994) recognized three major zones with reference to the distribution of fish in the Southern Ocean. These are, from south to north, the High-Antarctic Zone, the Seasonal Pack-Ice Zone and the Ice-Free Zone.

The High-Antarctic Zone is the region immediately adjacent to the continent and is covered by permanent ice for most of the year. It is characterized by the presence of

TABLE 7.2
Some Common Fish of the Southern Ocean

Group	Species	Common Name
Rajidae	*Raja georgiana*	
	Raja murrayi	Rays
	Raja eatoni	
Gadidae	*Micromesistius australis*	Southern poutassou or blue whiting
Nototheniidae	*Notothenia gibberifrons*	Bumphead notothenia
	Notothenia rossii rossii	
	Notothenia rossii marmorata	Marbled notothenia
	Notothenia squamifrons	Scaled notothenia
	Paranotothenia magellanica	
	Notothenia coriiceps coriiceps	
	Notothenia coriiceps neglecta	
	Notothenia kempi	
	Notothenia angustifrons	
	Nototheniops larseni	
	Pagothenia bernacchii	
	Pagothenia borchgrevinki	
	Patagonotothen brevicauda guntheri	Gunther's notothenia
	Dissostichus mawsoni	Antarctic toothfish
	Dissostichus eleginoides	Patagonian toothfish
	Pleurogramma antarcticum	Antarctic sidestripe or Antarctic silverfish
Channichthyidae	*Champsocephalus gunnari*	Antarctic icefish
	Channichthys rhinoceratus	Longsnoutcd icefish
	Pseudochaenichthys georgianus	South Georgia icefish
	Chionodraco rastrospinosus	Kathleen's icelish
	Chaenodraco wilsoni	

the euphausiid species *Euphausia crystallorophias* in the zooplankton and, in the coastal fish fauna, by the abundance of the genus *Trematomus*, few pelagic other nototheniids (*P. antarcticum* and the genus *Pagothenia*), and a high proportion of artedidraconids, bathydraconids and channichthyida. This ecologically defined zone covers all the coasts of the Antarctic Continent, most of the continental shelf, and the Peter I and Balleny Islands.

The Seasonal Pack-Ice Zone is limited to the north by the northern limit of the pack ice and to the south by the northern summer limit of the pack ice (Zwally et al. 1983a, 1983b). This intermediate Seasonal Pack-Ice Zone covers the Polar Frontal Zone between the Antarctic Coastal Current and the Antarctic Circumpolar Current. In some areas, such as the eastern Atlantic Ocean-western Indian Ocean sectors, this zone extends very close to the Antarctic Continent (Kock 1992). It is the most productive ecological zone of the Southern Ocean, with dense concentrations of krill, *Euphausia superba*. The fish fauna of this zone is mostly represented by myctophids. The South Orkneys Islands, South Sandwich Islands, South Shetland Islands and the northern tip of the Antarctic Peninsula lie within the Seasonal Pack-Ice Zone.

The Ice-Free Zone extends between the Subtropical Front to the north and the northern limit of the pack ice to the south. This zone is almost exclusively inhabited by mesopelagic and bathypelagic fish and by a coastal fish fauna dominated by notothenids of the genera *Notothenia*, *Lepidonotothen* and *Patagonothen*, harpagiferids and some channichthyids. It includes the following islands from West to East: South Georgia, Bouvet Island, Marion, Prince Edwards, Crozet, Kerguelen, Heard, and Macquarie Islands.

7.2.1 BENTHIC (DEMERSAL) SPECIES

The demersal fish fauna can be categorized into coastal and deep water faunas. The coastal fish fauna consists of two main groupings: the fauna of the Seasonal Pack-Ice Zone and the islands north of it, that inhabits the shelves of the Antarctic Peninsula, the islands of the southern Scotia Arc and the islands and seamounts north of the maximum extension of the pack ice, such as South Georgia and Kerguelen Islands; and the fauna of the High Antarctic Zone that is confined to the shelf and the upper slope areas of the Antarctic Continent.

The coastal fish fauna is characterized by the predominance (in terms of both species and biomass) of the genera *Notothenia* and *Lepidonothen*, and of *Champsocephalus gunnari*, and by the presence of the genus *Harpagifer*. The genus *Trematomus*, abundant in the High Antarctic Zone is represented in significant numbers by only three species: *T. hansoni*, *T. newnesi*, and *T. vacarius*. Fish biomass in the Seasonal Pack-Ice Zone, and the islands north of it, is dominated (or was dominated before exploitation) by a few species only: *Notothenia rossii*, *N. coriiceps* (in shallow waters), *C. gunnari* and *Lepidonotothen nudifrons*.

There are regional differences in the species composition of the fish fauna. A number of species common to the Atlantic Ocean sector, *Gobionotothen gibberifrons*, *Lepidonotothen nudifrons* and *Chaenocephalus aceratu*, for examples, are absent from the Indian Ocean sector, but have ecological equivalents in the similar *G. acuts*, *L. mizops* and *Channichthys rhinoceratus*. Other species are endemic to certain islands.

The principal components of coastal fish fauna in the High Antarctic Zone are also notothenioids, but the species composition is different from that of the Seasonal Pack-Ice Zone and the islands to the north. Two-thirds of the entire coastal fish fauna of the Southern Ocean are found here. Species diversity and richness are much higher than in the Seasonal Pack-Ice Zone (Hublold 1991), although the biomass is about an order of magnitude lower (Kock et al. 1984; Ekau 1990). Nototheniids are represented by the multispecific genus *Trematomus* and a number of predominately monospecific genera, such as *Pleurogramma*, *Aethotaxis* and *Pagathenia*. Only two species of *Notothenia* are present and Harpagiferids are absent. Most of the channichthyids (66%), bathydraconids (66%), and the artedidraconids (95%) in particular, are confined to the High Antarctic Zone. In addition to the notothenioids, the rajids and muraenolepids are also present.

Schroder et al. (1999) investigated the demersal fish fauna of the Weddell Sea. This fauna was dominated by one suborder, the Notothenioidei. Five families within this suborder accounted for more than 50% of the species and 90% of the fish biomass on the shelf (Gon and Heenstra 1990). This demersal fish fauna is dependent upon the structure of the benthic invertebrate communities supplying their diet and shelter. They also represent the link between the benthic communities and warm-blooded predators such as seals and penguins. Altogether, fifty-four species were found from the following families: Nothothenidae (13 species), Artedidraconidae (12), Bathydraconidae (9), Channichthyidae (9), Paralepdidae (1), Myctophidae (2), Muraenolepidae (1), Bathylagidae (1), Anotopteridae (1), Macrouridae (1), and Rajidae (2).

Ninety-three percent of all fish belonged to the Notothenioidei, including Nototheniidae (mostly *Trematomus* sp.) 35%, Channichthyidae 33%, Atredidraconidae 11%, and Bathydraconidae 6%. The only other family with numerical dominance was the macrourid *Macrourus wilsoni* (11% of all fish). The most widely distributed species were *Trematomus lepidorhinus*, present in every haul, and *T. scotii*, absent only in the deeper hauls, and two Channichthyids, *Chionodraco myersi* and *Cryodraco antarcticum*, present in nearly 90% of the hauls.

Barrera-Oro and Casaux (1998) investigated the fish distribution in Potter Cove in the South Shetland Islands. The fish were all demersal shallow-water fish (120 m deep) that spend all or part of their life cycles in inshore waters. The most frequent species were the nototheniids *Notothenia coriiceps* (previously known as *N. neglecta*), *N. rossii*, *Lepidonothen nudifrons*, *Trematomus newnesi*, *Gobionothen gibberifrons* and *T. bernacchii*, the harpagiferid *Harpagifer*

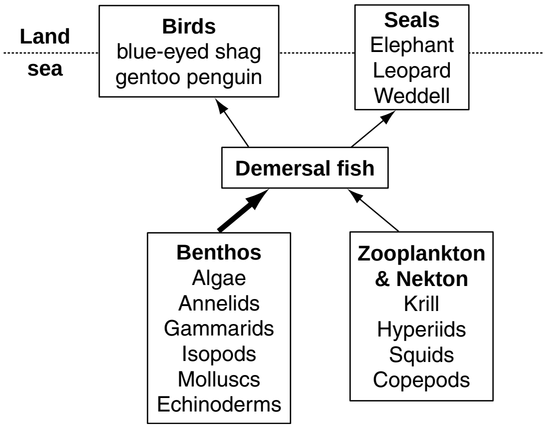


FIGURE 7.2 The role of demersal fish in energy flow through the Potter Cove, King George Island, ecosystem. (From Barrera-Oro, E., Casaux, R., *Ber. Polarforsch.*, 299, 161, 1998. With permission.)

antarcticus, and, less frequently, the bathydraconid *Parachaenichthys charcoti* and the channichthyid *Chaenocephalus aceratus*. *N. coriiceps* was the dominant species, both in number and biomass.

It is known that areas with high macroalgal diversity show greater fish abundance and this proved to be the case for the fish fauna of Potters Cove. The main pathways of energy flow through demersal fish in the food web of an Antarctic inshore shallow-water zone such as Potter Cove is shown in Figure 7.2. The demersal fish are the main predators on the benthos, feeding on all the organisms present below their own trophic level and also on zooplankton in the water column. On the other hand, the demersal fish are common prey of birds (primarily the Antarctic shag *Phalacrocorus bransfieldensis*) and seals.

7.2.2 BENTHO-PELAGIC SPECIES

The bathymetric range of the deep-sea bottom and bentho-pelagic fish fauna is not well known. Some notothenioids, such as *Pogonophryne macropogon*, *Bathydraco scotiae* and *B.antarcticus*, have been found as deep as 2,000–2,600 m. A number of zoarcids and liparidids have been caught as deep as 2,000–3,500 m (Anderson 1984). The deepest-living species so far recorded are the ophiidid *Holocmycteronus brucei* from 4,572 m in the Weddell Sea and the liparidid *Notoliparis kurchatovi* from 5,474 m in the South Orkney Trench.

7.2.3 MESOPELAGIC AND BATHYPELAGIC SPECIES

The mesopelagic species occupy the middle depth of the water column of the Southern Ocean and the benthopelagic species are those benthic species that migrate into the water column to feed. The oceanic pelagic fish fauna, both mesopelagic and bathypelagic, has its greatest diversity and its highest biomass in the Ice-Free Zone. This is due to the presence of a large number of species that have their center of abundance either in or north of the Polar Frontal Zone. The most abundant groups are the lantern fish (Myctophidae), deep sea smelts (Bathylagidae), barracudinae (Paralepididae), and bristlemouths (Gonostomatidae). Taxa from these families account for greater than 90% of the biomass of mesopelagic fish in the upper 1,000 m of the Weddel-Scotia sea region (Lamcraft et al. 1989).

Prominent species include *Electrona carlsbergi*, several *Protomyctophum* species such as *P. andriashevi* and *P. tenisoni* (Myctophidae), and *Benthalbella elongata* (Scopelarchidae). Although comparatively fewer, representatives of the pelagic fauna such as the mesopelagic *E. antarctica*, *Gymnoscopelus braueri*, *G. nicholsi*, *Protomyctophum bolini* (Myctophidae), *B. antarcticus* (Bathylagidae), *Borostomias antarcticus* (Stomiidae), and *C. microdon* (Gonostomatidae) are also common in the oceanic and slope areas of the Seasonal Pack-Ice Zone and High Antarctic Zone (Torres et al. 1984; Hubold and Ekau 1987; Duhamel et al. 1989). Kozlov (1995) reports that in the summer and autumn the total biomass of these species in the upper 100 m was 3.3–4.4 g fresh mass m^{-3} (Lancraft et al. 1989).

Many of the mesopeagic fish, particularly the myctophids, undertake diel and seasonal vertical migrations. In the spring and summer seasons, myctophids ascend to the epipelagic zone (50–200 m) and feed in the substratum of high summer plankton productivity. In the winter, they descend to greater depths (350–500 m) and inhabit the top layer of the Circumpolar Deep Water that contains the wintering populations of planktonic crustaceans (Lubimova et al. 1983, 1987). They have a diurnal feeding cycle; for example, *E. antarctica* feeds more during the day, when it is deeper, than it does at night (Rowedder 1979).

Larval mesopelagic fish dominate the ichthyoplankton of oceanic waters, especially the larvae of *Electrona* spp., *Gymnoscopelus* spp. and *Notolepis* spp. (Ascensio and Marina 1984; Efremenko 1986; Kellerman 1989a). The larvae of these groups also dominate the oceanic ichthyoplankton in the upper 500 m at South Georgia (Efremenko 1986; North 1987), in the Weddell Sea (Hubold 1990), and the southern Indian Ocean (Williams 1985b; Hully et al. 1991).

Myctophid biomass in the Southern Ocean has been estimated to be 70–130 million tonnes (Lubimova et al. 1987). On the basis of the most abundant myctophid species in catches of pelagic trawls, it appears that 80% of the biomass comprises four species: *E. carlbergi*, *E. antarctica*, *K. anderssoni* and *G. nicholsi*. Results of biomass assessments in the Polar Frontal Zone showed that *E. carlsbergi* accounted for between 40% and 50% of the total biomass of the four species, i.e., from 22.4 to 52 million tonnes (Kozlov 1995).

7.2.4 PELAGIC SPECIES

Antarctic pelagic fish have been derived from several faunal groups of different origin. In the absence of truly epipelagic species, those that occur are specialized notothenioids. Two relatively pelagic species are the large predators *Dissostichus elegenoides* in the Atlantic Sector, *D. mawsoni* in the Ross Sea and adjacent Eastern Antarctic waters, and the shoaling planktivore *P. antarcticum* (Eastman 1991). Their life cycles are not completely epipelagic in the proper sense (Kock 1992), because both are demersal-spawners and egg development is demersal, at least in *P. antarcticum*. In the Ross Sea, *D. mawsoni* live at depths of 300–500 m, often under fast ice (Eastman and DeVries 1981; Eastman 1991). The life cycle and time of spawning is largely unknown. The closely related *D. eleginoides* spawns in autumn and the pelagic eggs are widely dispersed across slope and oceanic waters, where the larvae hatch in the spring (Kock and Kellerman 1991; Kellerman 1989a).

P. antarcticum is the dominant pelagic fish in the High-Antarctic Zone, where it plays a fundamental role in the food web of the Antarctic marine ecosystem (Hureau 1994). Like young krill, juvenile *P. antarcticum* are important components of the cryopelagic feeding community and swim freely under the ice (Hureau 1994). In both the Weddell and Ross Seas, they are an important resource for top predators such as birds, seals and whales, as well as other notothenioid fish (Emerson 1968; Eastman 1985a, 1985b; Plotz 1986). In summer in the western Ross Sea, the pelagic fish fauna is dominated by this species, 97.6% in biomass (De Witt 1970; Guglielmo et al. 1998). *P. antarcticum* is the most abundant species of the Weddell Sea ichthyoplankton (Hubold 1991) and represents about 98% of the total ichthyoplankton living on the Weddell Sea continental shelf (Kellerman and Kock 1984).

7.3 MORPHOLOGICAL AND PHYSIOLOGICAL ADAPTATIONS

Two important characteristics of the Antarctic marine environment are the narrow annual temperature range, a temperature that is near or at the freezing point of seawater, especially in the deeper water and close to the continent. Because of this environmental stability, Antarctic fish have evolved to be most efficient at low temperatures. However, in the near-freezing water, they have needed to evolve systems to prevent freezing. The physiology and morphology of Antarctic fish, covering aspects such as buoyancy adaptations, cold adaptations, freezing resistance, metabolic adaptation, and white bloodedness in channichthyids, have been extensively studied in recent years (MacDonald et al. 1987; DeVries 1997; Di Priscu 1997; Wohrmann 1997).

7.3.1 Metabolic Adaptations

Temperate water fish are able to adjust to significantly large changes in their environmental temperature, i.e., they can acclimate to increases or decreases of temperatures, with such acclimation being achieved over an extended period of several weeks. Higher-latitude Antarctic fish, however, are only able to survive over a narrow range of temperatures and cannot tolerate temperatures beyond +4°C to +6°C, and these limits do not normally change, even after long periods of acclimation.

The consistently low temperatures present in the Southern Ocean mean that rates of biochemical reactions will be significantly slower than they would be in a temperate region. Yet Antarctic fish function efficiently at the low temperatures of their habitat. Wohlschlag (1964) found basal oxygen consumption of polar fish (both in the Arctic and Antarctic) to be 5–10 times higher than expected and considered this elevated rate, that he termed *cold adaptation*, to be an evolutionary adaptation to overcome the rate-depressing effects of temperature. It also means that more energy is required for maintenance and less, therefore, is available for growth. However, subsequent experiments on nototheniids, and one channichthyid from the Scotia Arc region, failed to demonstrate metabolic cold adaptation and it was suggested that Wohlschlag's experiments were influenced by stress and did not reflect true metabolic rates (Holeton 1974). Since that time, there has been considerable controversy as to whether cold adaptation exists (Clarke 1983, 1987, 1991). Everson (1977a) examined growth rates in Antarctic fish in relation to their warm-water relatives and found that their growth rates were slow, indicating little in the way of adaptation. The balance of evidence seems to suggest that the basal metabolic rate of Antarctic fish, both mesopelagic and demersal, is about twofold higher than for temperate water fish if extrapolated to the same temperature (Forster et al. 1987; Wells 1987; Torres and Somero 1988; Johnston et al. 1991).

On the other hand, compensation for decreasing temperatures in biochemical systems at the tissue level has been demonstrated for several species (Somero et al. 1968; Lin et al. 1976) and in terms of direct enzyme activities (Somero 1969; Johnston and Walsby 1977). These results show that, at the low environmental temperatures found in Antarctic waters, the enzymes of Antarctic fish are more efficient catalysts than those of temperate fish living at higher temperatures. Smith and Haschemeyer (1980) found that, in Antarctic fish, the protein synthesis rate in the liver was twice that predicted from theoretical temperature dependency relationships and three times the rate predicted in the white muscle. However, the low protein synthesis of 6% liver protein per day, compared with values of approximately 20% measured in tropical fish (Smith et al. 1980), nevertheless indicated a reduced metabolic rate. Thus, the enzyme systems of Antarctic fish exhibit features which seen to be related to their operation at low temperatures. These features (MacDonald et al. 1990) are: (1) most enzymes function best at 20–40°C, but those of Antarctic fish are most active near 0°C; (2) many Antarctic fish enzymes do not increase activity markedly at higher temperatures, which indicates that relatively little energy is needed to activate the enzymatic reactions; and (3) enzymes and other proteins of Antarctic fish tend to be less stable than those of warm water fish, and are easily denatured both by chemical agents and high temperatures. Under the assumption that the energetic costs of feeding and activity are comparable to those for temperate water species, the evidence of reduced basal metabolism, reduced growth, and reduced reproductive effort leads to a new concept of "cold adaptation" (Clarke 1980b).

7.3.2 FREEZING RESISTANCE

Depending upon depth, the water temperature in the coastal area of the Southern Ocean varies between −1.0°C and −2.0°C. The average year-round value is −1.87°C, the equilibrium temperature of ice and seawater, and well below the freezing temperature (0.08°C) of a typical marine teleost hyposmotic to seawater. Because the temperatures of the inshore regions of the Southern Ocean are usually below this, the fish must have some mechanism to avoid freezing. In Notothenioids, freezing is avoided by lowering the freezing point of the blood and other tissue fluids.

About one-half of the freezing point depression is due to NaCl; the other half is provided by solutes in the colloidal fraction of the fluid that exert their effect noncollectively. In most Antarctic fish species, these solutes are glycopeptides with molecular masses ranging from 2,000 to 33,700 Da; they contain a repeating unit of three amino acid residues in the sequence (Ala-Ala-Thr); a disaccharide is linked to each. In the lighter glycopeptides, Pro periodically substitutes Ala at its position in the tripeptide. Antifreeze glycopeptides are synthesized year-round in the liver, secreted into the circulatory system, and then distributed into extracellular fluids where their concentration approaches 3.5%. In the notothenid *Pagothenia borchgrevinki*, eight glycopeptides of different-sized molecules have been identified (DeVries 1988). The antifreezes depress the freezing point of water by a process termed absorption–inhibition (DeVries 1988).

Figure 7.3 compares the blood of a freshwater perch with that of an Antarctic notothenioid before and after dialysis to remove solutes less than 1 kDa (mainly NaCl, etc.). The change after dialysis indicated that sodium chloride and other small solutes normally account for the mild freezing-point depression of the perch plasma. After dialysis, the freezing point of the notothenioid rose from −2.2°C to −1.2°C, indicating that the glycopeptide molecules account for a significant part of the freezing-point depression of the blood.

Most of our knowledge on the antifreeze molecule's identification, tissue distribution, mechanisms of action, molecular structure, identification of the gene, relationships with kidney morphology, and phyletic distribution come from studies by DeVries and Lin 1977; Raymond and DeVries 1977; DeVries (1980, 1988, 1997); Ahlgren and DeVries 1984; Eastman and DeVries 1986; Ahlgren et al. 1988; Cheng and DeVries 1991; see also Eastman 1993.

7.3.3 BLOOD AND OXYGEN TRANSPORT SYSTEMS

The respiratory physiology of Antarctic fish has attracted a great deal of attention ever since Mathews (1931) established that the Channichthyidae (icefish) have no hemoglobin or respiratory pigment in their blood. The haematological features of many Antarctic Notothenioidei have been extensively investigated in the past decades (e.g., Everson and Ralph 1970; Hureau et al. 1977; Wells et al. 1990; Kunzmann 1996). These studies have demonstrated a clear difference between fish below the Polar Front and temperate and tropical fish in that Antarctic species are characterized by a reduction of erythrocyte number and the Hb concentration in the blood. In general, hemoglobin concentrations of Antarctic fish fall within the range of 4–5 g $(100\,\mathrm{ml})^{-1}$ of blood as compared to 7–12 g $(100\,\mathrm{ml})^{-1}$ for other teleosts, whereas the erythrocytes' counts generally fall within the range of $0.5\text{–}1.0\times10^6\,\mathrm{mm}^{-3}$ of blood compared

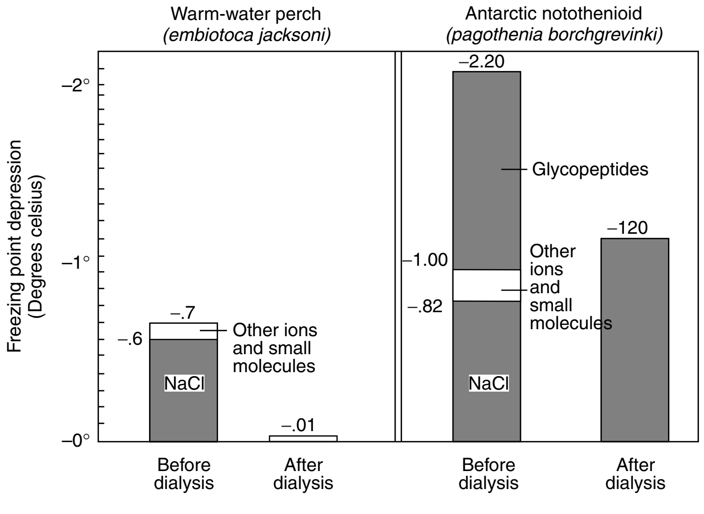


FIGURE 7.3 Comparison of the blood plasma from a warm-water Pacific perch and an Antarctic notothenioid after dialysis to remove solutes of molecular mass less than 1 kDa. The change after dialysis for the perch indicated that sodium chloride and other small solutes normally account for the mild freezing-point depression of the perch plasma. After dialysis, the freezing point of the notothenioid blood rose from −2.2°C to −1.2°C, indicating that the glycopeptide molecules account for a significant part of the freezing-point depression of the blood. (From Eastman, J.T. and DeVries, A.L., *Polar Biol.*, 4, 42–52, 1985. With permission.)

to 1.2×10^6 mm^{-3} for most other teleosts (Tyler 1960; Kooyman 1963; Hureau 1966; Everson and Ralph 1970; Wells et al. 1980; di Priscu and D'Avino 1989).

In the icefish, the oxygen is transported by simple physical solution in the blood plasma; consequently, the oxygen-carrying capacity is only about 10% that of notothenioids living in the same environment. In spite of this, the white-blooded fish are not sluggish sedentary species; they reach sizes of 60–75 cm and occupy a range of ecological niches, including active swimmers hunting for prey in the pelagic zone such as the South Georgia icefish *Pseudochaenichthys georgianus*. They have developed a number of adaptations that largely compensate for their presumed physiological "disadvantages" (Hemmingsen and Douglas 1970, 1977; Holeton 1970; MacDonald et al. 1987). These adaptations include low metabolic rate, large, well-perfused gills, large blood volume, large heart and stroke volume, large capillary diameter, and cutaneous respiration. The blood passages in the secondary gill lamellae are larger than those of any other teleost (Steen and Berg 1966; Jakubowski and Byczkowska-Smyk 1979) so that they may act more efficiently. Many species have reduced scale coverage (lacking in channichthyids) and this is assumed to facilitate cutaneous respiration. However, research by Hemmingsen and Douglas (1970) and Holeton (1970) indicate that it probably only accounts for between 2.8% and 3.0% of the total oxygen uptake. The blood volume (8–9% of the total volume) is much higher than in other nototheniids (Hemmingsen and Douglas 1970; Twelves 1972), and the size of the heart and the thickness of the cardiac muscle are much larger than in other teleosts (Everson and Ralph 1970; Holeton 1974). Everson and Ralph (1970) estimated that the cardiac output of *Chaenocephalus aceratus* was about ten times that of an equivalent cod and Holeton (1970) found a several-fold difference between this species and redblooded fish from the same locality. Thus, the increase in cardiac output and stroke volume in addition to the reduction in vascular resistance brought about by an increase in the bore of the blood vessels result in a large volume system operating at low pressure, with a higher blood-to-tissue oxygen gradient than that found in other fish. Although the blood has a low oxygen capacity, this is not a problem in cold Antarctic waters where the percentage oxygen saturation is high.

7.3.4 BUOYANCY ADAPTATIONS

The notothenioids are primarily bottom dwellers lacking swim bladders. Some nototheniids and channichthyids, however, show a trend towards the evolution of neutrally buoyant species (Nybelin 1947) that have become permanent members of the midwater community. The absence of competition from other midwater species and an abundant food supply (especially krill) have probably been responsible for this trend (Eastman 1980, 1985a). *P. antarcticum, Aethotaxis mitopteryx* and *Dissostichus mawsoni* are all neutrally buoyant. *D. mawsoni* is the largest predatory fish in the midwater of the Southern Ocean. In McMurdo Sound, *D. mawsoni* feeds predominantly on fish and mysid shrimps (Eastman 1985a). Evolutionary adaptations for buoyancy are reflected in morphological specializations such as reduced mineralization of the skeleton, reduced scale mineralization, and lipid storage (Eastman and DeVries 1978, 1981, 1982, 1985, 1986; DeVries and Eastmond 1985a, 1988). *P. antarcticum* is unique in storing lipids in large subcutaneous and intermuscular sacs. Lipid in *Dissosticus* is contained in adipose cells in subcutaneous and muscular deposits and accounts for 4.7% and 4.8% of body weight, respectively. In both species, the lipids consist primarily of triacylglycerols.

In the neutrally buoyant nototheniids, the skeleton is weakly calcified with a considerable amount of cartilage, resulting in a considerable reduction in weight. The scales are also incompletely mineralized. A subcutaneous lipid layer in *D. mawsoni* and subcutaneous lipid sacs in *P. antarcticum*, together with the high lipid content of the white muscles, provide buoyancy (Eastman and DeVries 1982). The liver of *D. mawsoni* is unique in that it contains large amounts of lipids (Estman and DeVries 1981). The lack of a swim bladder and the development of large pectoral fins in nototheniids may allow vertical migration over several hundred meters in a short time.

7.4 REPRODUCTION AND GROWTH

Information on reproductive characteristics and the early life history of Antarctic fish refers almost exclusively to notothenioids. Two recent reviews on reproduction in notothenioids are those of Duhamel (1987) and Kock and Kellerman (1991). An account of the early life history stages of Antarctic fish can be found in North and Kellerman (1990); two catalogues of Antarctic larval fish are those of Efremenko (1983) and Kellerman (1990a).

7.4.1 AGE AT SEXUAL MATURITY

As a consequence of their slow growth rates, slow metabolic rates, and relatively long life spans, many Antarctic fish do not reach sexual maturity until three to eight years. Length at first spawning may be from 55% of the maximum length ($L_{\max}$), but in many species it is not attained until 70–80% of $L_{\max}$. The only exception is *C. gunnari* at South Georgia, which may begin spawning at about 40% of $L_{\max}$ (Kock and Kellerman 1991). Male *Notothenia neglecta* (Everson 1970b), *N. rossii marmorata* (Olsen 1954; Shust 1978), *N. rossii rossii* (Hureau 1970) and *Chaenocephalus aceratus* (Kock 1981) mature approximately one year earlier than females. However, in other species, such as *N. kempi* (Shust 1978), *N. squamifrons* (Duhamel and Hureau 1981), *C. gunnari* and *Pseudochaenchthys georgianus* (Kock 1981), both sexes mature at the same age.

7.4.2 GONAD MATURATION AND DEVELOPMENT

The maturation of the ovary, i.e., the process of yolk deposition, takes place over two years, although spawning probably takes place annually thereafter. The development and maturation of the gonads of several species of Antarctic fish have been described by Dearborn (1965a), Everson (1970b, 1984b), Hureau (1970), and Kozlov (1980, 1982). Both the development and maturation proceed synchronously in individuals of the same species so that the spawning season is generally of limited duration. Complete annual cycles described thus far all show the general pattern described by Everson (1977b) for *Notothenia coriceps* at the South Orkney Islands. In this species, the ovary starts to increase in size in November, after being more or less constant at 3% of the body weight for the preceding six months (Figure 7.4). The increase is gradual over the period from six to eight months after spawning, followed by a rapid two-month increase (March–April) so that the gonad is nearly twice its March size when spawning takes place in May. The final maturation of the testes begins in December when there is a steady increase in size until spawning in May. There is then a steady reduction in size due to release and resorption of sperm (Figure 7.5).

Energy-loss during spawning is substantial and has been described as 50–60% in *N. rossii* at South Georgia (Kozlov 1980), although this does not only include the loss through the eggs. Lipid content in the muscle and liver decreases substantially in females of *N. rossii and N. coriceps* at South Georgia (Everson 1970b) in the course of gonad maturation.

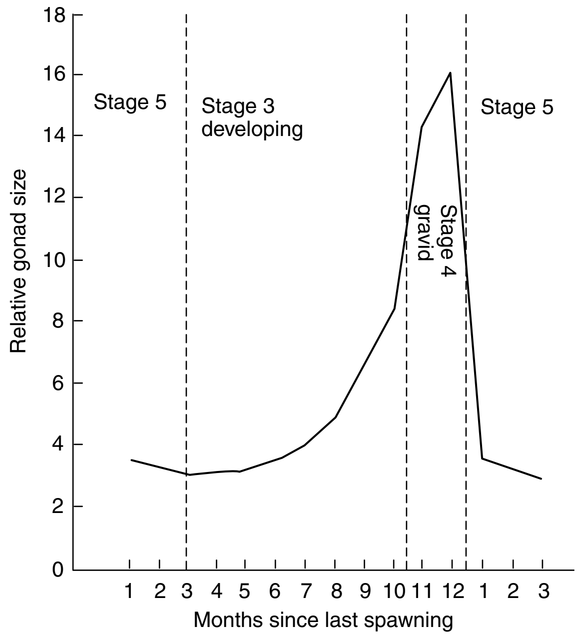


FIGURE 7.4 Probable seasonal pattern of relative female gonad size [(gonad weight / total weight)×100]. Morphological characteristics of stages: (1) Immature: ovary small and firm, no ova visible to the naked eye; (2) Maturing virgin: ovary 1/4 length of body cavity, firm, full of eggs; (3) Developing ovary: ovary large, contains eggs of two sizes; (4) Gravid: ovary large, when opened, large ova spill out; (5) Spent: ovary flaccid, contains few large and small ova. (From Everson, I., *Antarctic Ecology*, Vol. 2, Laws, R.M., Ed., 491, 1984b. With permission.)

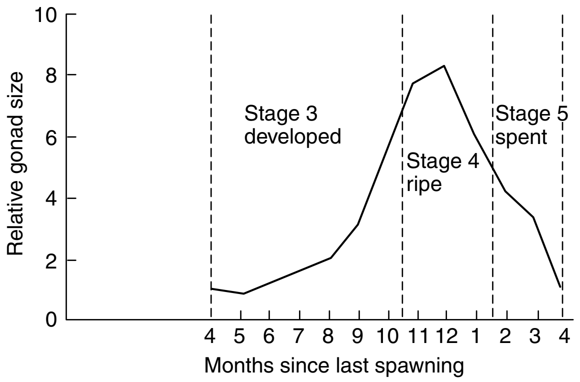


FIGURE 7.5 Probable seasonal pattern of relative male gonad size. Morphological characteristics of the stages: (1) Immature: testes small, translucent; (2) Developing: testes small, white, convoluted; (3) Developed: testes large, white, convoluted, no milt produced when cut; (4) Ripe: testes large, opalescent, white, milt produced when cut; (5) Spent: testes smaller, dirty-white in color. (From Everson, I., *Antarctic Ecology*, Vol. 2, Laws, R.M., Ed., Academic Press, London, 191, 1984b. With permission.)

7.4.3 OVA DEVELOPMENT AND FECUNDITY

Early studies by Marshall (1953) concluded that Antarctic fish produce relatively few, large, yolky eggs and larvae that hatch at an advanced stage. Egg size after fertilization ranges from 2.0 mm in *Lepidonotothen larseni* and *P. antarcticum* to 5.0 mm in *N. rossii* (Hubold 1990). In the Seasonal Pack-Ice Zone and around the islands north of it two groups of species can be distinguished with respect to egg size. The first group, exhibiting egg sizes of mostly 1.5–2.5 mm, comprises species of the genera *Notothenia*, *Lepidonotothon* and *Patagonotothen*, which are late-winter and spring spawners, and *Psilodraco breviceps* and *Harpagifer antarcticus*, which have high relative fecundity. The second group is made up of autumn-spawning members of the genus *Notothenia* and of icefish.

In the High Antarctic Zone, the only species with egg diameters less than 2.5 mm is *P. antarcticum*, which has an egg size of 2.0 mm (Hubold 1990). Members of the genera *Trematomus* and *Pagothenia* have egg sizes of about 2.5–4.3 mm. The largest egg sizes, 4.5 mm, are again observed in Channichthyids, Artedidraconids, and Bathydraconids produce eggs 3.0–4.0 mm. The trend to produce fewer but larger eggs towards higher latitudes is mostly confined to the family Nototheniidae.

Recent studies on *Notothenia neglecta* indicate that due to the large size of the ova yolk, deposition may take more than one year (Everson 1970b), so that there are two distinct classes of yolky oocytes present in a mature ovary. A biennial process of maturation has also been reported in other species, such as *P. borchgrevinki* (Andriashev et al. 1979) and *C. gunnari* and *Pseudochaenichthys georgianus* (Kock 1979).

As a consequence of the production of large, yolky eggs, fecundity is generally quite low. Overall fecundity ranges from about 100 eggs in *Paraliparis antarcticus* (Lisovenko and Svetlov 1980) to 238,000–546,000 and 40,000–200,000 in *Dissostichus eleganoides* and *Lepidonotothen squamifrons*, respectively. In the High Antarctic Zone, *Dissostichus mawsoni* has a potential fecundity of 472,000–1,343,000 eggs (Yukov 1982). Relative fecundity (i.e., the number of eggs per gram of body weight) is, in general, 4–30 for all channichthyids, most nototheniids, *Pseudochaenichthys georgianus*, and *Harpagifer* spp. A higher relative fecundity of about 50–250 eggs is found in several late-winter- and spring-spawning species of *Notothenia*, in the dragon fish *Psilodraco breviceps*, and in the eel cod *Muraenolepis microps*. Fecundity in different populations of the one species, as well as in different genera of one family (e.g., *C. gunnari*, *Notothenia* and *Trematomus*), normally decreases with higher latitudes (Permitin and Sil'yanova 1971).

7.4.4 SPAWNING

Spawning dates are now fairly well known for a good number of species (Hureau 1966, 1970; Everson 1970b; Permitin and Sil'yanova 1971; Permitin 1973; Keysner et al. 1974; Duhamel 1987; Kock 1989; Kellerman 1990a, 1990b). Of the species for which data is available, 30% of all individuals spawn in the summer, 43% in the autumn, 17% in the winter, and 10% in the spring. Approximately 71% of the species spawn in the late summer and autumn (March–June), with peak spawning occurring around May–June (54%). Only 28% of the species spawn during the eight months of the year between July and February. Those species spawning in the summer (January–April), especially in the early summer (February), have a longer spawning period than fish spawning in the autumn and winter. Species spawning between January and April have an average spawning period of over 61 days, while those spawning from May to December have an average spawning period of 48 days.

Spawning migrations have been described for several species. The marbled notothenia, *N. rossii*, undertakes regular migrations from the feeding grounds in the northeast to the spawning area in the southeast of the Kerguelen Plateau, probably assisted by a prevailing southward-flowing current (Meissner et al. 1974). South Georgia icefish in spawning condition are found only in inshore waters, whereas those caught offshore are less advanced in their maturation, indicating an onshore-migration movement. Males generally start spawning migrations earlier than females (Kock 1981).

Based on the lack of oil droplets, the eggs of most species are considered to be deposited on the bottom (demersal), or to float loosely on the sea floor (benthopelagic), where they are protected against the lower-salinity surface water and damage by drifting or freezing ice. White et al. (1982) found that the developing eggs of *Notothenia neglecta* at Signey Island are free-floating, but become negatively buoyant after 14 days when they sink to the bottom, whereas those from South Georgia floated throughout the whole period of their embryonic development. Protection by nest-guarding has been described in *Harpagifer bispinis* and *Pagothenia bernacchii* (Daniels 1979; Moreno 1980).

7.4.5 HATCHING PERIOD AND LARVAL DEVELOPMENT

Although the spawning season for most Antarctic fish is relatively short, there is a considerable time lapse between spawning and hatching (Burchett et al. 1983). Burchett et al. (1983) found that the time between spawning and first hatching varied from 60 days in *Notothenia squamifrons* to 270 days in *Chiionodraco* sp. However, hatching primarily occurs in the late winter and spring (August–October) regardless of the spawning timing. Fish spawning in the spring and early summer have a short embryonic period, hatching at the end of summer. Marshall (1953), Everson (1970b), North and White (1982), Burchett (1983a), and Efremenko (1983) all found that the larvae of Antarctic fish species were hatched at a large size and with an average length of 10 mm.

The large size of the larvae is a consequence of the large eggs with ample food reserves. The larger larvae have a smaller food requirement per unit weight, and are capable of swimming more actively in search of food than smaller larvae (Marshall 1953). Even though relatively large, the early postlarvae are able to feed only on the smallest zooplankton (Daniels 1979; Hoshiai and Tanimura 1981; Burchett 1983b). Because these food items, especially larval copepods, are most abundant immediately following the summer phytoplankton bloom, the development of the fish larvae needs to be synchronized such that yolk reserves are used up as copepod larvae become available at peak abundance. Figure 7.6 gives a calendar of events in the early life history of two species, *Harpagifer bispinis* and *Notothenia neglecta*, which fit well with the life cycle of primary production and thus the production of copepod larvae as food.

During the first few weeks after hatching, the larvae do not migrate far away from the spawning area, but remain over the shelves (Efremenko 1983). After they develop into fingerlings, they may disperse away from the continental shelves to deeper water. This dispersal has been recorded in species such as *Notothenia neglecta* (White et al. 1982) and *N. rossii marmorata* (Burchett 1982, 1983a) in the Scotia Sea, where the young fish may be carried by currents into lower latitudes from the South Orkneys and South Shetland Islands to South Georgia and the South Sandwich Islands.

7.4.6 REPRODUCTIVE STRATEGIES

Reproductive strategies of Antarctic notothenioids have been reviewed by Kock and Kellerman (1991) and North and White (1991). Two groups of notothenioids can be distinguished with respect to egg size. The first group comprises species with a moderately high fecundity that spawn numerous smaller eggs, resulting in a large number of larvae. This strategy is common among late winter/spring spawners in the Seasonal Pack-Ice Zone, e.g., *Nototheniops larseni*, *Notothenia gibberifrons*, *N. squamifrons* and *N. kempi*, and *P. antarcticum* in the High Antarctic Zone. Their larvae are small-particle feeders that utilize mainly copepod eggs, nauplei, and copepodite stages, as well as pelagic molluscs such as *Limacina* sp. (Hubold 1985a; Balbontin et al. 1986; Kellerman 1987, 1990a, 1990b). The second group produces

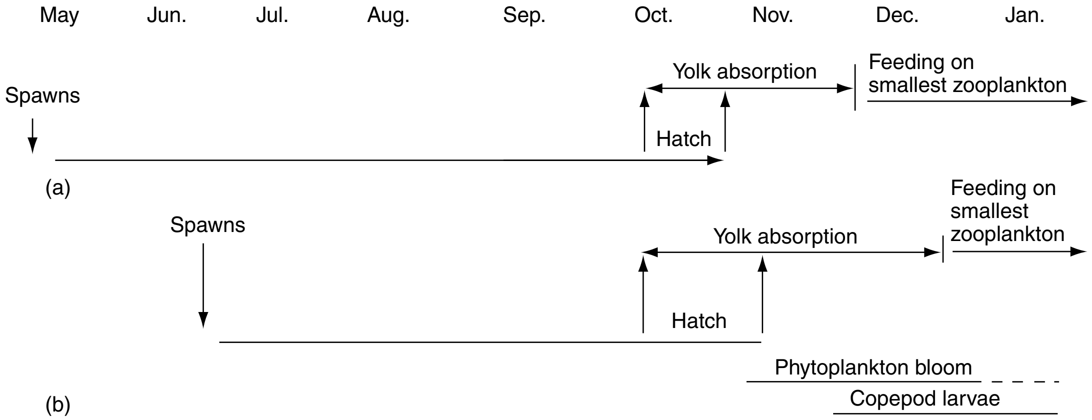


FIGURE 7.6 Schematic representation of egg and larval development of two Antarctic fish; (a) *Notothenia neglecta*, and (b) *Harpagifer bispinis*. (From Everson, I., *Antarctic Ecology*, Vol. 2, Laws, R.M., Ed., 191, 1984b. With permission.)

fewer, larger eggs that release correspondingly large larvae, e.g., icefish, *Trematomus*, and some larger-sized *Notothenia*. Most of these are large-particle feeders. Icefish, for example, commence feeding on larval stages of euphaudiids and fish larvae (Kellerman 1986).

The majority of species hatch in spring and early summer when zooplankton populations increase following the onset of the spring phytoplankton bloom. Spring-hatching larvae originate from eggs spawned from early autumn and exhibit a wide range of lengths at hatching (5–17 mm), indicating that different food-size spectra are utilized by the feeding larvae (Williams 1985b, Balbontin et al. 1986; Kellerman 1986), thus allowing for size-dependent resource partitioning by the abundant co-occurring larvae (Kellerman 1987; Hubold and Ekau 1990). A number of species hatch during the winter. They all have large larvae emerging from large and yolky eggs 4–5 mm in diameter. These larvae have lower relative food requirements and large search volumes so that they can cope with food scarcity under winter ice cover. However, the larvae of some species form part of the cryopelagic community that feeds on the ice algal communities or on the copepod larvae associated with the ice (Knox 1986, 1990). Besides the trophic niche segregation by larval size variation in spring, there exists a temporal sequence of hatching periods by species throughout the summer. This is thought to be related to the sequential reproductive peaks of calanoid copepods (Kellerman 1986, 1987).

7.5 AGE, GROWTH, MORTALITY AND BIOMASS STRUCTURE

7.5.1 Size and Age

Investigations of age are generally carried out by investigation the growth rings of otoliths. To a lesser extent, growth increments in scales have been used. Considerable difficulties have been encountered in such age estimations and age estimates have varied widely between investigators.

The coastal fish fauna is dominated by small species up to 45 cm. Harpagiferids and Artedidracnids (with the exception of some of the *Pogonophora* spp. that grow up to 30–35 cm) are typically less than 15 cm long. Bathydraconids generally do not grow larger than 45 cm. However, the largest species among the coastal fish are found in this family; *Dissostichus eleginoides* and *D. mawsoni* attain maximum sizes of 215 cm (>100 kg) (Duhamel 1987) and 174 cm (ca. 70 kg) (Yukov 1982), respectively. About two-thirds of the channichthyids grow larger than 45 cm.

In the Seasonal Pack-Ice Zone and around the islands north of it, about 45% of the notothenioids attain sizes of more than 45 cm, whereas in the High Antarctic Zone, 90% of the notothenioid species are less than 45 cm long and 65% do not grow larger than 30 cm.

Disregarding epipelagic migrants from the north, the pelagic fauna comprises mostly small forms. Myctophids, with the exception of *Gymnoscopelus* spp. that grow to 15–20 cm, are typically 8–12 cm long (Hulley 1990). Other abundant species, such as *B. antarcticus*, and *Notolepis coasti* attain sizes of 20 and 40 cm, respectively (Gon 1990; Post 1990).

Maximum ages reported for small-sized (20–23 cm) nototheniids, such as *Lepidonotothen larseni*, *L.nudifrons*, or *Patagonotothen guntheri*, in the Seasonal Pack-Ice Zone and around the islands north of it were 8–10 years (Radtke and Targett 1984; Shlibanov 1990). Similar-sized (20–30 cm) High Antarctic nototheniids, such as *P. antarcticum*, *P. borchgrevinki*, or *Trematomus* spp., were estimated to be 25–20 years old (Ekau 1988; Hubold and Tomo 1989).

Chamaesocephalus gunnari, *Chaenocephalus aceratus*, and *Pseudochaenichthys georgianus* at South Georgia, and *Channichthys rhinoceratus* at the Kerguelen Islands, attain ages of 12–15 years (Hureau 1966; Kompowski 1990). Ages of 19–22 years have been recorded for *Nothothenis rossii* and *G. gibberifrons* at South Georgia (Boronin and Frolkina 1976). Ages of more than 30 years have been estimated in *Aethotaxix mitopteryx* from the Weddell Sea (Ekau 1988) and *Dissostichus mawsoni* from the Ross Sea (Burchett et al. 1984). Amongst the myctophids, *Electrona* and *Gymnoscephalus* species live up to five years (Linkowski 1985).

7.5.2 GROWTH

The growth model commonly applied to Antarctic fish has been the von Bertalanffy growth formula. As a result of the variation in age estimates described above, the shape of the corresponding growth curves may vary considerably. Some species, such as *Lepidonotothen squamifrons*, *Harpagifer antarcticus*, *C. gunnari*, *Trematomus bernacchii*, and *P. antarcticum* also exhibit considerable differences in their growth performance between different areas.

Some trends are apparent from the various studies of growth performance (Kock 1992). Growth performance of notothenioids in the Seasonal Pack-Ice Zone and around the islands north if it appear to be higher than in the High Antarctic Zone. However, growth of *P. antarcticum* does not differ between the (warmer) Antarctic Peninsula region and the (colder) Weddell Sea (Hubold and Tomo 1989). Growth performances of *Dissostichus* species and other larger nototheniids and channichthyids are similar to that of North Sea fish. Values of growth performance for two Antarctic myctophids, *E. antarctica* and *Gymnoscopelus nicholsi*, at South Georgia are within the range observed for other myctophids (Linkowski 1985). Hence, growth has evolved some compensation for low temperatures. Although low temperatures probably impose a general constraint on growth in Antarctic fish, other ecological constraints, such as the seasonal food supply, seasonal variations in its energy content (Clarke 1988) and variations in food-particle size, are likely to affect growth rate, growth performance, and maximum size more than temperature. These factors may also largely account for differences in growth performance between species of the Seasonal Pack-Ice Zone and the islands to the north of it and the High Antarctic Zone.

7.5.3 MORTALITY

In common with studies of fish elsewhere, the instantaneous rate of natural mortality (*M*) of Antarctic fish has proved difficult to determine with accuracy. Estimates of natural mortality from both size- or age-dependent and independent methods are available for only some the exploited stocks and for *Notothenia coriiceps* (Everson 1984b), *Trematous newnesi* (Radthe et al. 1989), *Lepidonotothen nudifrons* (Radtke and Hourigan 1990) and *H. antarcticus* (Daniels 1983). Estimates vary widely, for example, in *C. gunnari*, from 0.19 (Pauly 1980) to 0.60 (Beverton and Holt 1956), with corresponding longevities of 24.2–7.7 years. Mortality estimates for *N. rossii* are 0.13 to 0.39. Estimates for two myctophid species were 0.86 (longevity $t_m = 5.3$ years) in *Electrona carlsbergi* and 1.14 ($t_m = 4.0$) in *Gymnoscopelus nicholsi*.

7.5.4 BIOMASS ESTIMATES

Five different methods have been used to calculate the biomass or stock size of Antarctic fish:

1. Production estimates
2. Hydro-acoustic surveys
3. Micronekton net catches
4. The "swept area" method
5. Virtual population analysis (VPA)

Standing stock biomass derived from production estimates has only been calculated once for *N. coriiceps* at Signey Island. The biomass estimate of 194 kg ha^{-1} (19.4 t km^{-2}) was considered to be too high (Everson 1970b).

Results of hydroacoustic surveys have so far been published only for myctophids. Myctophid biomass between 48° and 56°S and 8° and 48°W, which was mostly composed of *E. carlsbergi*, but also included *E. antarctica*, *Gymnoscopelus nicholsi*, *Protomyctophum choriodon*, and *Kreffrichthys anderssoni*, was estimated to be two million tons in the summer-autumn period of 1987–1988 (Filin et al. 1990). The total biomass of Antarctic myctophids has been estimated to be 70–200 million tons (Lubimova et al. 1987). Based on micronekton net catches, the biomass of mesopelagic fish in the marginal ice zone of the Scotia Sea between the surface and 1000 m has been estimated to be 3.27 t km^{-2}.

The "swept area" method extrapolates the mean number of research-vessel catches per unit area swept by the net to the whole area under investigation (Saville 1977). This method assumes a random distribution of fish in the area and 100% efficiency of the gear in catching all the fish in the trawl's path. These assumptions are rarely met. Biomass estimates from VPA and the swept area method suggest that a fish biomass of ca. 750 kt was present on the shelf round South Georgia before the beginning of commercial exploitation in 1969–1970. By 1975/1976, fish biomass was only ca. 40% of the initial value, owing to the removal of *N. rossii*. Fish biomass on the Kerguelen shelf prior to exploitation in 1970/1971 should have been on the order of 420–550 kt, with *N. rossii* and *L. squamifrons* making up 50% and 25% of the biomass, respectively. This would correspond to a biomass of 4–5 t km^{-2}. Since the 1980s, the biomass is unlikely to be considerably more than 125 kt, owing to the low stock sizes of *N. rossii* and *L. squamifrons*.

The maximum stock sizes for single stocks before commercial exploitation could have been:

N. rossii	South Georgia	580 kt
N. rossii	Kerguelen	180–290 kt
L. squamifrons	Kerguelen	120 kt
Patagonotothen guntheri	Shag Rocks	100–200 kt
C. gunnari	South Orkney Is. Antarctic Peninsula	280 kt

Fish biomass in the High Antarctic Zone appears to be one order of magnitude lower that in the Seasonal Pack-Ice Zone and around the islands to the north of it. It has been estimated to be 0.9 t km^{-2} on the shelf of the eastern Weddell Sea and only 0.3 t km^{-2} in Gould Bay in the inner Weddell Sea (Ekau 1990). Stock size of the most dominant species in the Weddell Sea, *P. antarcticum*, was estimated to be 600 kt (Hubold 1991).

7.6 FEEDING ECOLOGY

7.6.1 Feeding Niches and Food Availability

As mentioned previously, although notothenioids are primarily bottom-dwelling species, they have nevertheless occupied a wide range of ecological niches. Table 7.3 lists selected common Antarctic fish species according to their feeding niches. Although the feeding niche of a fish is determined by a complex set of dimensions (habitat, prey species, prey size, etc.), there is a broad vertical distribution of feeding niches. Antarctic fish can be grouped into (1) demersal species (bottom dwellers) feeding on sedentary and motile benthic animals; (2) demerso-pelagic species (above the bottom) feeding on motile benthic animals and nekton swimming above the bottom; and (3) pelagic (free-swimming) species feeding on zooplankton and pelagic larval and adult fish.

Antarctic coastal fish can be roughly segregated into five categories according to their dominant prey:

1. Benthos feeders that feed on the infaunal and epifaunal polychaetes, mollusca, and crustaceans, especially amphipods
2. Fish and benthos feeders that prey on fish, cephalopods, and epibenthic organisms such as mysids and caridean shrimps; typical representatives are *Dissostichus* spp. and *Chaenocehalus aceratus*.
3. Plankton and fish feeders that utilize euphausiids, copepods, pteropods, and fish; typical examples are *N. rossii*, *Pseudochaenichthys georgianus*, and *Chionodraco* spp.
4. Plankton and benthos feeders that rely on euphausiids, salps, hyperiids, and epibenthic organisms such as mysids; typical examples are *L. squamifrons*, *Cygnodraco mawsoni*, and *Eacovitzia glacialis*.
5. Plankton feeders that are primarily dependent on euphausiids, copepods, pteropods, and htperiids; typical representative are *C. gunnari*, *Leoidonotothen larseni*, *Chaenodraco wilsoni*, and *P. antarcticum.*

Food composition of the mesopelagic (200–1000 m) fish is best documented for myctophids. The main prey items of the myctophids, *E. antarctica*, *E. carlsbergi*, *Krefftichthys andersoni*, *Gymnoscopelus braueri*, *G. nicholsi*, and *G. opisthopteris*, were copepods (primarily *Calanus propinquus*, *Metridia gerlachei*, *Calanoides acutus*), euphausiids (mostly *Thysanoessa macrura* and *E. superba*), hyperiids (primarily *Thermisto gaudichaudii*) and pteropods (*Limacina*

TABLE 7.3
Ecotypes of Selected Species of Antarctic Fish Based on Body Morphology, Diet, and Depth of Capture

Demersal fish species	Zone[1]	Demerso-pelagic fish species	Zone[1]	Pelagic fish species	Zone[1]
Raja georgiana	3	*Nototheniops larseni*	2, 3	*Pleuragramma antarcticum*	5,6
R. murrayi	2	*N. rossii marmorata* (adult)	2, 3	*Dissostichus mawsoni*	5, 6
R. eatoni	2	*N. rossii rossii* (adult)	2, 3	*D. eleginoides*	3
Notothenia giberrifrons	2, 3	*P. magellanica*	2, 3	*Micromesistius australis*	3
N. rossii marmorata (juv)	2	*Pagothenia hansoni*	2, 3	*Electrona antarctica*	6
N. rossii rossii (juv.)	2	*T. newnesi*	2, 3	*Gymnoscopelus nicholsi*	6
N. coriiceps neglecta	2	*Champsocephalus spp.*	2, 3	*Notolepis coatsi*	6
N. angustifrons	1, 2	*Chaenocephalus aceratus*	2, 3	Larvae and postlarvae of many fish species and young of *Champsocephalus gunnari* and Myctophidae	
N. kempi	2, 3	*Pseudochaenichthys georgianus*	2, 3		
N. cyanobrancha	2				
N. squamifrons	2, 3				
Paranothenia magellanica	1, 2				
Trematomus spp.	2, 3				
Harpagifer spp.	1, 2				
Artedidraco spp.	2, 3				
Pogonophyrne spp.	3, 4				
Muraenolepis microps	2, 3				
Psilodraco breviceps	2				
Pseudochaenichthys spp.	2				
Channichthys rhinoceratus	2				
Chionodraco spp.	2, 3				

[1] Zone 1, littoral, 0–3m depth; Zone 2, sublittoral, 3–200m depth; Zone 3, archidemersal, 200–1000m depth; Zone 4, abyssodemersal, 1000+m depth; Zone 5, epipelagic, 0–200m depth; Zone 6, mesopelagic, 200–1000m depth.

Source: From Bengston, J.L., *Selected Papers Presented to the Scientific Committee of CCAMLR 1987–1984*, Part 1, CCAMLR, Hobart, 1–226, 1985a. With permission..

spp.) (Lubimova et al. 1987; Kozlov and Tarverdiyera 1989). Among the other abundant mesopelagic fish, *Notolepis coasti* and *N. antarctica* probably fed primarily of *E. superba*. Pelagic early life stages of notothenioids rely primarily on copepods, pteropods, and fish larvae as food. Larval and postlarval nototheniids and *Harpagifer* spp. are small-particle feeders preying on copepod eggs, nauplei, copepodites, small cyclopoid and calanoid copepods, pteropods, and tintinnids.

As discussed above, the development of yolky eggs over the winter allows the larval fish to hatch at an advanced stage that coincides with the phytoplankton bloom and abundant zooplankton grazers, especially copepods. Many of the zooplankton species that the pelagic fish feed on spend their summer months in the epipelagic zone (0–200 m) and the winter period (May–August) in deeper water or under the ice (David 1955, 1958,1965; Hopkins 1971). Both demersal and pelagic fish benefit from the vertical migration and swarming behavior of the invertebrate zooplankton. In the winter, the deeper-depth distribution of the zooplankton brings them near the sea bottom in shallow areas on the continental shelves. This allows both the demersal and demerso-pelagic fish to prey on the zooplankton not available to them at other times of the year (Kompowski 1980a; Naito and Iwami 1982).

In the summer, zooplankton abundance in the surface water increases as a consequence of vertical migration (Foxton 1956) and reproductive and growth cycles. Many pelagic fish, especially in their larval and juvenile stages, feed on the concentrated zooplankton at this time. For example, juvenile *C. gunnari* is often a by-catch species in krill harvesting (Kompowski 1980b). Krill, salps, gammarid amphipods, and hyperiids are often found in the stomachs of demersal and demerso-pelagic fish such as *Notothenia kempi*, *N. gibberifrons*, *N. rossii*, *Chaenocephalus aceratus*, and *Chionodraco* spp. (Permitin and Tarverdiyera 1972, 1978). When the epipelagic concentration of summer zooplankton (especially in the top 50 m) extends into the nearshore sublittoral zone, they become available to demersal species present in that zone. Pelagic zooplankton have been identified in the stomach contents of *N. rossii* juveniles in the nearshore waters of South Georgia (Hoshiai 1979) and krill are a common item in the diet of *N. gibberifrons* from the shallows of the South Shetland Islands (Takahashi 1983).

Demersal fish, as well as some demerso-pelagic species, feed principally on benthic invertebrates (polychaetes, molluscs, and amphipods) (Targett 1981; Burchett et al. 1983). Typical examples are *Gobionotothen acuta*, *Indonotothenia cyanobranchia*, and *Paranotothenia magellanica* in the Ice-Free Zone and *T. bernacchii* and *Dolloidraco longedorsalis* in the High Antarctic Zone. The species composition of the benthic community varies with depth, substrate, and to a lesser extent with season (Daniels 1982); this is reflected in the diets of the fish. Many infaunal species are unavailable to the fish, with the possible exception of *N. gibberifrons* (Moreno and Osorio 1977). The epifaunal invertebrates are important prey items for most of the benthic fish and are available year-round (Burchett 1983).

Krill are a major component of the diet of demersal, demerso-pelagic, and pelagic Antarctic species. Table 7.5 compares the importance of krill in the diet of seven Antarctic fish species. The percentage composition ranges from 1.8% to 100%; in the same species, it varies according to the time of the year and the availability of krill.

7.6.2 Niche Changes Over the Life Cycle

A number of species change their feeding niche at least once during their life-cycle. For example, *N. rossii mamorata* spends the first year after hatching in subsurface water far from the coast, feeding on krill and copepods. They then migrate towards the coasts and live for the next five to six years close to the bottom in nearshore kelp beds where they feed primarily on amphipods. Hoshiai (1979) found that at South Georgia, juvenile *N. rossii mamorata* feed on hyperiid amphipods, gammarid amphipods, a shrimp (*Chorismus antarcticus*), an epitokous nereid polychaete (*Neanthes kerguelensis*), the fry of two species of fish, *N. rossi mamorata* and Bathydraedonidae sp., algae, and ctenophores (Hureau 1970; Burchett 1983a; Linkowski et al. 1983). After attaining maturity, they leave the inshore waters for the offshore feeding grounds at 150–300 m depth from where they ascend into the midwater zone to feed on krill, fish, and salps (Latogurskij 1972; Tarverdiyeva 1982; Checnun 1984; Duhamel 1987).

7.6.3 Feeding Behavior

The demersal and demerso-pelagic fish show great diversity in feeding behavior and the type of prey consumed (Richardson 1975; Targett 1981; Daniels 1982; Takahashi 1983). Diversity in diet and feeding is greatest among demersal and demerso-pelagic nototheniids, especially in nearshore communities under 90 m deep (Burchett 1982; Burchett et al. 1983). Demersal nototheniids feed primarily on amphipods, isopods, fish (mostly larvae, postlarvae, and young fish), polychates, decapods, gastropods, and bivalves (Targett 1981; Daniels 1982; Linkowski et al. 1983; Takahashi 1983). Studies on channichthyids by Permatin and Tarverdiyera (1978b) and Daniels (1982) have demonstrated that they are specialized feeders. Most channichthyids are planktivorous feeders, with the exception of *Chaenocephalus aceratus* and *Channichthys rhinoceratus*, which consume a high proportion of fish (Hureau 1970; Williams 1983).

In addition to ontogenetic shifts in the composition and size of the prey, considerable variations in food consumption can exist both locally and seasonally. Figure 7.7 illustrates the temporal variation in the proportion of the three major prey items of *C. gunnari* around South Georgia. Although *E. superba* was the dominant prey item in most years, the proportion of hyperiid amphipods and mysids varied from year to year.

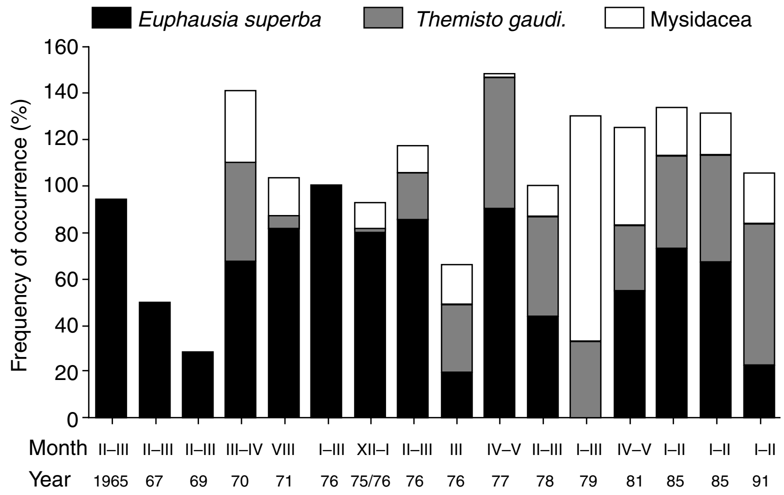


FIGURE 7.7 Temporal variation in the proportion of the three major prey items of *Champsocephalus gunnaru* around South Georgia. The proportion of prey items is based on the "frequency of occurrence" method. Data sources: Permitin and Traverdiyeva 1972; Linkowski and Rembiszewski 1979; Kompowski 1980a; Kock 1981; Wilhelms 1986, 1988; Kock et al. 1992. (From Kock, K.H., *Antarctic Fish and Fisheries*, Cambridge University Press, Cambridge, 135, 1992. With permission.)

The most extensive studies of the feeding behavior of Antarctic fish have been carried out in nearshore waters in depths of 0–70 m. Around islands such as South Georgia and Kerguelen, the shallow, nearshore areas with depths of 0–30 m are often dominated by brown algae such as *Macrocyctis pyrifera*, *Himanothallus grandifolius*, and *Durvillaea antarctica* (Burchett 1982; Duhamel 1982), which provide a specialized habitat, not only for fish, but also for their prey. Burchett et al. (1982) and Burchett (1983c), working at South Georgia, found that much of the benthos upon which the fish feed were nocturnally active. SCUBA-diving observations and net hauls confirmed that the fish were also active only at night.

Linkowski et al. (1983) investigated the food habits of five species of Nototheniidae (*Notothenia neglecta*, *N. rossii mamorata*, *Trematomus newnesi*, and *P. antarcticum*). The diets of the first three species were benthic organisms with amphipods (especially representatives of the families Lysianassidae and Eusiridae), 79–82.9% for *N. neglecta* and 79–75.6% for *N. rossi mamorata*. While the diet included polychaete worms, amphipods, isopods, and gastropods, pelagic salps made up 41.9% of the total number of stomach components and 70.7% by weight. *T. newnesi* fed principally on *E. superba*, which, over the summer, comprised 94.5% of the stomach contents by weight.

La Mesa et al. (2004) have reviewed the role of notothenioid fish in the food web of the Ross Sea shelf waters (Figure 7.8). Here, notothenioids dominate the fish fauna comprising 76.6% of the species, 91.6% of the abundance, and 91.2% of the biomass. Unlike the linear phytoplankton the *E. superba* consumers of the *E. superba* food chain hypothesized for much of the Southern Ocean, the food web of the Ross Sea is nonlinear, with complex prey-predator interactions. Notyothenioid fish play a key role as predators: they occupy most of the trophic niches available in the ecosystem, relying on benthic, zooplanktonic, and nektonic organisms as prey. They are an important food resource for each other and for most of the top predators living on the shelf. This is especially true for *P. antarcticum*, which constitutes >90% of the midwater fish fauna. Along with *E. crystallorophias*, its ecological role in the Ross Sea is equivalent to that of myctophids and *E. superba* elsewhere in the Southern Ocean.

South Polar Skuas, Antarctic Petrels, Adélie and Emperor Penguins, Weddell Seals, and Minke and Killer Whales are the higher vertebrate components of the food web, and all prey on notothenioids to some extent. Based on the frequency of occurrence of prey items in the stomachs of fish, bird, and mammal predators, *P. antarcticum* and *E. crystallorophias* are the key species in the food web of the Ross Sea. *P. antarcticum* is a component of the diet of at least 11 species of nototheniids, bathydraconid and channichthyid fish; at frequencies of occurrence from 71% to 100%, *P. antarcticum* especially important for *Dissotichus mawsoni*, *Gvozdarus svetovidovi*, and some channichthyids. At least 16 species of notothenioids serve as prey for bird and mammal predators. *P. antarcticum* is the most important and is a major component of the diet of the South Polar Skua, Adélie and Emperor Penguins, and Weddell Seals at a frequency of occurrence from 26 to 100%. *E. crystallorophias* is consumed by some nototheniid and channichthyid fish and is also of importance in the diet of Emperor and Adélie Penguins.

Around Kerguelen and South Georgia, *N. neglecta* actively graze on the macroalgae that appear to be an important dietary component at certain times of the year (Burchett 1983c; Burchett et al. 1983). Algal consumption has also been observed by Everson (1970a), Hureau (1970), Daniels (1982), and Linkowski et al. (1983) for equivalent subspecies at the South Orkney Islands, South Shetland Islands, and the Antarctic Peninsula.

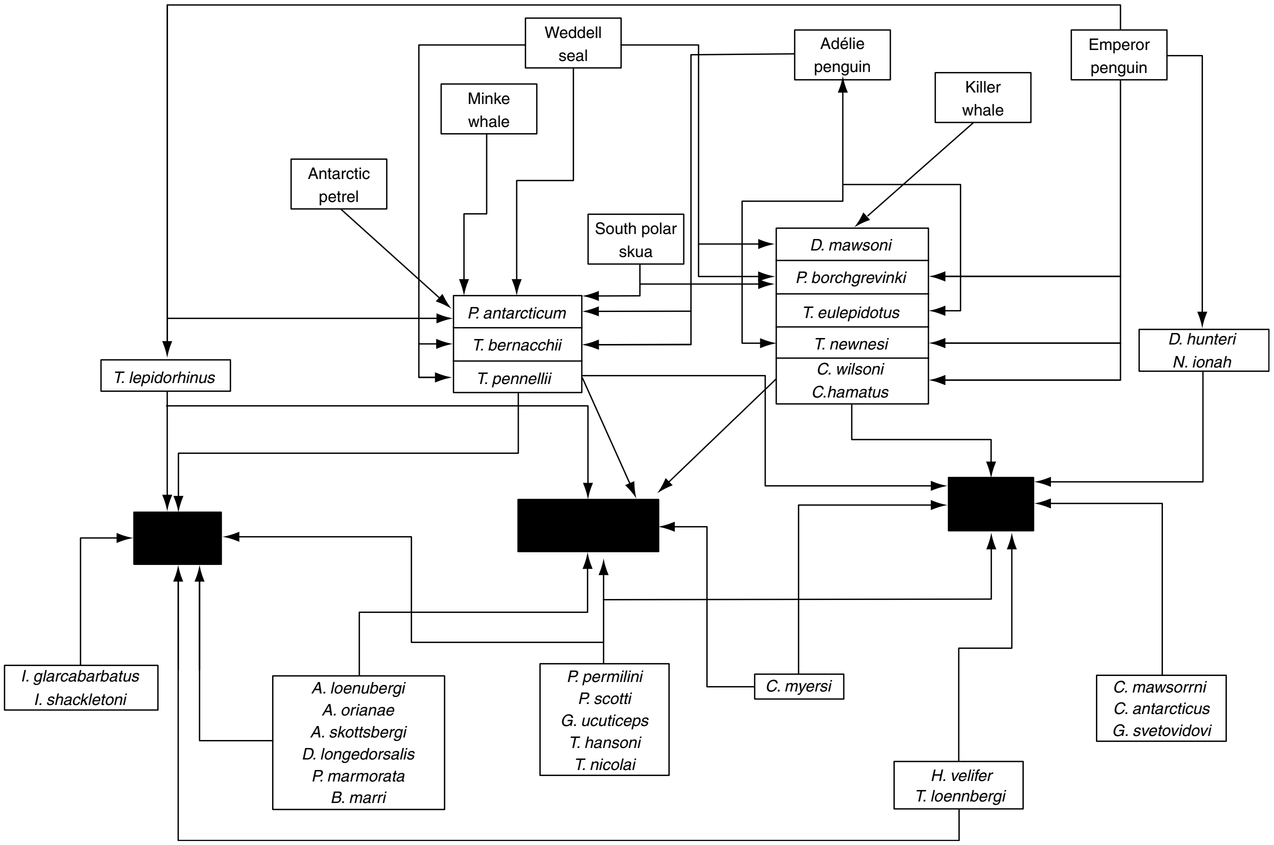


FIGURE 7.8 Diagram showing the position of notothenioid fish in the food web of the Ross Sea. (From La Mesa, M., Eastman, J.T., Vacchi, M., *Polar Biol*., 27, 353, 2004. With permission.)

Diets for individuals of the same species vary between localities (Rowedder 1979; Naito and Iwami 1982; Linkowski et al. 1983). For example, with *Notothenia gibberifrons*, *Notothenia larseni*, *Trematomus scotti*, and *Harpagifer bispinis*, individuals of similar size caught at the same time of the year but at different localities have significant differences in prey taken and the amount of food eaten (Daniels 1982). Richardson (1979) at the South Orkney Islands investigated the feeding habits of *N. neglecta* in shallow water (1–20 m) and found that the diet consisted of benthic animals (amphipods, gastropods, bivalves) and did not record any pelagic species. On the other hand, Permitin and Tarverdoyera (1978a) studied samples from deeper water (down to a depth of 170 m or more) and noted a predominance of pelagic animals (*E. superba*, fish, hyperiid amphipods) in their diet.

Differences in the diets of fish of different sizes have also been noted by a number of authors for many species, including *P. antarcticum* (DeWitt and Hopkins 1977). *Pogonophyrne* sp. (Wyanski and Targett 1981), *N. gibberifrons*, *C. gunnari* (Takahashi 1983), *P. magellanica* (Blankley 1982), *N. neglecta* (Showers et al. 1977) and *Dissostichus eleganoides* (Duhamel and Pletkowsic 1983). In all these species, prey size, prey quantity consumed, and numbers of different prey types taken increased with fish size.

Seasonal changes have also been reported in the diets of many demersal and demerso-pelagic fish. Burchett (1983c) found that juvenile *N. rossii* have a more varied diet over the summer months. There were definite seasonal variations in the numbers of amphipods, bivalves, and polychaetes consumed. (Daniels 1982) found differences in the composition of the diet and amount of food consumed in similar-sized individuals of *N. gibberifrons*, *Notothenia nudifrons*, *Nototheniops larseni*, and *T. scotti* collected at the same time at different times of the year.

Eastman (1985a) examined the stomach contents of nine species of notothenioid fish near the southern limit of their range in ice-covered McMurdo Sound (Figure 7.9). Pelagic species with reduced or neutral buoyancy fed exclusively on nektonic organisms. *P. borchgrevinki* fed in the platelet ice layer on the underside of the sea ice and in the water beneath the ice, predominantly on small (2–3 mm) copepods and amphipods. *Dissistichus mawsoni*, the largest Antarctic fish, was a neutrally buoyant midwater predator that ate primarily fish and mysids. *Pleurogrmma antarcticum* was a shoaling midwater species that ate copepods, mysids, and other fish. *Gymnodraco acuticeps* was predominantly piscivorous, with amphipods and fish eggs being the only other significant food items in the diet.

The other six species were trophic generalists confined primarily to benthic habitats. *Pagothenia bernacchii*,

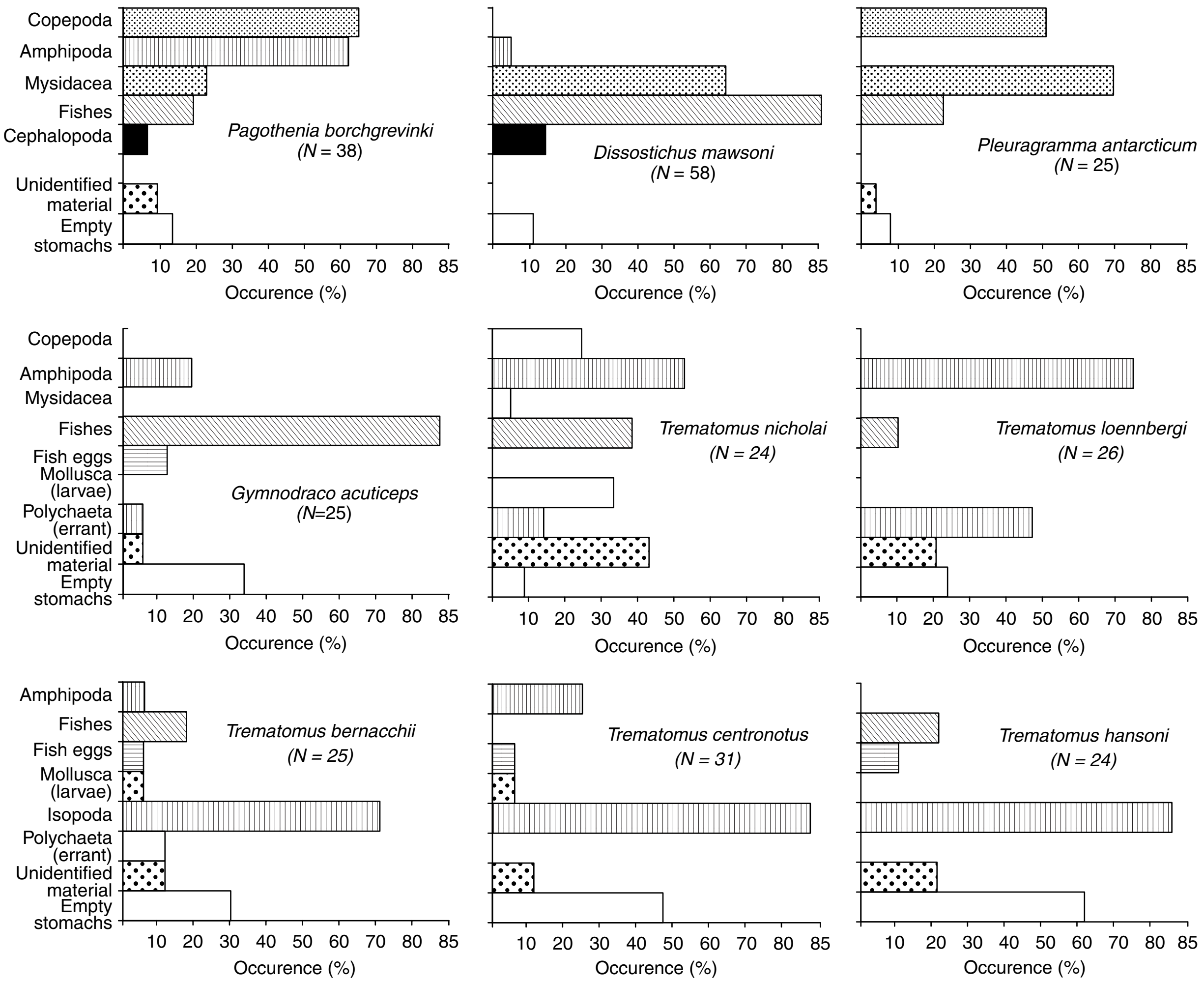


FIGURE 7.9 Diets by percentage frequency of occurrence for nine species of notothenioid fish from McMurdo Sound. (From Eastman, J.T., *Antarctic Nutrient and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 430–456, 1985a. With permission.)

Trematomus centronotus, and *P. hansoni*, for example, were typical benthic species that fed primarily on errant polychaetes. *T. nicholai* was a shallow-water benthic species that preyed actively on moving organisms (copepods, amphipods, small fish, molluscs and errant polychaetes), some of which may have been captured in the water column. *T. loennbergi* fed predominantly on amphipods and errant polychaetes.

One of the interesting findings of this study was that fish, especially *Pleurogramma*, were of wide occurrence in the diets of McMurdo fish. Fish were a dietary item in eight of the nine species, and two of these eight species, *Dissostichus* and *Gymnodraco*, were predominantly piscivorous. *Pleurogramma* was the most common prey species consumed, being present in four of the eight species, including *Pleurogramma*. In the Ross Sea, *Pleurogramma* ate copepods and adult euphausiids, with copepods dominant by number and euphaudiids by weight (DeWitt and Hopkins 1977). Near the Antarctic Peninsula, euphausiids are most important in the diet, both by number and volume (Daniels 1982). In the northern part of the Weddell Sea, small *Pleurogramma* consumed copepods, polychaetes, and chaetognaths (Kellerman and Kock 1984). In the southern and eastern Weddell Sea, the most abundant food items in the diet by number were copepods, gastropods, and euphausiids, with euphausiids dominant by weight (Hubold 1985b) (Figure 7.10). In Prydz Bay, East Antarctica, copepods and larval euphausiids were the most important dietary item by weight (Table 7.4) (Williams 1985b). Fish are, in general, present in the diet of *Pleurogramma* only as incidental items (Hubold 1985b; Williams 1985b). In contrast, Eastman (1985b) found that in the inner McMurdo Sound fish constituted 22% of the diet by occurrence, including 13% cannibalism. The heavy cover of ice and the reduction in euphausiid abundance are probably the reasons for this difference.

The Antarctic silverfish, *P. antarcticum*, is the only true pelagic fish among the Notothenioidea (Andriashev 1965) (Figure 7.10). In the Ross Sea, the pelagic fish fauna is dominated by this species (Granata et al. 1998) (92% in numbers and 96.7% in biomass), and northern midwater fish, such as myctophids, are excluded from the area by the steep temperature gradient over the edge of the outer shelf (DeWitt

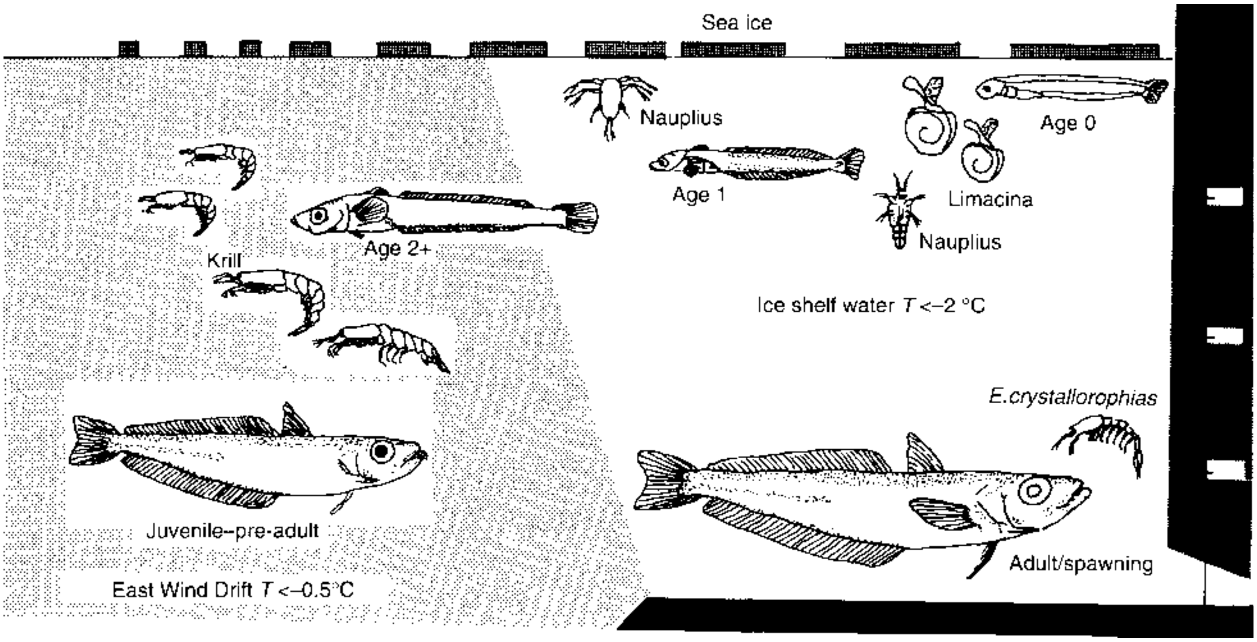


FIGURE 7.10 Schematic life cycle of *Pleurogramma antarcticum* in the Weddell Sea. (Redrawn from Hubold, G., *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 445, 1985a. With permission.)

1970). In the Weddell Sea in 1979–1980, 95% of the larval fish taken in bongo nets were *P. antarcticum* (Hubold 1985a). The importance of this species as food for predatory vertebrates is reflected in its occurrence in their diet. It is present in the diet of all McMurdo Sound fish that either live in the water column or rise from the bottom to feed in the water column (Eastman 1985b). It is the main food of the Antarctic cod (*D. mawsoni*) (Eastman and DeVries 1981), and is also an important component of the diet of Weddell Seals (*Leptonycotes weddelli*) (DeWitt and Tyler 1960; Dearborn 1965b; Testa et al. 1985), of whales (Andriashev 1965), of Gentoo (*Pygoscelis papua*), Adélie (*P. adeliae*), and Emperor (*Aptenodyptes forsteri*) Pengiuns (Norman 1937; Emerson 1968; Volkman et al. 1980), of South Polar Skuas (*Catharacya maccormicki*) (Young 1963b), and of Antarctic Petrels (*Thalassoica antarcticus*) (Hubold 1985b). Emerson (1968) noted that Adélie Penguins can live successfully and rear chicks in areas nearly devoid of euphausiids if the water is rich in *Pleurogramma*.

Sabourenkov (1990) has reviewed Soviet research on the feeding of myctophids. Their diet in open waters in both winter and summer consists primarily of certain species of copepods. Myctophids of the 5–11 cm length group feed exclusively on small planktonic organisms. Larger myctophids, such as *E. antarctica* and *Gymnoscephalus nicholsi*, also take macroplanktonic organisms, including *E. superba*.

7.6.4 KRILL CONSUMPTION BY ANTARCTIC FISH

A number of studies (e.g., Latogurskij 1972; Permitin and Tarveridiyera 1972; Tarveridiyera 1972, 1982; Naumov and Permitin 1973; Rowedder 1979; Kompowski 1980a; Lubimova and Shust 1980; Tarveridiyera and Pinskaya 1980; Kock 1981, 1985; Checkunova and Naumov 1982; Takahashi 1983; Williams 1985b) have shown that krill are an important component of the diet of Notothenioidea, especially those nototheniids and channichthyids that are adapted for temporary or permanent pelagic life. Kock (1985) studied the feeding ecology and food intake of four species of channichthyid fish (*C. gunnari*, *C. aceratus*, *Pseudochaenichtjys georgianusm*, *Chionodraco rastrospinosus*) and three nototheniids (*Notothenia rossi mamorata*, *N. gibberifrons*, *N. larseni*) in western Antarctic waters off South Georgia. Data from South Georgia are summarized in Table 7.5. Although *C. rastrospinosus* consumes krill in other Southern Ocean localities, it did not do so at South Georgia. The proportion of krill found in the diets of these species ranges up to 100%. For the purposes of calculating the amounts of krill consumed, Kock (1985) estimated the weight percentages at 50% for *N. rossi*, *C. gunnari*, and *N. larsenim*, 10% for *C. aceratus*, and 60% for *C. rastrospinosus* and *P. georgianus*. Before the onset of commercial exploitation, the total consumption of krill by the seven species off South Georgia was probably 5×10^6 t y^{-1}. *N. rossi* and *C. gunnari* probably accounted for more than 80% of this annual consumption. Due to the substantial reduction in the stock sizes of the fish due to commercial harvesting, the consumption of krill by fish has declined markedly (Table 7.5) (e.g., for *N. rossi* from an estimated 160.8×10^3 before exploitation to 9.3×10^3 t in 1980–1981).

Consumption of euphausiids (mainly *E. superba* and *E. crystallorophias*) by fish inhabiting Antarctic shelf waters has been estimated at 24–29$\times 10^6$ t y^{-1} (Lubimova and Shust 1980). Consumption by the ice fish *C. gunnari* in western Antarctic waters has been assessed at 3–4$\times 10^6$ t in 1975–1976 (Kock 1981).

TABLE 7.4
Stomach Contents of Pelagic Fishes in the Region of Prydz Bay. Data for Food Items are Given as Percentage by Number and Percentage by Weight (e.g., 18.31; 0.22)

	Gymnoscopelus nicholsi	Gymnoscopelus brauerei	Notolepis coatsi		Cryodraco antarcticus		Pagetopsis macropterus		Chaenodraco wilsoni		Electrona antarctica		Krefftichys anderssoni		Pleuragramma antarcticum		Trematomus scotti		Trema tomus sp.	
Polychnetes	–	–	18.31	0.22	–	–	–	–	–	–	1.49	0.14	–	–	0.08	1.23	–	–	–	–
Chaetognaths	–	–	36.52	0.50	–	–	–	–	–	–	0.83	0.15	–	–	–	–	–	–	–	–
Ostracods	–	–	–	–	–	–	–	–	–	–	2.81	0.33	–	–	–	–	–	–	–	–
Copepods	40.91	2.87	12.68	0.72	–	–	–	–	–	–	47.85	12.02	76.22	64.58	64.21	48.28	48.81	76.78	98.11	90.08
Amphipods	18.19	5.75	–	–	–	–	–	–	–	–	7.45	27.24	1.11	4.58	–	–	–	–	–	–
Euphausiids																				
Euphausia superba	27.27	89.98	28.17	96.24	50.0	97.92	–	–	–	–	0.99	12.26	–	–	9.16	4.45	–	–	–	–
E. crystallorophias	–	–	–	–	–	–	60.0	22.53	37.5	73.68	–	–	–	–	20.97	17.83	–	–	–	–
E. frigida	–	–	–	–	–	–	–	–	–	–	0.99	2.80	–	–	–	–	–	–	–	–
Thysanoessa macroura	13.64	2.40	12.68	0.72	–	–	–	–	–	–	5.13	7.80	22.20	23.76	–	–	–	–	–	–
Unidentified euphausiids	–	–	–	–	–	–	20.0	68.0	62.5	26.32	4.80	5.66	–	–	–	–	51.19	23.21		
Total euphausiids	40.91	92.38	40.85	96.96	50.0	97.92	80.0	90.53	100.00	100.0	11.91	28.52	22.20	23.76	30.13	22.28	51.19	23.21		
Decapods	–	–	1.41	3.27	–	–	–	–	–	–	5.46	1.01	–	–	–	–	–	–	–	–
Crustaceans unidentified	–	–	–	–	50.0	2.08	–	–	–	–	8.11	6.79	0.048	0.05	0.17	0.70	–	–	–	–
Molluscs	–	–	–	–	–	–	–	–	–	–	6.29	18.19	–	–	0.18	2.46	–	–	1.26	6.11
Fish	–	–	–	–	–	–	20.0	9.6	–	–	0.33	0.47	–	–	0.60	20.88	–	–	–	–
Unidentified remains	–	–	–	–	–	–	–	–	–	–	7.45	3.10	4.36	7.64	–	–	–	–	0.63	3.82

Source: From Williams, R., *Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, Heidleberg, 452–459, 1985b. With permission.

TABLE 7.5
Consumption by Six Notothenioids Around South Georgia

	Krill Consumption (1×10^1)		
Species	**1975–1976**	**1977–1978**	**1980–1981**
Notothenia rossii	160.8	42.0	9.3
N. gibberifrons	18.0	9.0	5.5
Nototheniopsis larseni	1.0	0.9	—
Champsocephalus gunnari	630.0	156.2	354.0
Chaenocephalus aceratu	33.7	33.1	12.4
Pseudochaenichthys georgianus	131.0	11.8	27.9
Total	974.5	253.0	409.1

Source: From Kock, K.-H., *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, Heidelberg, 437, 1985. With permission.

The relationship between euphausiids and pelagic fish has been less intensively studied. There is general information on the diets of *Notolepis coasti* (Solynik 1965), *E. antarctica* (Solynik 1967) and various species caught in the Scotia Sea area (Rembiszewski et al. 1978). More information is available on the diet of *P. antarcticum* (DeWitt and Hopkins 1977; Rowedder 1979; Gorelova and Gerasinchuk 1981; Eastman 1985b; Hubold 1985b; Granata et al. 1998). The most comprehensive study of the feeding habits of pelagic fish is that of Williams (1986b) in the Prydz Bay region, East Antarctica. Ten of the eleven species studied had euphausiids as a significant component of their diet. Only *Trematomus* sp. juveniles had no euphausiids in their stomachs. The other ten species fell into three groups on the basis of the contribution of euphausiids to their diet. In the first group that included *N. coatsi*, *Gymnoscopelus* spp. and the juveniles of *Cryodraco antarcticus*, *Pagetopsis macropterus* and *Chaenodraco wilsoni* euphausiids were the dominant part of the diet (30–100% by number and 90–100% by weight), with other prey being definitely secondary. The second group contains the general plankton feeders in which euphausiids formed a major part (12–52% by number and 23–26% by weight), but are secondary to copepods (35–76% by number and 48–79% by weight) (*P. antarcticum*, *K. andersoni*, and *T. scotti*) or codominant with copepods and amphipods (*E. antarctica*). The last group comprises *Chionodraco* sp., in which fish predominated in the diet (55%). Thus the commonly encountered fish in the Prydz Bay region depended heavily on euphausiids, and in some areas specifically on *E. superba*, for their food. While the large fish take adult krill, there is a significant predation by juvenile fish on the younger stages of krill. Estimates of the importance of krill in the diets of seven Antarctic fish species are given in Table 7.6. It can be seen that krill consumption differed between the regions, ranging from 3.7 to 100%. In genera, consumption is highest in the mid-Antarctic region, ranging from 38.5 to 100%.

7.6.5 FEEDING COMMUNITIES

It is clear from the above discussion that a number of different pelagic and benthic feeding communities can be distinguished (Kock 1984).

1. A *cryopelagic community* closely associated with drifting or fast ice in Antarctic high latitudes, formed mainly by juvenile and adult *Trematomus* spp. that feed on ice-associated amphipods and copepods. The fish cling to the undersides of the ice when resting and hide in ice crevices and holes when disturbed. Other fish that feed on the ice-associated organisms and in the top few meters of the water column include the pelagic nototheniid *P. borchgrevinki* and juveniles of *Pleurogramma antarcticum* (Bradfield 1980; Eastman 1985b; Hubold 1985b; Knox 1986).
2. A specific *epipelagic krill-fish community* has been suggested by several authors because about 40 notothenioid and mesopelagic species have been encountered in association with krill swarms. This community is composed mainly of juvenile notothenioids living at the border of swarms, and of various icefish, Antarctic cod, and mesopelagic species that undertake temporary and regular migrations from the bottom or deeper layers to subsurface waters to feed on krill (Efremenko 1983; Williams 1985b). This vertical migration has been confirmed by echo sounder and visual observations (Olsen 1955; Basalaev and Petuchov 1969). Efremenko (1983) reports that the most frequently encountered mesopelagic species in the Scotia Sea were eight species of the families Myctophidae (*Elecrtona antarctica*, *K. andersoni*, *Protomyctophum bolini*, *Gymnoscopelus baureri*, *G. nicholsi*, *G. opsthopterus*), Bathylagididae (*B. antarcticus*) and Paralepidae (*N. coatsi*). These fish spawn at a depth below 200 m and all their eggs and prelarvae have been collected between 200 and 1000 m. The vertical distribution of the larvae and prelarvae depends on the season. At the end of autumn and during the winter they are present in the warmer waters below 200 m, but in the spring and summer they are also found in the surface waters (0–100 m). The larval stages of 27 notothenioid species have been found over the continental shelf between 0 and 200 m. These larval notothenioids all feed on zooplankton, including the larval stages of euphausiids.
3. Various *nearshore* and *offshore benthic* and *benthopelagic communities* have been distinguished by several authors (Richardson 1979; Targett 1981; Takahashi 1983). The dominant species in each

TABLE 7.6
Estimates of the Importance of Krill in the Diet of Antarctic Fish

Species	Locality	Percentage of Krill		Source
Notothenia rossii	W.A.	F	90–100	3,4, 6, 8, 14, 19
	S.G.	F	15.2–90.4	5, 10, 11, 12, 13
	S.G.	B	40.2–56.2	1, 5, 9, 15
Champsocephalus gunnari	W.A.	F	90–100	3, 5, 6, 8, 14, 19
	W.A.	B	95	5, 16, 18
	S.G.	F	18.1–94	5, 10, 11, 12, 13
	S.G.	B	42–90	1, 5, 9, 15
Nototheniopsis larseni	S.A.	F	20.6–95	2, 13, 14, 16, 19
	W.A.	B	38.5–92	15, 16, 17
Notothenia gibberifrons	W.A.	F	22.2–97.6	11, 13, 14, 16
	S.A.	B	3.7–5.7	15
	S.G. (winter)	B	18	1
Chionodraco rastrospinosus	W.A.	F	98.1	19
Chaenocephalus aceratus	W.A.	B	10–90	7
Pseudochaenichthys georgianus	S.G.	F	25–87.4	7
	S.A.	F	38.5–100	7
	W.A.	B	>60%	5, 11, 14, 19

1, Chekunova and Naumov (1982); 2, Daniels (1982); 3, Freytag (1977); 4, Gubsch (1979); 5, Kock (1981); 6, Kock (1982); 7, Kock (1985); 8, Kock et al. (1985); 9, Kompowski (1980a); 10, Latogurskij (1972); 11, Linkowski and Rembiszewski (1978); 12, Naumov and Permittin (1973); 13, Permittin and Tarverdiyera (1972); 14, Permittin and Tarverdiyera (1978); 15, Rowedder (1979); 16, Takahashi (1983); 17, Targett (1981); 18, Tarverdiyera (1982); 19, Tarverdiyera and Pinskaya (1980); W.A., West Antarctica; S.G., South Georgia; S.A., Scotia Arc; F, frequency of occurrence; B, biomass.

Source: From Kock, K.-H., *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, Heidelberg, 437, 1985. With permission.

community partition the prey resources by vertical separation. Prey overlap is low in some of the nearshore communities, but may be high in offshore communities where krill is at least temporarily abundant, forming the staple food of most species. In these situations, krill is a nonlimiting resource and thus interspecific competition is reduced to a minimum (Takahasi 1983). Off South Georgia, for example, where krill is only temporarily abundant, the icefish *Champspcephalus gunnari* and *Pseudochaenichthys georginus* feed almost exclusively on krill when it is available. When a shortage of krill occurs as it did in 1988–1978, *C. gunnari* substituted part of their diet with hyperiids and mysids and *P. georgianus* increased the proportion of fish in their diet (Kock 1981).

Many benthic feeding species, such as the plunder fish and some of the Antarctic cod, generally take the same species; it therefore appears that there could be competition for the same food resource. However, interspecific competition is reduced as the various species take different proportions of the same prey species. For example, in morphologically similar *N. gibberifrons* and *Nototheniops nudifrons*, the former primarily exploits sedentary polychaetes while the latter feeds on errant polychaetes (Targett 1981).

In addition to the resident species preying on krill, a considerable number of species migrate from north to south of the Polar Front into Antarctic waters in the summer to feed on krill. Various mesopelagic species, such as the daggertooth *Anotopterus phargo*, the paralepid *Notolepis rissoi*, the nototheniid *Paranotothenia magellanica*, and part of the population of the southern blue whiting *Macromesistius australis*, undertake such migrations from the Patagonian shelf.

An alternative classification is that of Kock (1992), who distinguishes three principal shelf trophic systems: inshore sublittoral systems, inshore deep-water systems, and offshore systems:

1. *Inshore sublittoral systems*. This system (depth less than 30 m) is characterized by areas of sand and mud with boulders and stones harboring somewhat dense beds of macroalgae. Principal prey organisms are lysianassid and eusirid amphipods, isopods, decapods (*C. antarcticus*), molluscs, and fish (Hureau 1970; Moreno 1971; Moreno and Bahamonde 1975; Richardson 1979; Burchett et al. 1983).
2. *Inshore deep-water systems*. These comprise the deeper parts (less than 30 m) of the fjords and bays where a sparse covering of filamentous algae and diaoms in the upper parts gives way to bare mud as the depth increases. Major prey organisms are

nudibranchs, gastropods, ophiuroids, large scavenging amphipods, and caridean shrimps (*Notocrangon antarcticus*) (Burchett et al. 1983).

3. *Offshore systems.* These include the entire shelf of the islands and the continent. Main prey organisms on the bottom are amphipods, molluscs, and fish, but more important (at least seasonally) are prey organisms in the water column. These include copepods, hyperiids, euphausiids, and pelagic fish. Staple food of pelagic species around the Kerguelen Islands is *Thermisto gaudichaudii*, *Euphausia frigida*, and *E. vallentini*, and myctophids (Chechun 1984; Duhamel 1987). Principal pelagic prey items in the Scotia Arc and the Antarctic Peninsula are *E. superba* and fish and around South Georgia to some extent *T. gaudichaudii*, mysids and salps (Permitin and Traverdiyeva 1978a, 1978b; Kock 1981; Targett 1981; Takahashi 1983), *E. crystallorophias*, *P. antarcticum*, copepods. To some extent also krill form the main pelagic prey in the High Antarctic Zone (Kock et al. 1984; Takahashi and Nemoto 1984; Eastman 1985a, 1985b; Schwarsbach 1988).

The trophic communities in the High Antarctic Zone differ from those in the Seasonal Pack-Ice Zone in that the number of species feeding primarily on benthic or epibenthic organisms is several-fold higher. Another feature is the existence of the cryopelagic habitat discussed above.

Pelagic feeders have much less diverse diets than benthic feeders because of the lower diversity of pelagic prey compared with benthic prey. All abundant coastal fish species, both in the Seasonal Pack-Ice Zone and the High Antarctic Zone, are pelagic feeders, often exceeding the biomass of benthos feeders by one or two orders of magnitude.

Figure 7.11 depicts the central role that fish play in the marine Antarctic ecosystem (Hureau 1994). Hureau (1994) considers that this role is comparable to that of *E. superba*, at least in the High Antarctic Zone. The key role of fish as prey for birds and squid, and as predators of krill and other zooplankton, is clearly summarized in Figure 7.11. Their impact on krill resources is of the same magnitude of that of the present populations of whales and squid but remains much below that of the birds.

7.7 FACTORS CONTROLLING THE DISTRIBUTION, ABUNDANCE, AND TROPHIC ECOLOGY OF ANTARCTIC FISH

7.7.1 Role of Sea Ice

As discussed previously, the extent and abundance of the sea ice cover varies considerably. There are long-term increases in the winter maximum at the scale of years in, e.g., the Bellingshausen Sea, with concomitant decreases in other areas (Zwally et al. 1983a, 1983b). As melting occurs, the

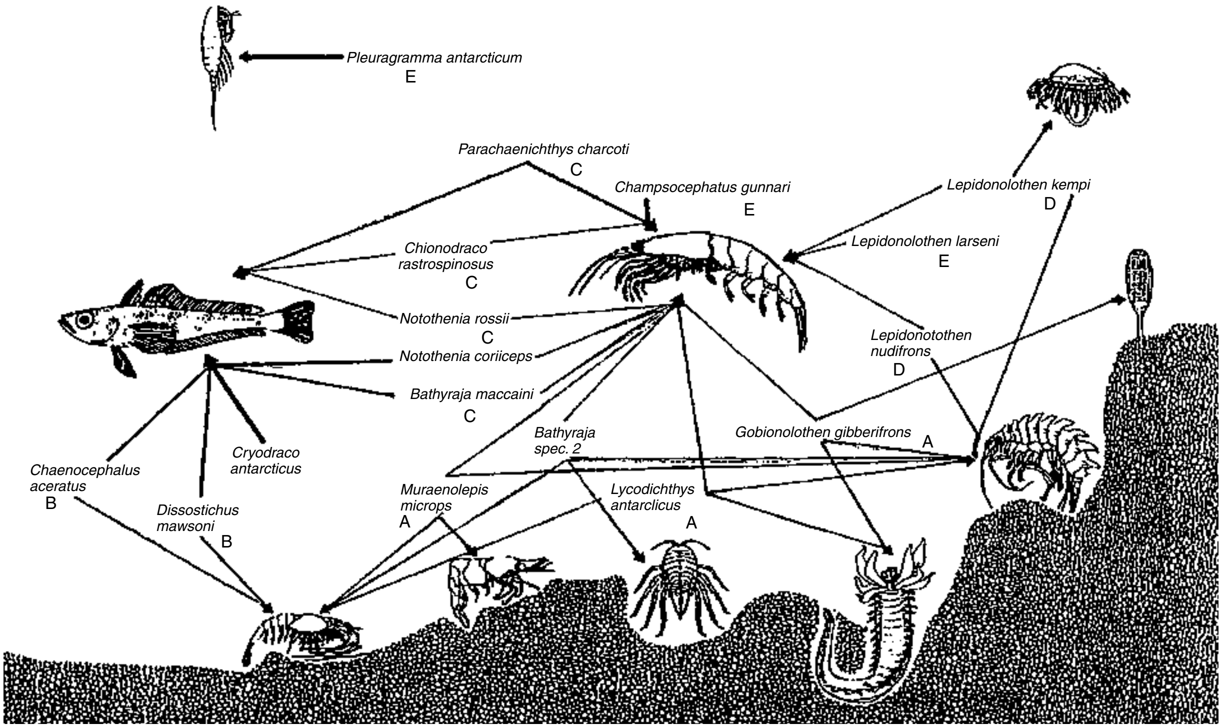


FIGURE 7.11 The role of fish in the Antarctic marine ecosystem. (From Hureau, J.-C., *Polar Biol.*, 14, 311, 1994. With permission.)

marginal sea ice zone is the site of intensive microalgal blooms. A specific feature of the Antarctic Peninsula area is an oscillation between several consecutive high-ice years (Stammerjohn and Smith 1996). Variation in sea ice can have major impacts on primary productivity and the zooplankton that feed on it. Consequently, planktonic food available to the epipelagic fish also varies. In addition, the sea ice provides a feeding habitat for a range of cryopelagic and other larval and adult fish.

7.7.2 HYDRODYNAMIC PROCESSES

The Circumpolar Antarctic Current and the westward setting of the Antarctic Coastal Current, especially the locality of reformation, set the spatial and temporal scales for the residence time of pelagic midwater fish, especially their planktonic life stages, with the cyclonic motion pattern resulting in the formation of gyres that act as retention mechanisms between the two currents The number and extent of cyclonic gyres show considerable variability. These gyres are important in the retention of larval fish within specific areas. Variability of the geostrophic currents induced by wind-field anomalies in late winter (Zwally et al. 1983a, 1983b; Stein 1992) can dissolve retention properties of the gyres and lead to a substantial deterioration of the larval environment and/or increased dispersal.

The extent and magnitude of upwelling is also highly variable and this can impact primary production and, consequently, the abundance of zooplankton, especially copepods, that provide a major food resource for epipelagic fish.

7.7.3 FOOD WEB DYNAMICS

As discussed in Chapter 9, several seabirds, such as penguins, albatrosses, petrels, shags and the South Polar Skua, feed primarily on midwater fish (Kock 1992). As discussed, midwater fish feed on a variety of zooplankton and micronekton species. Krill and other euphausiids, calanoid copepods, polychaetes, and also gelatinous zooplankton are also major prey items (Kock 1992). Krill, as a food resource, is taken by all development stages of the fish (Williams 1985). Notothenioid larvae consume eggs and sometimes nauplei (Kellerman 1987, 1990b). Furcilia stages are subject to predation by channichthyid larvae hatched in late-winter and spring (Kellerman 1986, 1989). Thus the winter survival of krill furcilia larvae will impact the nutritional environment of channichthyid larvae in late-winter and spring, whereas the food supply for winter hatching icefish larvae will be controlled by the abundance of krill furcilia during the winter. Several studies have found better survival of furcilia larvae in winters with a greater extent in annual sea ice cover (Quetin et al. 1998b).

Further important prey sources of larval fish in the Seasonal Pack-Ice Zone are cyclopoid copepods, eggs, nauplei and copepodites of calanoid copepods, tintinnids and pteropods (Kellerman 1987, 1990b). The calanoids *Calanoides acutus* and *C. propinquus* undergo annual vertical migrations. Ascent to the surface is sequential; upon the pack-ice retreat in the spring, copepodites of *C. acutus* are the first to migrate into surface layers, followed by the primarily herbivorous *C. propinquus* (Andrews 1966; Voronina 1970, 1972; Atkinson 1991; Quetin et al. 1996). The spawning of these species is highly variable, coinciding with the spring bloom. Thus peak abundance of copepod eggs and nauplei as principal food of larval nototheniids may vary between years on a scale of months (Kellerman 1996).

7.7.4 LIFE HISTORY PROCESSES

Egg sizes of Antarctic fish vary considerably, e.g., 3.8–5.0 mm in channichthyids and 1.6–2.5 mm in nototheniids and harpagiferids. In addition, some species produce eggs of different sizes. Incubation times also show considerable variation. As discussed, the breakup and retreat of the sea ice canopy shows considerable variation on a scale of weeks to months (Stammerjohn and Smith 1998). Larvae hatched well in advance of ice decay and the subsequent onset of the production cycle may be exposed to unfavorable feeding conditions.

8 Seals

CONTENTS

8.1 INTRODUCTION

Seals are well adapted to the cold waters of polar seas because their dense fur and a layer of blubber beneath their skin provide effective thermal insulation. These insulating layers are effective in air as well as in water and consequently seals suffer little heat loss in air, even at the low temperatures which occur in the Southern Ocean.

The order Pinnipeda, to which the Antarctic seals belong, evolved in the Northern Hemisphere, probably from two separate stocks. One stock, arising from a dog-like ancestor in the North Pacific, gave rise to the walruses and the related eared seals, the Otariidae. Another stock, derived from an otter-like ancestor in the North Atlantic, radiated to produce the true seals, the Phocidae. Early in the radiation of the phocid seals during the Miocene, the subfamily Monachinae originated in the Mediterranean region and spread across the Atlantic. One group, the Lobodontini, colonized the Atlantic during the Miocene or early Pliocene, at a time when the region was much warmer than it is today. The Lobodontini eventually radiated to produce four very distinct and successful Antarctic seals. They are the crabeater seal *Lobodon carcinophagus* (Figure 8.1), the Ross Sea *Ommatophoca rossii* (Figure 8.3), the leopard seal *Hydrurga leptonyx* (Figure 8.2), and the Weddell seal *Leptonychotes weddelli* (Figure 8.4). The species listed above have been estimated to amount to about 50% of the world's seal stocks, and because individuals of these species tend to be larger than other seals they comprise about 79% of the biomass

(Laws 1977a). However, Laws (1985) believes that population increases in these species which have occurred in recent years suggest that these species may amount to considerably more than 79% of the biomass.

The elephant seals were another group of monachine seals that invaded the Southern Hemisphere. They developed no special adaptation for the Antarctic ice environment and the main distribution of the southern elephant seal *Mirounga leonina* (Figure 8.5) is north of the Polar Front. Otarid seals originated in the northeast Pacific and early in their radiation crossed the equator and radiated to give rise to eight species of southern fur seals (genus *Arctocephalus*) (Repenning et al. 1971). The southern fur seal, *Arctocephalus australis*, probably gave rise to a number of closely related species. One of the most numerous of which is the Antarctic fur seal, *Arctocphalus gazella* (Figure 8.6). It is found on the islands south of the Polar Front, but generally on those that are not surrounded by sea ice.

The ecology of Antarctic seals has been the subject of a number of reviews (Turbott 1952; Scheffer 1958; Bonner and Laws 1964; Carrick 1964; King 1964; Laws 1964, 1977a, 1977b, 1984a, 1984b; Øritzland 1970a; Ray 1970; Erickson and Hoffman 1974; Stirling 1975; Gilbert and Erickson 1977; Kooyman 1981a, 1981b, 1981c, 1981d; Bonner 1985a; Siniff 1991; Costa and Croker 1996). Studies of Antarctic seals have added much to the development of pinneped and mammalian studies in general. For example, studies have developed an understanding of age determination, reproduction, population dynamics, energetic, behavior, and diving physiology.

8.2 SPECIES COMPOSITION AND DISTRIBUTION

8.2.1 General

Although seals feed exclusively at sea, their pups are born on land or ice and remain at their birth site until weaned. In most parts of the world seals must return to land, at least during the breeding season, so that their distribution is discontinuous and limited to areas where suitable islands or reefs occur. In polar regions, however, some species breed on drifting pack ice and this ability has allowed them to colonize a much larger geographic area, and enabled their breeding system to closely match their prey distribution. However, the pack ice is an unstable environment where pups may crawl into the sea and be crushed between the floes.

Habitat has greatly influenced our state of knowledge of the species concerned. Best known are the Weddell seals, which breed on fast ice, and the beach-breeding elephant and fur seals. Least known are the crabeater, leopard, and Ross seals, which inhabit the pack ice.

8.2.1.1 Crabeater Seal

FIGURE 8.1 Crabeater seal *Lobodon carcinophagus*.

The crabeater seal (Figure 8.1) is one of the most remarkable, but least known, of the marine mammals of the world. Its population probably numbers between 15 and 40 million, making it one of the most abundant large mammals in the world. More than one in every two seals in the world is a crabeater seal and the population biomass of the crabeaters is about four times that of all other pinnipeds put together.

Crabeater seals are large seals, although slender in comparison with their length, and they are very active creatures. Female adults are 230–260 cm in length and 200–227 kg in weight. Males are slightly smaller (Bertram 1940). When freshly molted in January or February the coat is mainly dark brown above and fawn below. The pattern becomes slightly mottled, particularly in young animals, with patches of darker color on a lighter ground. The pattern is more conspicuous on the flanks behind the flippers and around the posterior end of the body.

8.2.1.2 Leopard Seals

The leopard seal (Figure 8.2) is one of the largest and most mobile of the phocids (Kooyman 1981b). As in other lobodontine seals the female is slightly longer than the male. While the largest recorded specimen was 358 cm long (Hamilton 1939), females generally average 291 cm and males 179 cm in length. Average weights are 367 kg for

FIGURE 8.2 Leopard seal *Hydrurga leptonyx*.

females and 324 kg for males, but some large female leopard seals estimated to weight 500 kg have been hauled out at South Georgis (Kooyman 1981a). Despite their size leopard seals have a slender appearance and they are lithe and graceful in the water and on the ice. The fore-flippers are long and the tapered head and neck sinuous. The head is large with a huge gape. Unlike most seals they move rapidly when on the ice and land.

8.2.1.3 Ross Seal

Mystery surrounds the Ross seal (Figure 8.3). It may be the least abundant of the Antarctic seals, although Gilbert and Erickson (1977) believe that it could be as numerous as the leopard seal. It frequents the heavy pack ice that even modern ice breakers can penetrate only with difficulty; hence it is not often seen.

Ross seals are the smallest of the Antarctic phocids. Of the few which have been measured the largest female was 256 cm long and weighed 204 kg, and the largest male 208 cm and 216 kg (Ray 1981). They are stout thickset animals, with short necks, and an extraordinarily long snout set on a wide head. The eyes are large, up to 7 cm in diameter, although the eye openings are no longer than those in comparable phocids. The anterior flippers, which reach nearly 22% of the standard body length, are proportionally the largest of any phocid (Ray 1981).

8.2.1.4 Weddell Seal

The Weddell seal (Figure 8.4) has the most southerly distribution of any mammal. It is another very large phocid. As with other ice-breeding seals, females are larger than males. In early spring, when the seals are fat, both males and females may commonly weigh around 400–500 kg (Kooyman et al. 1973). Adults grow up to 3 m in length. In contrast to the leopard seal, the snout of the Weddell seal is short and the head seems small for its body.

Weddell seals are strongly spotted with irregularly shaped patches. The background color is blue–black with silver gray spotting, the underside being paler in color. As the hair ages it fades to a yellowish hue with darker areas of the back becoming rusty brown. The coat of a new-born pup is a very light or silvery gray with no traces of the spotting that is characteristic of the adult until the molt begins at about 9–21 days after birth.

FIGURE 8.4 Weddell seal *Leptonychotes weddelli*.

8.2.1.5 Southern Elephant Seal

The southern elephant seal (Figure 8.5) is the largest of all the pinnipeds and one of the largest mammals excluding the whales. There is a striking sexual dimorphism, which is opposite to that shown in lobodontine seals. Fully grown males reach a length of 4.5 m and weigh about 4,000 kg. The female is very much smaller reaching a length of 2.8 m and a weight of about 900 kg.

Adult males are recognizable by their inflatable proboscis, which plays an important part in agonistic behavior during the breeding season. The coat of the elephant seal is composed of rather sparsely distributed short, very stiff recurved hairs. The color is generally a uniform brownish color though there is considerable variation from a very dark chocolate to a pale sandy color. Adults of both sexes are much scarred, especially the males, as a result of

FIGURE 8.3 Ross seal *Ommatophoca rossii*.

FIGURE 8.5 Southern elephant seal *Mirounga leonine*.

wounds on the neck and chest received during the breeding season. The young are born with a coat of jet black woolly hair which is shed at about 3 or 4 weeks, exposing a coat that is steely-black above and silvery below.

8.2.1.6 Antarctic Fur Seal

The Antarctic fur seal (Figure 8.6) is the only eared seal (family Otariidae) that lives in polar waters. As an otarid it is very much more mobile on land than the phocids. It is a medium-sized seal with adult males reaching a length of 200 cm and a weight of around 125–200 kg. As in the elephant seal the female is smaller than the male, up to 140 cm long and weighing about 50 kg. The fur is composed of two layers, an outer coarser layer of guard hairs, and an under layer of very fine under-fur fibers. It is this layer which provides the fur seal fur for commerce after the removal of the guard hairs. The layer of air trapped in the fur provides thermal insulation as the fur seals do not have as a well developed blubber layer as found in the phocid seals.

The color is gray to brownish on the back and sides while the throat and breasts are creamy and the belly is dark brown. In adult males a heavy mane is developed around the neck and shoulders. The new-born pup is clad in a black coat.

8.2.2 DISTRIBUTION

The Antarctic seals are essentially distributed in circumpolar latitudinal zones, except where the Antarctic Peninsula and Scotia Arc intervene, extending the breeding distribution of some high latitude species northwards (e.g., Weddell and leopard seals), and some lower latitude species southwards (Laws 1984a) (Figure 8.7). Changes in the physical properties of the environment, while exerting strong direct influence on distribution, most likely have strong indirect effects on both the quality and quantity of breeding substrate, the nature of foraging habitat, and on distribution and abundance of potential prey (Croxall 1992). Important physical barriers affecting overall distribution are the Polar Front and the Subtropical Convergence. The breeding of three species is strictly limited to the south of the Polar Front (crabeater, Ross and Weddell seals). The greatest numbers of seals are located in the pack ice region. The distribution of the ice-breeding seals may be most strongly influenced by the effects of the nature and extent of ice on the availability of breeding sites with suitable access to water for mating and feeding. The four species that occupy the pack ice region have become specialized in terms of habitats and their utilization so that little ecological overlap occurs (Siniff 1991). The elephant seals and the fur seals, although not directly affected by ice, are influenced by the effects of ice on prey populations which originate in areas of seasonal ice cover.

FIGURE 8.6 Antarctic fur seal *Arctocephalus gazelle*.

8.2.2.1 Distribution

As all seals must give birth to their pups on land or ice, their distribution during the breeding season are determined by the availability of suitable habitats. Fur seals and elephant seals breed on ice-free beaches, and in the Antarctic region these only occur on islands in the Scotia Arc and other isolated islands close to the Polar Frontal Zone (Bonner 1981). Competition for breeding sites between fur and elephant Seals is slight since the former breed mainly on rocky shores and the latter on sandy beaches. The breeding stock of the fur seal is concentrated at Bird Island, Willis Island, and the neighboring coasts of South Georgia. Smaller colonies are present on the South Orkney Island, Elephant and Clarence Islands, South Sandwich Islands, Bouvetya, Heard, and MacDonald Islands, and Isles Kerguelen (Figure 8.7).

Elephant seals are circumpolar, but they appear to be subdivided into three main breeding stocks (Laws 1960b) (Figure 8.7). The first is centered on South Georgia and includes breeding populations in South America, the Falkland Islands, the South Orkney Islands, and possibly Bouvetya (Laws 1984a). The second group breeds at Isles Kerguelen, Heard Island, Marion, and Prince Edward Islands, Crozet Island, and Amsterdam and St. Paul Islands. The third stock is found at Macquarie Island and the New Zealand Subantarctic Islands. Although branding and tagging experiments have demonstrated movements within the three geographic areas covered by the three groups, no interchange between them has been observed (Dickinson 1967; Ingham 1967; Hunt 1973; Scoloro 1976).

Weddell seal breeding colonies have been recorded from fast ice areas adjacent to the Antarctic Continent and the off lying islands in every region that has been visited during the breeding season. Suitable habitat occurs wherever tidal or glacial action forms cracks large enough to be used as breathing or exit holes (Stirling 1969a). The long-term tagging programs at McMurdo Sound (Stirling 1971a; Siniff et al. 1977b; Siniff 1982) and Signey Island (Croxall and Hiby 1983) have shown a general fidelity to the general area of the colony of birth with no evidence of long-range movements. However, they have been reported from pack ice habitats outside the breeding season (Smith 1965; Bester et al. 1995). Stewart et al. (1998, 2000) found that some weaned pups leave their coastal niches and spend most of their first winter foraging in distant ice and open water,

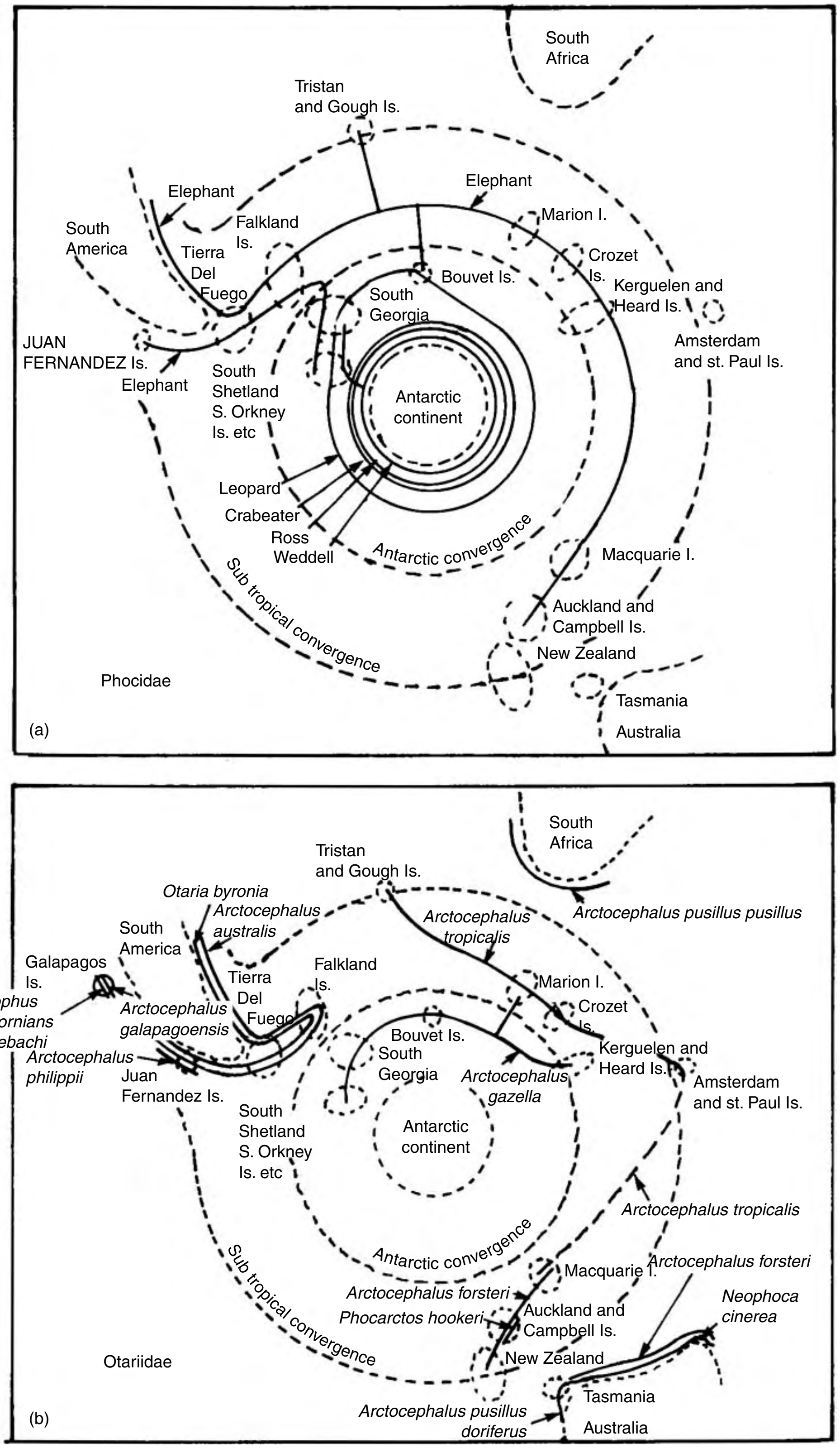


FIGURE 8.7 The geographical distribution of the southern seals. The thick lines are drawn to join the breeding localities of (a) Phocidae, and (b) Otariidae. (Redrawn from Laws, R. M., *Antarctic Ecology*, Laws, R. M., Ed., Academic Press, London, 621, 1984. With permission.)

polyna habitats. They hypothesized that young seals may spend several years in such habitats before returning, when sexually mature, to natal colonies. Stewart et al. (2003) tested this hypothesis by monitoring weaner pups by satellite telemetry. They found that while some of the seals dispersed into the pack ice and open water, others remained near the coastal fast ice habitat. Seals dispersing into the pack ice habitat will be subject to greater risk from predators.

The remaining three species have severed their attachment to the land and spend the whole of their lives in drifting pack ice which surrounds the continent. Due to logistic difficulties observations on their breeding have been limited and have been largely confined to the Antarctic Peninsula (Siniff et al. 1979; Bengston and Siniff 1981) and the vicinity of the South Orkney Islands (Øritzland 1970b). Unconsolidated pack ice, covering 30–70% of the water surface, is the preferred spring and summer habitat of Crabeater Seals (Siniff et al. 1970; Erickson et al. 1971) where they form family groups in the spring composed of a male, female and pup (Siniff et al. 1979; Shaughnessy and Kerry 1989). The length of time the family group remains together is uncertain, but is considered to be 14–21 days. Gilbert and Erickson (1977) found that crabeater seals were predominantly distributed close to the edge of the pack ice in cake and brash ice where there was access to open water and food. As the ice edge recedes during the summer the crabeater seals move southwards (Bonner and Laws 1964; Solynik 1964).

Two predators have played a significant role in the evolution of the crabeater's life history: the killer whale (*Orcinus orca*) and the leopard seal. Killer whales actively prey on crabeaters of all ages while the leopard seal preys primarily on newly weaned pups or animals in their first year (Siniff and Bengston 1977; Laws 1984a).

The breeding distribution of the leopard seal is similar to that of crabeater seals, perhaps due to the importance of krill and crabeater seals in its diet (Gilbert and Erickson 1977). They are often found in the sea around penguin colonies, and are frequently hauled ashore, or on fast ice off the coast or offshore islands. Leopard seals are usually observed in the summer as solitary animals (Erickson et al. 1971; Gilbert and Erickson 1977), with higher densities near the pack ice edge, similar to the crabeater seal (Laws 1984a). Population size has been estimated to be between 220,000 and 440,000 animals (Laws 1984a).

The Ross Sea is the least known of the Antarctic seal species. From the limited data that is available it appears that the breeding distribution is circumpolar but there is evidence that they are very much more abundant in some areas than others. One such area is the King Haaken VII Sea (Condy 1976), and they may be more abundant near Cape Adare than further south in the Ross Sea (Ray 1981).

8.2.2.2 Nonbreeding Distribution

In contrast to the breeding distribution, the nonbreeding distribution is less well known for the fur, elephant, and Weddell seals than for the pack-ice species.

Very little is known about the pelagic distribution of the fur seal. Adults fur seals are absent from their breeding grounds between May and October. Fur seals tagged at South Georgia have been sighted at the South Orkney Islands, the South Shetland Islands, and Tierra del Fuego (Hunt 1973; Payne 1979). Payne (1979) suggested that Antarctic fur seals may undertake a seasonal migration similar to that exhibited by northern fur seals in the north Pacific.

In the case of the elephant seal, sightings of marked seals reported by Laws (1984a, 1984b) indicate that these seals disperse widely up to 2,000 km from their breeding grounds (Laws 1960b; Dickinson 1967; Ingham1967; Scolaro 1976; van Aarde and Pascel 1980). They have been recorded from the Antarctic Continent and as far north as South Africa, Tasmania, New Zealand, Mauritius, and the Rodriguez Islands.

Nonbreeding Weddell seals range into the pack ice during the winter. Although the winter distribution of crabeater seals is unknown, it is likely to be in the pack ice zone. In some years, large numbers of crabeater seals have been recorded at Signy Island and South Orkney Islands, which are near the pack ice edge. During the nonbreeding season, leopard seals range widely, many migrating northwards (most of the sightings at the Subantarctic Islands occur at this time) and occasionally individuals are reported from the coasts of Patagonia, South Africa, southern Australia, Tasmania and New Zealand (Bonner 1985a). The most northerly record is from Rarotonga in the Cook Islands at 21°S (Berry 1961). Possible seasonal movements of Ross seals are unknown. The only sighting of a Ross seal north of 55°S has been made at Heard Island (Ingham 1960).

8.2.3 HABITAT PREFERENCES

On land in the breeding season the Antarctic fur seal shows a preference for rocky shores and small beaches in sheltered coves (Bonner 1968). At other times of the year it is more widely dispersed in more open areas, and, at South Georgia in tussock grassland behind the beaches. Elephant seals tend to occupy the more open beaches in the breeding season, and at South Georgia they are found in muddy wallows in low-lying tussock grass (Laws 1960b).

Weddell seals form pupping colonies on the fast ice in the spring, along the shorelines, associated with broken ice, tide cracks and hummocking (Stirling 1971a; Siniff et al. 1977b; Kooyman 1981c). They enlarge existing cracks with their canine teeth to form holes for hauling out (Stirling 1969b), but are unable to make new holes. Although females usually return to the same colony, year after year, they will pup at other sites should cracks not open at the colony site used in the previous year (Stirling 1969c).

The most detailed studies of Weddell seal distribution and movements have been made in McMurdo Sound (Smith 1965; Stirling 1969c, 1971b; Siniff et al. 1971a, 1977b). Most of the seals remain in McMurdo Sound throughout the year but local movements occur as the distribution of the breathing holes changes. By mid-December, the pups have been weaned and many seals move south to occupy cracks near Cape Armitage and Scott Base which form as the sea ice breaks up. Others disperse north, some to Cape Bird where in the late summer they haul out on stony beaches, bared as the push ice retreats. Sub-adults tend to move to more peripheral areas than the adults. During the winter the seals move back to the breeding areas as the sea ice reforms. An unusual habitat found at White Island on the McMurdo Ice Shelf is a land-locked colony of some 20–30 seals which over-winter beneath the ice (Stirling 1972; Kooyman 1981c).

The habitat of the pack ice species is very different in that they show preferences for particular types of ice (Gilbert and Erickson 1977). Highest densities of crabeater seals have been recorded in the summer within 120 km of the ice edge. Densities are closely correlated with dominant floe size, not ice cover, and in the summer they are most abundant in cake and brash ice with a cover of about 7–8 octas (a measure of the percentage of ice cover, maximum 8, minimum 1) (Figure 8.8); densities are lowest in areas with larger crabeaters at around midday, with some regional year-to-year variability (Condy 1977b). In spring their family groups are associated with larger hummocked floes, and the immatures can be found in large concentrations of several thousands, associated with the fast ice remaining in the bays (Bengston and Siniff 1981).

In the summer, leopard seals generally occur as solitary animals and like the crabeater seals they show higher densities near the pack ice edge. Although their predatory activities in the vicinity of penguin colonies have attracted a lot of attention relatively few are seen in inshore waters (Laws 1981). The daytime haul-out patterns and distribution in relation to floe size are similar to those of crabeater seals.

Ross seals are usually seen as solitary individuals and their highest densities are associated with larger floes than is the case for other species, typically where the ice cover is about 6–8 octas (Gilbert and Erickson 1977).

8.3 ABUNDANCE

Different methods have been used to assess the abundances of the different species of Antarctic seals (Laws 1981; SCAR/SCOR 1983b). For the colonial breeding species (fur, elephant and Weddell seals) counts of pups raised by a factor related to the age structure of the population is the

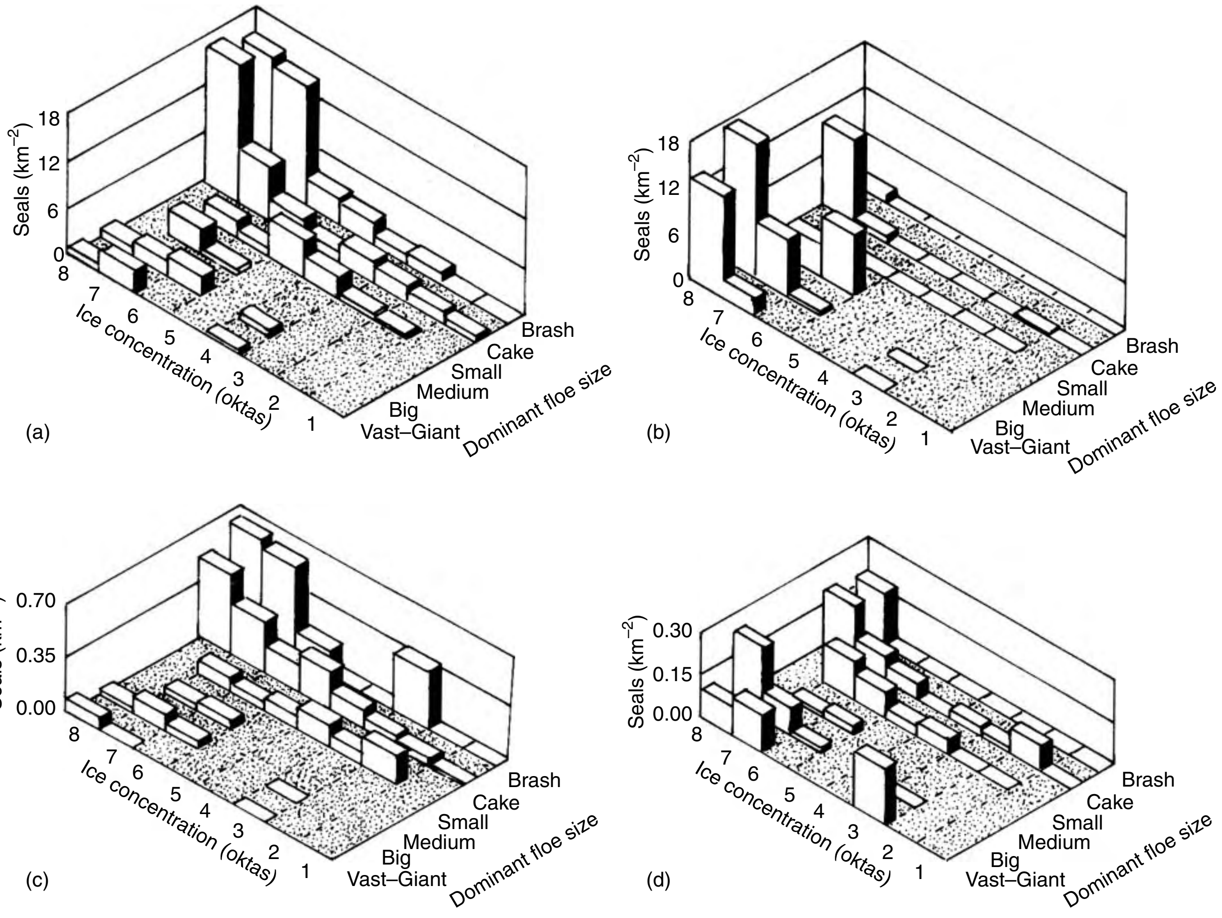


FIGURE 8.8 Typical seal densities in each floe size and concentration class for the four pack ice seal species during 1972. (Redrawn from Gilbert, J. R., Erickson, A. W., *Adaptations Within Antarctic Ecosystems*, Llano, G., Ed., Smithsonian Institution, Washington, DC, 703, 1977. With permission.)

method generally used determine population. For the pack ice species, estimates are calculated from stratified random strip census counts supported by surveys from ships or aircraft.

Prior to exploitation in the nineteenth century Antarctic fur seals were estimated to number from 1 to 2 million individuals (Bonner 1976). Following the slaughter of these seals, their reduction to some hundreds of individuals and the collapse of sealing (Bonner 1964; Laws 1977a, 1981), the stocks began to recover (see Chapter 16). This recovery has been dramatic and has been reviewed by Bonner (1976), Laws (1973, 1977a), Payne (1977, 1978), Boyd (1993), and Costa and Crocker (1996). Bonner (1981) estimated that the annual pup production in 1978 was 138,000, corresponding to a total population of about 554,000; by 1982, it was estimated that there were probably over 900,000 (Laws 1985). Mean annual population growth rate was 16.8% between 1958 and 1972 (Payne 1977). Since this period of population expansion, the annual increase has declined to 9.8% between 1976 and 1990 (Boyd 1993). Boyd estimated a total population size of around 1.5 million seals in 1993.

Laws (1960b) on the basis of information then available, concluded that the total mid-year population of the southern elephant seal was 600,000 ± 100,000. This estimate was updated by McCann (1980a) to approximately 750,000, with the South Georgia stock comprising 350,000, Macquarie Island 136,000, Isles Kerguelen 157,000, and Heard Island 80,000. Elephant seals are increasing in some areas and declining in others. Condy (1977a) estimated a decline of approximately 69.5% at Marion Island between 1951 and 1976. A more recent evaluation (SCAR/SCOR 1983c) indicates that the elephant seals throughout the Antarctic and Subantarctic might be declining at a rate as high as 8–11% per annum. Counts of elephant seals at the Vestfold Hills from 1958 to 1988 indicate that the population had declined by half to two-thirds, similar to the reported decline of the breeding population on Kerguelen.

The Weddell seal population has been estimated at 800,000 individuals and is thought to be stable (Laws 1984a). A few populations adjacent to bases declined due to the harvesting of Weddell seals for dog food. This practice has now ceased.

The most carefully planned and executed estimates of the four Antarctic pack ice seals are those described by Erickson et al. (1971), and Gilbert and Erickson (1977) based on investigations made from icebreakers in 1968, 1979, 1972, and 1973 (Figure 8.8). A variety of parameters affected these estimates, including activity patterns, haul-out rates, transect width, light conditions, and the ability to spot seals behind drift ice. Gilbert and Erickson (1977) concluded that there were six residual pack ice regions and estimated their overall seal densities in February to March, within the range of 1.86–6.56 individuals km^{-2}, to give a conservative population estimate of 14,858,000 Crabeater Seals. However, as they point out juveniles are probably under-represented in the estimates, and the recorded densities are likely to be low. In 1984 (Laws 1984a) considered that an estimated population of 15 million could well be conservative and that a population of 30–40 million was not unlikely, as the species appeared to be increasing at a comparatively rapid rate. Due to the nature of the limited surveys that have been carried out to date, any conclusions about absolute numbers or population trend in crabeater seals is premature.

Leopard seals are estimated to total between 220 and 440,000, with the population on the increase (Laws 1984a). The least reliable estimate is that of 220,000 for the Ross seal. In percentage terms, the estimated populations associated with the residual pack ice regions represent 92.36% crabeater, 1.35% leopard, 1.35% Ross, and 4.93% Weddell seals (Laws 1984a). Bester et al. (1995) investigated the distribution of the pack ice seals off the Princess Martha coast. The species composition was 94.4% crabeater, 3.4% Ross, 1.4% leopard, and 0.8% Weddell. While the species composition of the seals within the pack ice remains remarkably constant, the inshore ratios change. For example Ray (1970) found 43% Weddell seals in counts on the western side of the Ross Sea. Estimates of the total population of all six species are given in Table 8.1. From this table, it can be seen that the total population estimated at some 18 million in the early 1970s had risen to possibly some 33 million in 1982.

8.4 SOCIAL ORGANIZATION AND REPRODUCTIVE BEHAVIOR

The social and reproductive behavior of the six Antarctic seals varies widely and is, in part, associated with breeding habitat and predatory pressure. Crabeater, leopard, and Ross seals inhabit an unstable area of shifting pack ice that varies from place to place and day to day. Floe size, surface features and the proportion of sea covered also vary. Weddell seals breed in areas of predictable fast ice, permitting association with specific sites. Elephant and fur seals have developed social systems adapted to female aggregation, terrestrial parturition, and seasonal breeding at specific sites.

TABLE 8.1
The Number of Genera and Species of Each Species of Seals Found in the Southern Ocean, Showing the Number Restricted to the Area and the Number Found Further North

Species	Population Size 1982 $(\times 10)^3$	Status
Fur	930	Increasing
Elephant	750	Stable some decreasing
Crabcaler	30000	Increasing
Leopard	220–140	Increasing
Ross	220	Not known
Weddell	800	Stable some colonies decreasing
Total	33140	Increasing

Source: From Laws, R. M., *Antarctic Ecology*, Vol. 2, Laws, R. M., Ed., Academic Press, London, 491, 1984. With permission.

8.4.1 ICE-BREEDING SPECIES

Very little is known of the social organization of the pack ice breeding species. Aspects of the social organization and reproductive behavior of crabeater seals have been described by King (1957), Øritzland (1970a), Corner (1972), Siniff and Bengston (1977), and Siniff et al. (1977a, 1979). Crabeater seal overall mean densities in the pack ice range from about 4.83 individuals km^{-2} in the summer to about 0.5 individuals km^{-2} in the winter and spring. During the breeding season the seals form pairs when a pregnant female hauls to give birth on a suitable floe and is joined by a male either before or after parturition. Pups are born in September and October, with most births occurring in early to middle October (Figure 8.9a). Lactation lasts for about 4 weeks during which time the pup increases in weight from about 20 to 113 kg, while the mother loses about 50% of her weight. During this period the male defends an area of about 50 m round the family group from other males and leopard seals. Competition for mates must occur as the males frequently bear wounds characteristic of interspecific encounters. After the pup is weaned the male maintains close contact with the female preventing her from leaving the floe and often biting her on the upper back and neck. This is probably precopulatory behavior as the female returns the male aggression. Copulation probably occurs on the ice, unlike that of most ice-breeding species where it occurs in the water (Stirling 1975). Perhaps this is because copulating seals would be vulnerable to predators such as killer whales and leopard seals in the water (Table 8.2).

The social organization and mating strategies of the leopard and Ross seals are less well known than that of the crabeater. Ross seals are almost solitary, although groups of up to 13 have been recorded (Laws 1964). During the summer their closest observed spacing was 1 km and the average overall density was about 0.09 individuals km^{-2}. In the spring the density is probably about 0.02 km^{-2} (Gilbert and Erickson 1977). Very few Ross seal pups have been recorded. The greatest number is eight recorded near the Balleney Islands (Tikhomirov 1975). Pups are probably born in November, later than those of the Crabeater Seals. Males do not appear to accompany the females as in the Crabeater Seal, and perhaps this is because copulation occurs in the water.

Leopard seals are mostly solitary inhabitants of the pack ice zone (Laws 1964; Marlow 1967; Øritzland 1970a; Siniff et al. 1970; Erickson et al. 1971; Hofman et al. 1973). They are not known to form aggregations except for occasional small groups on the ice floes (Hofman et al. 1977). Along the Antarctic Peninsula females haul out alone in November and December, deliver their pups, and remain with them to weaning (Figure 8.9b). The breeding behavior of the males and females is practically unknown, and copulation is presumed to take place under water after the pups have been weaned (Harrison 1969; Siniff et al. 1980; Harrison et al. 1982).

The Weddell seal is quite different in its social organization and reproductive behavior from the other ice-breeding species and this difference has been described by Stirling (1969c, 1971b), Kaufman et al. (1975), Siniff et al. (1977b) and Siniff (1982), Mansfield (1985). In the summer, outside the breeding season, Weddell seals probably move to the outer edge of the fast ice and the inner zones of the pack ice, although dispersal may be limited in some areas. They are nearly always single when found in the pack ice in summer. The main density in the pack ice at this time is about 0.14 individuals km^{-2}, whereas in the winter it may be about 0.002 individuals km^{-2}, assuming an even distribution as the pack ice spreads (Gilbert and Erickson 1977).

In spring, pupping colonies form on the nearshore fast ice. Several females may share a single breathing hole, giving birth (in September to November, depending on the latitude) to pup on the sea ice surrounding it (Figure 8.9c). Pups are suckled until weaning at about 6 weeks. They weigh about 15 kg at birth, and by 10 days they have about doubled in weight. They are weaned at about 110 kg between 6 and 7 weeks.

During the winter and spring there is intraspecific competition for space, and nonbreeding seals and subadults are excluded from the preferred breeding areas. In the breeding season the males spend most of their time in the water beneath the cracks, where they defend aquatic territories against other males (Siniff et al. 1977b). This enables them to have exclusive access to all females using the same breathing hole or length of crack. The mature female ovulates just before the pup is weaned in late November–December and underwater mating occurs then; observations of such mating are limited (Kaufman et al. 1975). Unlike the pack ice seals, lactating female Weddell seals leave the pups periodically to feed. Leaving the pups to feed occurs more frequently as the pups grow. The pups first enter the water at 2–3 weeks after birth (Stirling 1969a).

8.4.2 LAND-BREEDING SPECIES

In contrast to the ice-breeding species, the two land-breeding species—the fur seal and the elephant seal—are highly polygynous and gregarious in their breeding behavior. They may also form large aggregations at other times.

The breeding grounds of the fur seal tend to be rocky or shingle beaches, and the seals return to their breeding grounds year after year, showing strong fidelity. The males come ashore and establish territories averaging 60 m^2 in late October, which is 2 or 3 weeks before the females haul out (Figure 8.9d). Territory size declines to about 22 m^2 later in the season when the beaches are fully occupied. Bulls defend their territories with displays, vocal threats and fighting encounters, which often result in severe wounds. Successful fighting and territory maintenance means that the bulls are on site to mate with the oestrous cows in their territories. Territories are held from late October to late December for an average period of 34 days during which the bulls do not feed (McCann 1980b).

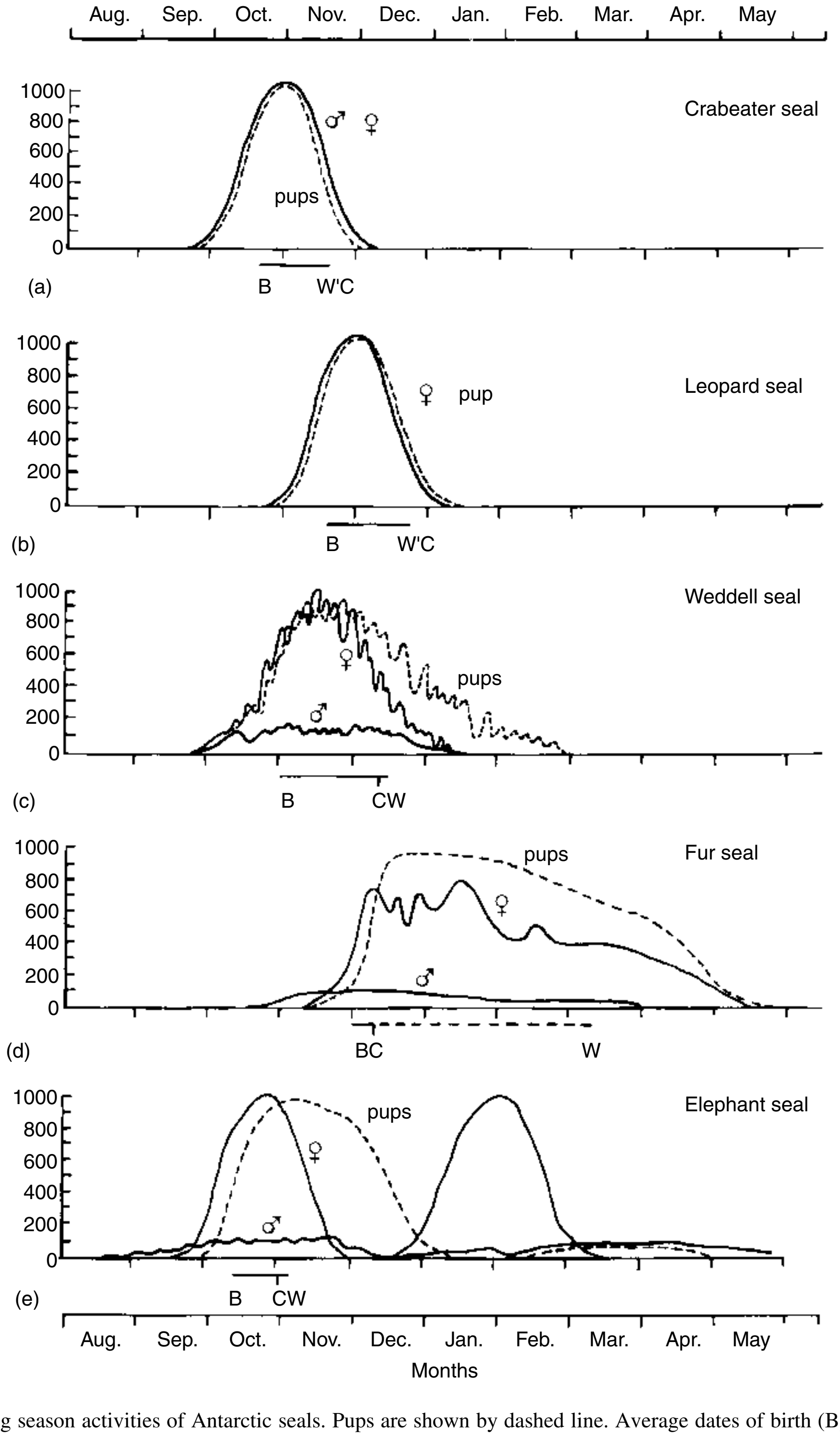


FIGURE 8.9 Breeding season activities of Antarctic seals. Pups are shown by dashed line. Average dates of birth (B), conception (C), and weaning (W) are indicated. (a) Crabeater seal; Antarctic Peninsula, family groups and mated pairs in pack ice; (b) Leopard seal, Antarctic Peninsula, female and pup pairs on ice; (c) Weddell seal, McMurdo Sound, haul-out of mature males, females and pups on fast ice for breeding; fluctuating curves reflect aquatic activity (data from Kaufman et al. 1975); (d) Fur seal, Bird Island, haul-out of mature males and females for parturition, lactation and mating. Note the suckling period is broken by feeding trips to sea. Data to early March from Bonner (1968), extrapolated to May from other reports; (e) Elephant seal, South Georgia. Adult haul-out for moult in January–May is also shown (data from Laws 1956a, and McCann 1980a). Hypothetical curve inferred from very limited observations. (Redrawn from Laws, R.M., *Antarctic Ecology*, Vol. 2, Laws, R.M., Ed., Academic Press, London, 621, 1984. With permission.)

TABLE 8.2
A Summary of the Various Life History Aspects of the Four Species of Antarctic Seals that Live in the Pack Ice Zone

Species	Habitat	Pattern of Distribution	Food	Pupping and Matting Characteristic	Predaor Preasure	Annual Pupping/ Pregnancy Rates
Weddell (*Leptonychotes weddelli)*	Usually heavy, persistent ice, close to Antarctic continent	Ciumped, particularly during breeding, pupping and moulting seasons	Fish : a few species	Polygamous, males defend underwater territories, breeding at end of lactation	Little, killer whale: rarely leopard seal	Pupping: 0.47–0.90: Pregnancy 0.85–0.95
Crabeater(*Lobodow carcinophagus*)	Pack ice. Floes	Dispersed(group sizes average 2–3)	Krill: mostly one species	Serial monogomy, males defend female/pup pairs, breeding in male/female paris after weaning.	Intense, leopard seals and killer whales	Pregnancy: 0.90–0.97
Leopard (Hydrurga leptonyx)	Pack ice, floes	Dispersed, single animals most common	Birds (penguins) seals (crabeater weanlings) fish; krill, cephalopods	Mostly unknown, female alone with pup, breeding proposed within one month after weaning	Some, killer whales	Pregnancy: 0.47, 0.61, 0.85 and 0.93 (four data sets)
Ross (*Ommatophoca rossii)*	Pack ice, floes	Dispersed	Mostly cephaloopods and a few fish species	Mostly unknown, female alone with pup, breeding may occur about one month after weaning	Some killer whales and perhaps leopard seals	Pregnancy: 0.88 and 0.90 from two small data sets

Source: From Siniff, D. B., *Amer. Zool.,* 31, 147 1991. With permission.

A cow produces a pup about 2 days after coming ashore. For about 8 days she remains with the pup suckling it at about 6-h intervals. At the end of this period she comes into oestrous and is mated by the bull in whose territory she occurs. After mating, the females go to sea to feed. They are away for 3–6 days and then they return to suckle their pups for 2–5 days. This pattern is repeated for the whole of the lactation period which lasts from 110 to 115 days until April (Bonner 1968; Doidge and Croxall 1983). The pups grow rapidly; males gain weight at an average of 98 g day^{-1} from a birth weight of 5.9 kg, while females born at 5.4 kg grow more slowly at about 84 g day^{-1} (Payne 1979).

Elephant seals also form harems but they are of a different kind to those of fur seals. In September the bulls arrive to take up positions on the preferred beaches which are generally sand or shingle, and shortly afterwards the cows haul out to give birth (Figure 8.9e). The cows are gregarious and form groups which quickly attract the larger bulls to join them. These territorial bulls drive off intruding bulls usually by threat alone and very exceptionally by fighting. Pups are born about 8 days after haul-out and, unlike the fur seal, the cows do not go to sea until the pups are weaned. Both cows and bulls go without food on the breeding beaches, living on their reserves of blubber, the female for over 3 weeks and some of the males for up to 3 months. As the season advances the groups of cows increase in size and may coalesce, reaching a maximum in October. The larger groups may have several bulls among them, but one of these is usually clearly dominant. Subordinate bulls lower in the dominance hierarchy are found around the groups of cows and in the water offshore (Laws 1956).

At birth the pups weigh about 45 kg. The weight is doubled in about 11 days and quadrupled at the end of lactation, which lasts for about 3 weeks. The cows come into oestrous about 19 days after they give birth and are mated over a receptive period of about 4 days by the dominant bulls (McCann 1980a). Adult male elephant seals reach sexual maturity at about 4 years, but do not achieve physical maturity or breeding status until at least 7 years. The dominant bulls, the beach-masters, probably only have one or two seasons of dominance, but during this time they pass their genes to a large number of offspring as they achieve the great majority of matings (McCann 1981a).

8.5 FEEDING ECOLOGY

8.5.1 Food Consumption

Understanding the feeding ecology of Antarctic pinnipeds is essential to our understanding of the role of this important group of animals in the Southern Ocean ecosystems. As Laws (1984a) points out there are many difficulties in establishing the qualitative and quantitative aspects of their feeding. These difficulties are due to the vast areas the pinnipeds occupy, the inaccessibility of the pack ice and fast ice regions, and the lack of opportunity of observing feeding directly except on rare occasions. Nevertheless, some generalizations can be made, mainly on the basis of the records of stomach contents from collected animals (Figure 8.10). Recent reviews of food consumption include those of Øritzland (1977), Laws (1977b, 1984a) and Costa and Croker (1996). Table 8.3 updates their calculations with estimates of stock sizes and prey selection.

The crabeater seal is a specialist feeder with over 90% of its diet made up of krill, with small amounts of fish, squid and other invertebrates. The crabeater's dentition is very complex, with each cheek tooth having a main backwardly directed cusp, flanked by one anterior and one posterior cusp (Figure 8.11). When the teeth occlude they leave a small gap forming a strainer which enables the retention of krill while expelling the water taken in with the prey. King (1961) described the straining mechanism of the crabeater, including a bony projection on the mandible which closes the gap between the last upper cheek tooth and the scoop-like lower jaw. Racovitza (1900) described the crabeater as swimming with the mouth open in krill swarms, while Wilson (in Kooyman 1981a) reports it as catching invertebrates one by one.

Little is known about the feeding behavior of Ross seals. Cephalopods appear to be an important component of their diet (about 57%), although fish (about 37%) have also been found (Barrett-Hamilton 1901; Wilson 1907). King (1969) suggested that Ross seals may take larger cephalopods (up to 7 kg in weight) than other seals. However, Øritzland (1977) states that, of the cephalopods that he found in Ross seal stomachs, 92% were small.

In contrast to the above two species, the leopard seal is an opportunistic predator, taking a variety of prey, including krill, squid, fish, penguins, and seals. Leopard seals are perhaps best known for their predation on penguins. At the landing place of most Antarctic penguin rookeries, one or more leopard seals lie in wait to take the toll of birds as they arrive and depart. This predatory behavior has been described by Penny and Lowry (1967), Hunt (1973), and Muller-Schwarze and Muller-Schwarze (1975). They pursue, catch, and kill penguins in the water, dismembering them by powerful jerks of the head. Penguins, however, are a temporary food resource when the birds are concentrated on the breeding colonies (late January and February). Where it has been possible to identify the sex of the predatory seals, they have all been males.

Another important food for leopard seals is the flesh of other seal species. Although five other species of seal have been identified as being preyed upon by leopard seals (Wilson 1907; Bertram 1940; Laws 1964; Erickson and Hofman 1974; Gilbert and Erickson 1977; Siniff and Bengston 1977; Siniff et al. 1979; Bengston 1982; Siniff 1982; Stone and Siniff 1983), the most important species is the crabeater. The importance of crabeater seals in the diet of leopard seals is supported by the observations of Condy (1976), Siniff and Bengston (1977), Siniff et al. (1979), Siniff (1982), and Siniff and Stone (1985), who all emphasized the high rate of scarring of crabeater seals. The spacing of the scars on the flanks of the majority of these seals is consistent with leopard seal attacks. Up to 93% of the seals encountered during census surveys had such scars. Crabeater seals older

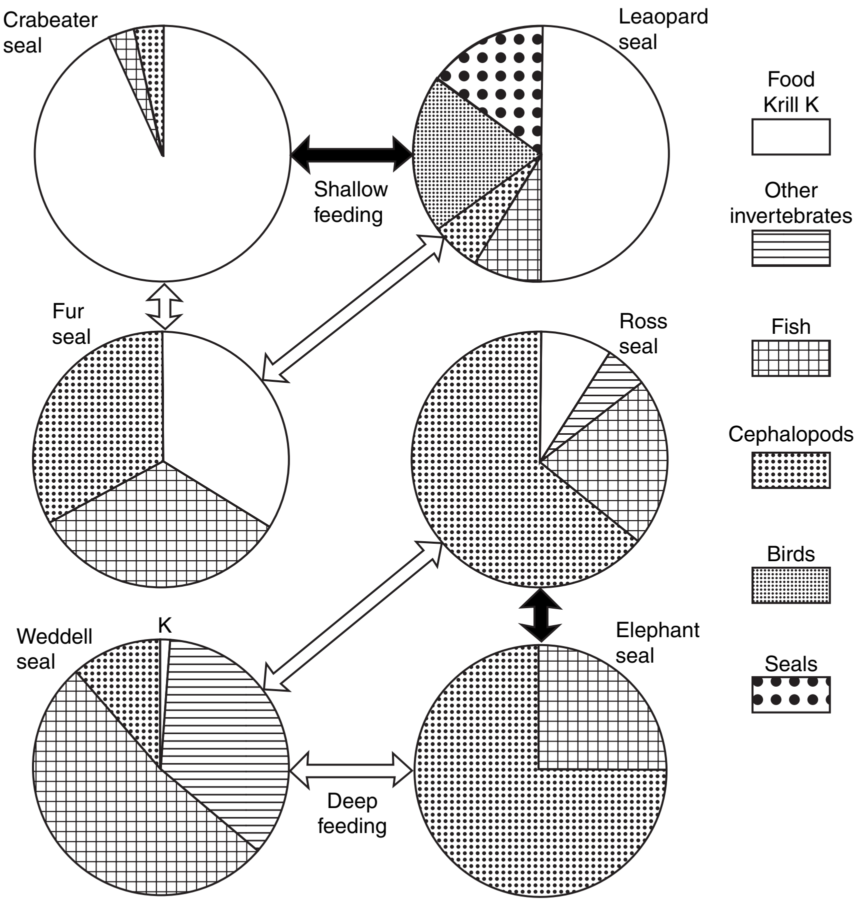


FIGURE 8.10 Percentage composition of stomach samples of Antarctic seals. Black arrows, major similarities in diet; white arrows, minor similarities in diet. (Redrawn from Laws, R.M., *Antarctic Ecology*, Vol. 2, Laws, R.M., Ed., Academic Press, London, 621, 1984. With permission.)

then 1-year-old are seldom attacked and flesh wounds on adults are rare (Laws 1977a).

In view of their predatory behavior, it is surprising that leopard seals take substantial quantities of krill. Like those of the crabeater, the teeth of the leopard seal are intricately cusped and when the jaws are closed, they interlock to form an efficient strainer (Figure 8.11). Øritzland (1977) concluded that overall the leopard seal take 37% of krill in its diet, but Hofman et al. (1977) at Palmer Station on the Antarctic Peninsula found a much higher proportion of 87%. The latter sample was biased towards the younger age classes which may take krill more frequently than the older ones.

Øritzland's (1977) samples from the pack ice comprised 58% krill, 16% penguins, 12% fish, 9% cephalopods, and 3% seals. Siniff and Stone (1985) have broadly confirmed Øritzland's conclusions. From samples taken along the west coast of the Antarctic Peninsula during November–March, they found 45% krill, 10% penguin (mainly Adelie), 35% seal of which were mostly crabeater, and 10% fish and squid. On the basis of all the published information, Laws (1984a) suggested that the overall relative proportions are 50% krill, 20% penguins, 14% seals, 9% fish, and 6% cephalopods.

Siniff and Stone (1985) have shown that in the Antarctic Peninsula area the diet of leopard seals changes over the year (Figure 8.12). They found that the consumption of crabeater seals rose sharply in November, when the newly weaned crabeater pups became available (Siniff et al. 1979). After November, the proportion of crabeater seals in the diet continued to rise until early February, after which there was a sharp decline in crabeater consumption accompanied by an increase in krill consumption. This decline in crabeater seals in the diet coincides with the ability of growing young animals to escape predation. Krill probably remain an important component of the diet over the winter as a high level of krill consumption (60%) was recorded in September. Penguins were an important dietary item in mid-February when young penguins were fledging and entering the sea. Cephalopods were a major food item in January but some were taken throughout the year. These findings confirmed the view that leopard seals are very catholic in their choice of food. Peaks in the incidence of the various groups of prey in the diet apparently occur when the prey is most available and vulnerable, or when opportunities to take other prey are few.

Analysis of the stomach contents of Weddell seals indicates that a variety of prey is taken including fish (Dearborn

TABLE 8.3
Rough Estimates of Food Consumption of Antarctic Seals. Feeding Rate Estimated at 7% of Body Weight for all Seals Except Elephant Seals, which were Assumed to Consume 6% of Body Weight Daily. Elephant Seals were Assumed to Feed 290 days year^{-1}, all others 335 days year^{-1}

Species	Crabeater	Leopard	Ross	Weddell	Elephant	Fur	Total
Stock size ($\times 10^2$)	30000[a]	400[a]	220[b]	730[b]	741[a]	1108[a]	33199
Mean wt (t)	0.193	0.272	0.173	0.246	0.500	0.500	–
Antartic biomass ($\times 10^2$ t)	5790.0	108.8	38.1	176.6	370.5	55.4	6542.4
Individual consumption							
kg d^{-1}	14	19	12	17	30	3	–
t y^{-1}	4.53	6.38	4.05	5.77	8.70	1.17	–
Annual consumption of stock (1×10^2) and average food item frequencies (% in brackets)[c]							
Euphausllids	127.4(94)	1.15(45)	0.08(9)	0.04(1)	–	0.44(34)	129.11
Cephalopods	2.72(2)	0.13(5)	0.57(64)	0.46(11)	4.48(75)	0.43(33)	8.79
Other inventebrates	1.36(1)	–	0.04(5)	1.48(35)	–	–	2.88
Fish	4.08(3)	0.13(5)	0.20(22)	2.23(53)	1.16(25)	0.43(33)	8.68
Birds	–	0.25(10)	–	–	–	–	0.25
Seals	–	0.89(35)	–	–	–	–	0.89
Total	135.56	2.55	0.89	4.21	6.09	1.30	151.06

Modified from øritzland (1977) and Laws (1977b) with data from SCAR/SCOR (1983c) and Siniff and Stone (1985).

[a] Stock estimates from SCAR/SCOR (1983)

[b] Sock estimates from Gilbert and Erickson (1977)

[c] Percentages for leopard seals from siniff and Stone (1985), for leopard seals from Orizland (1977), for crabeater, Ross and Weddell seals: and from Laws (1977b) for elephant and Antarctic fur seals.

Source: From Bengston, L., *Selected Scientific Papers Presented to the Scientific Committee of CCAMLR 1982–1984, Part II*, 43, 1985. With permission.

1965b; Calhaem and Christoffel 1969; Kooyman 1981c; Burns et al. 1998), squid (Clarke and MacLoed 1982b) and crustaceans, including krill (Lindsay 1937; Bertram 1949). Clarke and MacLoed (1982b) analyzed the contents of eight stomachs of seals taken at Deception Island. The majority contained fish, as well as crustaceans, isopods, amphipods, and krill. All of the stomachs contained stones, as is common in leopard and crabeater seals (Bengston 1982). From 336 lower beaks found in the stomachs they were able to estimate the frequency and biomass of eight species, six squid and two octopuses. Cephaopods were the predominant food taken in contrast to Weddell seals in the McMurdo Sound area where fish were the main prey occurring in 97% of the stomachs sampled (Kooyman 1981c).

Burns et al. (1998) determined the diet of adult and juvenile Weddell seals in McMurdo Sound from both scat and stable isotope analyses. The remains of the pelagic fish *Pleurogramma antarcticum* were recovered from between 70 and 100% of the scats. However, stable isotope and dive data analyses indicated that while most seals foraged predominantly on pelagic fish and squid some juveniles concentrated on shallow benthic *Trematomus* Testa et al. (1985) found that over a limited period in December the large Antarctic cod *Dissostichus mawsoni* was an important prey species in McMurdo Sound.

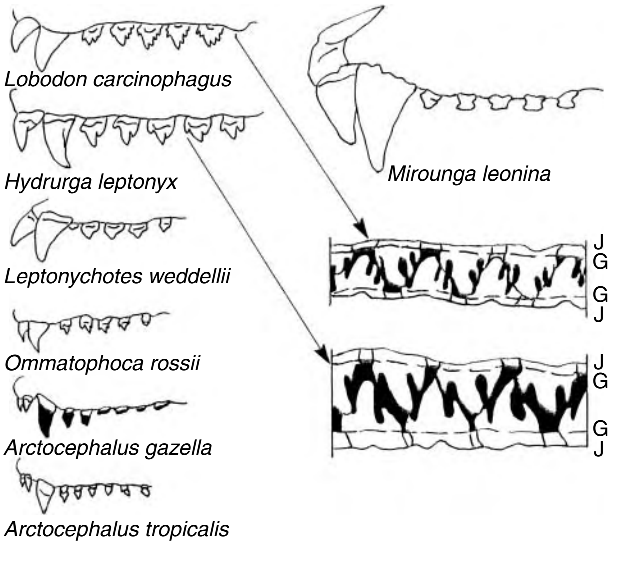


FIGURE 8.11 Maxillary dentitions of six Antarctic seals and one Subantarctic species. Inset, enlarged diagram of opposed jaws to show the sieve (J, jaw; G, gumline). (After Laws, R.M., *Antarctic Ecology*, Laws, R.M., Ed., Academic Press, London, 1984; From Costa, D. P. and Crocker, D. E., Antarc. Res. Ser., 70, 287–301, 1996. With permission.)

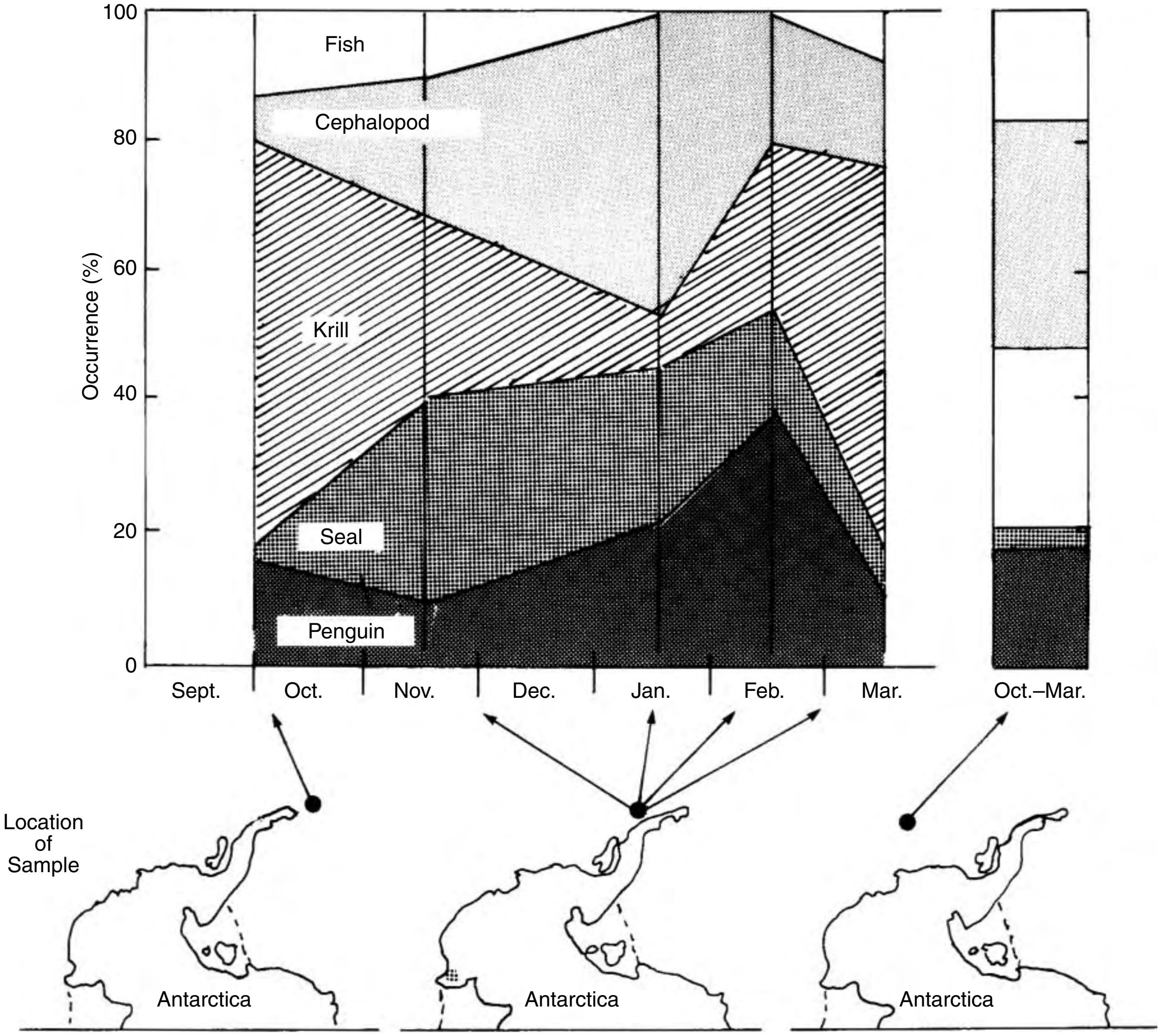


FIGURE 8.12 Frequency of occurrence (%) of food items in the stomachs of leopard seals in relation to time of the year. Sample size and date as follows: Sept.–Oct., $n = 38$ specimens with food in stomachs (data from Øritzland 1977); pooled data for Oct.–March, $n = 39$ specimens with food (data from Tikhomirov 1975) not broken down by month; Nov.–March, n = 66 specimens with food (data from Siniff and Stone 1985). (From Siniff, D.B. and Stone, S., in *Antarctic Nutrient Cycles and Food Webs*, Sigfried, W.R., Condy, P.R., and Laws, R.M., Springer-Verlag, Berlin, Heidelberg, 555, 1985. With Permission.)

It appears that there is considerable geographic variation in the diets of Weddell seals in Antarctic waters. Casaux et al. (1997) investigated the diet of Weddell seals at the South Shetland Islands. The diet was diverse and comprised both benthopelagic and benthic-demersal species. Fish were the most frequent (95.7%) and numerous (46.2%), but molluscs were the most important by mass (65.8%). Octopods, mainly *Pareledone charcoti*, constituted the bulk of the diet (53.1% by mass), but the importance of the remaining molluscs was negligible. The majority of the fish belonged to five species: *Gymnoscophalus nicholsi*, *Electrona antarctica*, *Lepidonotothen nudifrons*, *Gobionotothen gibberifrons*, and *Nototheniops nubelini*. The myctophid, *G. nicholsi*, was the most important fish prey, and the contribution of benthic-demersal species was low.

Lake et al. (2003) investigated the variation in Weddell Sea diets at four coastal locations in East Antarctica. In the southern fjords of the Vestfold Hills the diet was benthic fish and prawns, whereas in the northern area the diet was dominated numerically by *P. antarcticum*. Along the Mawson coast, the diet was spatially homogeneous, but varied over time. Squid, *Psychroteuthis glacialis*, was an important prey item for a short time in the spring, and octopus was also abundant. The variety in the diet composition demonstrated both flexibility in the Weddell seals' foraging response and the range of different prey items available to Weddell seals over the Antarctic continental shelf and slope. However, in most southerly area (McMurdo Sound), the seals take multiple prey species, which may minimize the coupling between Weddell seal population dynamics and the dynamics of their prey.

Little information is available on the pelagic food habits of elephant seals. Laws (1956) noted that young elephant seals may feed on amphipods for a short time after weaning. Only 35 of the 139 stomachs that he examined contained food; of these 83% had cephalopod remains and 26% fish. On the basis of these results and evidence from other studies (Murphy 1914; Matthews 1929), Laws concluded that elephant seal's year-round diet probably includes 75% cephalopods and 25% fish (Laws 1977b; McCann 1983). Clarke and MacLoed (1982a) identified eight species of cephalopods from five to six families in the stomachs from elephant seals at Signey Island. Four of these species were in the size range eaten by sperm whales.

As with elephant seals there is little information on the feeding of fur seals during their pelagic phase. However, it is clear that in the Antarctic Peninsula region and at South Georgia during the breeding season krill are a staple food for lactating females (Doidge and Croxall 1985; Costa and Crocker 1996; Reid and Arnould 1996). Fish and squid are taken by juvenile and nonbreeding adults (Bonner 1968; North et al. 1983). One of the most comprehensive studies is that of Doidge and Croxall (1985) who examined 79 stomachs collected at Schlieper Bay, South Georgia and 238 collected at Bird Island. They estimated that in the summer krill consumption varied from 75 to 92% by weight, but that in the winter the males consumed only 20% krill, with 30% squid and 50% fish. At Heard Island, Green et al. (1989, 1991) found that fur seals during the breeding season fed mainly on fish in contrast to those in the peninsula region. Pelagic myctophids constituted more than 50% of the fish taken by seals at the beginning of the summer and at the end of the season when there was an influx of nonbreeding males. From October to December fish from the surrounding shelf area (various benthic nototheniid species and the bentho-pelagic ice fish *Champsocephalus gunnari* and skate *Bathyraja* spp.) comprised the bulk of the catch. Laws (1977b) concluded that the overall diet of the Fur Seal was approximately 34% krill, 33% cephalopods, and 33% fish.

Casaux et al. (1998) investigated the diet of Antarctic fur seals at the South Shetland Islands. Overall fish were the most frequent prey (74.5%) and predominated by mass (54.4%), whereas krill predominated by number (94.2%). The importance of the remaining taxa represented in the samples (octopods, hyperiids and bivalves) was negligible. Among the fish myctophids represented 85.2% of the fish mass, with *G. nicholsi* and *E. antarctica* being the main prey. There, two species dominated in 1997, whereas the channichthyid *Cryodraco antarcticus* and the nototheniid *G. gibberifrons* were dominant in 1996.

At Marion Island, Klages and Bester (1998) found that the two fur seals on the island *Arctocephalus gazella* and *Arctocephalus tropicalis* fed predominantly on fish of the family Myctophidae. The seven species of myctophids that formed numerically 90 and 86% of the prey for *A. gazella* and *A. tropicalis*, respectively, all showed seasonal fluctuations in their contribution to seal diets. *Electrona carlsbergi*, *E. subaspersa*, *Metelectrona ventralis*, and *Gymnoscopelus fraseri* increased in the winter in both species of fur seals, whereas *Gymnoscopelus piabilis*, *Protomyctophum choridon*, and *P. tensoni* showed the opposite trend.

8.5.2 FEEDING AND DIVING BEHAVIOR

The depth of feeding dives and the timing of feeding activities differ among the various species of Antarctic seals. Ross, Weddell, and elephant seals appear to feed at great depths, up to several hundred meters, with diurnal feeding patterns that may vary seasonally (Laws, 1984a). Crabeater, fur, and leopard seals, on the other hand, are shallow feeders generally utilizing the upper portion of the water column, usually feeding to depths of about 60–80 m in summer, mainly feeding at night and being hauled out on land or ice, or swimming at the surface during the day.

Laws (1984a) has suggested three reasons why elephant seals probably feed at depth in the water column. First, the very similar northern elephant seal, *Mirounga angustitostris*, take prey species usually found between 100 and 300 m (Huey 1990); second, southern elephant seals take prey similar to that of sperm whales, which feed at great depths; and, third, their eyes have a visual pigment—a deep-sea rhodopsin—simiar to that found in deep-water fishes and which has been suggested as an adaptation for detecting bioluminescence of deep-sea squids (Lythgoe and Darnell 1970).

Southern elephant seals dive continuously, day and night, for the entire trip to sea which lasts between 2 and 8 months. Females who have just completed lactation depart and forage at sea for 10 weeks, return to molt, and then depart for an 8-month foraging trip during which gestation occurs. While at sea, they spend 90% of their time under water, with dives averaging 20 min (maximum dives of up to 2 h), followed by surface intervals of less than 4 min. Their diving patterns follow a diurnal cycle with the deepest dives occurring during the day and the shallowest at night. Modal dive depths are 300–600 m with a maximum reported dive depth of 1,430 m.

Elephant seals' large size, high energy storage capacity, low at-sea energy expenditure, and ability to fast while breeding may enable them to utilize foraging areas distant from breeding grounds, where prey is associated with reliable oceanographic features (Costa 1991a; Le Boeuf et al. 1993). In their investigation of seasonal movements of foraging areas of adult elephant seals at Marion Island, Jonker and Bester (1998) found that the longest residence time of post-breeding females during their foraging migrations was in areas at the outer edge of their feeding range (1,460 km). Residence time occurred both to the north and south of the island, largely within the inter-frontal zones south of the Antarctic Polar Front and between the Subtropical Convergence and the Subantarctic Front. Post-molting females traveled further a field (2,122–3,133 km) to the Antarctic Polar Front, to inter-frontal zones south of the front (within the pack ice edge), as well as to the Antarctic Continental Shelf. It is clear that elephant seals travel considerable distances to feed on areas associated with oceanographic features where prey might be concentrated.

Ross seals are also thought to be deep divers although only a limited amount of information is available. Their oversized eyes, as well as the presence of very large squid remains in their stomachs (King 1969), suggest that they may be adapted for feeding at great depths. Bengston and Stewart (1997) found that Ross seals dived continually when in the water at night. Dives averaged 110 m deep and 6.4 min long, the deepest dive being 212 m and the longest 98 min. There appears to be a peak haul-out in the middle of the day, indicating nocturnal feeding (Gilbert and Erickson 1977; Condy 1977b).

The diving patterns of the Weddell seal is better known than that of any other species of seal. It has been extensively studied (Kooyman 1981c, 1981d) by using time-depth recorders attached to free-diving seals. Dives of 200–400 are most common and one dive has been measured at 600 m. Because the latter dive was to the sea floor, the Weddell seal may be capable of even greater dives. The duration of such dives were 15 min or less. A typical pattern based on the record of diving behavior over 4 days in September is depicted in Figure 8.13. Kooyman (1981d) identifies two types of dives: deep dives and exploratory dives. Exploratory dives were shallow and of longer duration. Daytime dives were to a maximum depth of 600 m, whereas at night the maximum depth was 270 m, and the average depth 40 m. There were also more exploratory dives during the day. Plotz et al. (2001) investigated the foraging behavior of Weddell seals in Drescher Inlet of the Weddell Sea. They found that the seals foraged within two depth layers. The levels being from the sea surface to 160 m where temperature and salinity varied considerably, and near the bottom from 430 to 450 m, where temperature was lowest and salinity highest. The seals foraged almost exclusively in the upper water column at night.

Fur seals are tied to the shore for breeding and rely on the availability of nearby prey resources to produce milk to provision the young. Female Fur Seals must optimize the time they spend feeding at sea to the time spent nursing the pup onshore (Costa et al. 1989; Costa 1991a, 1991b; Lunn et al. 1993). Movements into the Southern Ocean for foraging can be estimated from diving behavior and assumed swimming speeds (Kooyman et al. 1986). These calculations suggest a maximum range from the breeding colony of 150 km from the continental shelf, for a 4 or 5-day foraging trip from South Georgia. Whereas Bengston et al. (1991) tracked a radio-tagged fur seal foraging from Seal Island for a maximum distance of 240 km. Although we have considerable information about diving and foraging behavior

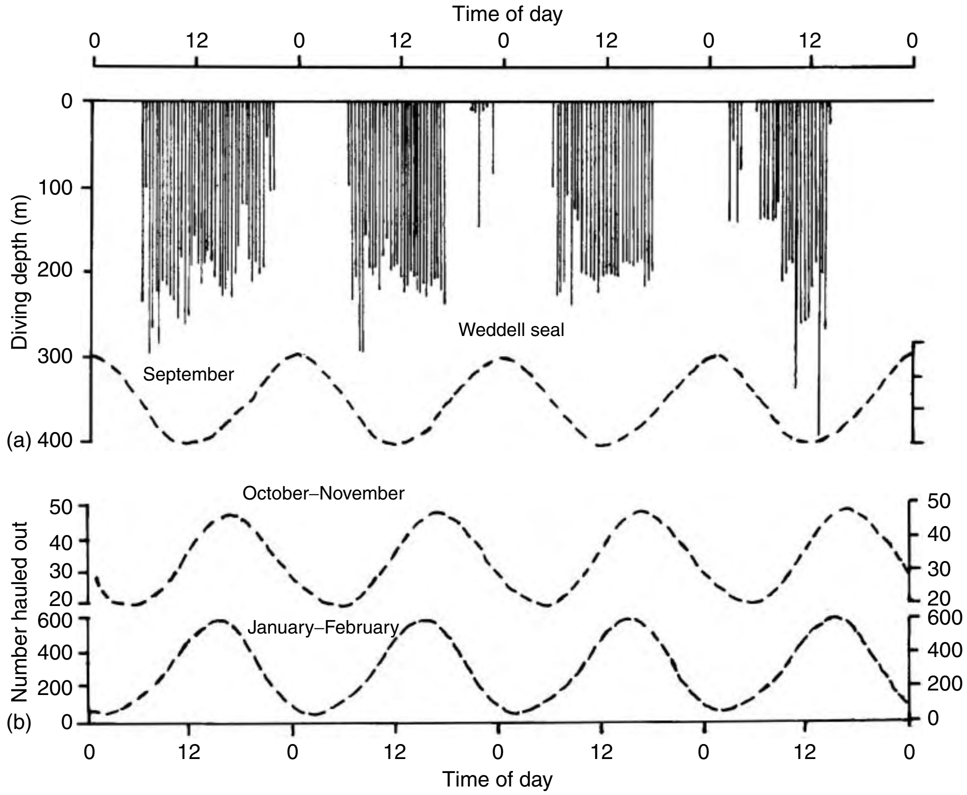


FIGURE 8.13 (a) Diagrammatical representation of typical Weddell seal time/depth diving pattern over 4 days in September (after Kooyman 1981d); (b) Described haul out pattern for September. Actual haul out cycle for McMurdo Sound Weddell seals during October/November and January/February, reported over 4 days, for comparison with the diving pattern of experimental animal (data from Kaufmann et al. 1975; Stirling 1969c). (From Laws, R.M., in *Antarctic Ecology*, Vol. 2, Academic Press, London, 621, 1984a. With permission.)

during the summer breeding season, almost nothing is known about its distribution and foraging ecology during the winter months.

Kooyman and Davis (1980) and Kooyman et al. (1982) have investigated fur seal diving behavior at Bird Island, South Georgia. In Figure 8.14, a typical diving pattern of a female fur seal feeding on krill off South Georgia is depicted. Like the Weddell seal, there is a diurnal pattern with most of the dive activity taking place at night. Diving depths are shallower than in the Weddell seal, most being between 20 and 50 m in depth, with a maximum depth of 100 m, and with dives to shallower depths at night. In Figure 8.14, a comparison of the diurnal pattern is made with that of the diurnal variation in the depth of the krill. It can be seen that there is a clear correlation between prey availability and diving depth.

8.5.3 Amounts of Food Consumed

Laws (1984a) and Bengston (1985) have analyzed the available data and estimated the amount of food consumed by Antarctic seals. They concluded that elephant seals feed for some 255–315 days annually varying according to age and sex, fur seals for 325–336 days, and the pack ice seals for about 335 days. However, the quantities of food consumed are somewhat difficult to estimate. Øritzland (1977) estimated an average meal size as follows: Weddell seal, 23 kg; Leopard seal, 16 kg; Crabeater seal, 8 kg; and Ross seal, 6 kg. Data on captive seals can give some estimate of daily feeding rates: 6–10% of body weights; less for elephant seals (Keyes 1968); 4–7% (Geraci 1975); adults 6%, young 19% (Ray in Sergeant 1973); 5% (Samuelson in Sergent 1973; Øritzland 1977); 5%. These estimates of 4–10% are for captive animals under different conditions and higher temperatures than wild Antarctic seals.

Laws (1977b) accepted Øritzland's (1977) tentative estimates of an average daily food intake of 7% of body weight for pack ice seals, a similar rate for fur seals, and 6% for elephant seals when not fasting. He applied these percentages to the feeding periods listed above to arrive at the following suggested daily food intake averaged over the year: 55 g food kg^{-1} for the elephant seal; 62 g kg^{-1} for the fur seal; and 64 g kg^{-1} for the pack ice seals. Thus the average annual food consumption would be about 20 times mean body weight for elephant seals, 23 times for fur seals, and about the same consumption for pack-ice seals.

8.5.4 Energy Requirements

The energetic values of the different foods consumed varies (Laws 1984a): for krill it is about 4.2–4.3 kJ (g wet wgt)$^{-1}$ (Clarke and Prince 1980); for lipid-rich myctophid fish 5.6–8.0 kJ g^{-1}; and for nototheniid fish about 4.1 kJ g^{-1}, compared with 3.5 kJ g^{-1} (range 2.9–4.5) for squid (Croxall and Prince 1982). Thus the ratio of energy content of krill, fish, and squid eaten by seals is probably about 1.00:0.94:0.80. The energetic value of seal prey is about 20.5 kJ g^{-1}, which is about four to five times the energy value of krill. The energy value of penguins is probably similar to that of krill.

Pinneped energetics have been reviewed by Lavigne et al. (1982, 1986). Naumov and Chekunova (1980) calculated the energy expenditure and needs for crabeater seals from generally accepted equations for mammalian energy balances. A total metabolic energy expenditure of 16,867 kcal day^{-1} (70,672 kJ day^{-1}) was calculated for a

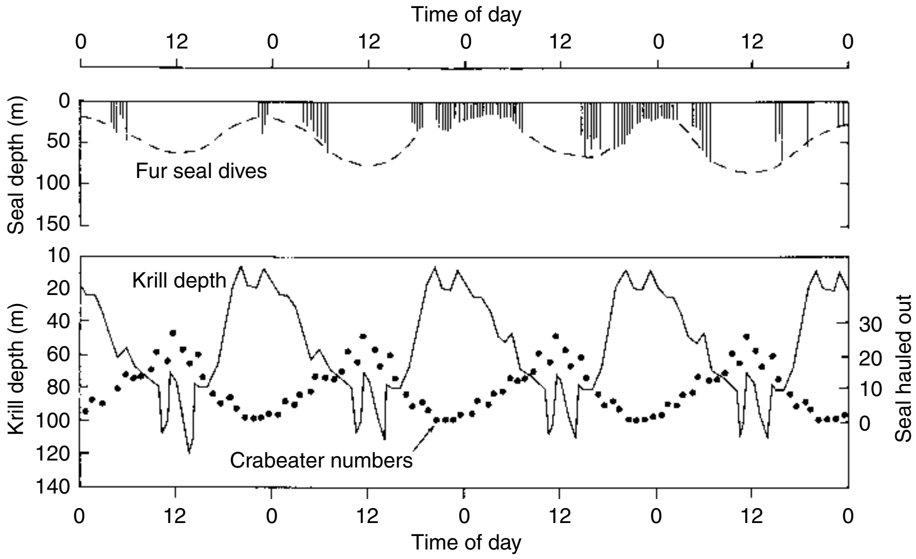


FIGURE 8.14 Diagrammatic representation of typical fur seal diving patterns over 4 days in January compared with the diurnal variation in mean depth of krill in the Scotia Sea in summer (data from Everson 1984a), and diurnal variation in Crabeater seal numbers hauled out in pack ice on January 15, 21, and 23 at about 69°40′ E (data from Condy 1977b). (From Laws, R.M., in *Antarctic Ecology*, Vol. 2, Academic Press, London, 621, 1984a. With permission.)

190 kg female. Growth energy requirements were calculated at 782 kcal day^{-1} (3,277 kJ day^{-1}). They further estimated that a female spends over 51% of her energy resource on reproductive metabolism. They calculated that their 190 kg seal must consume 10.4% of its body weight (20 kg) daily to satisfy energy requirements of 22,062 kcal day^{-1} (92,440 kJ day^{-1}). They also estimated that it would feed intensively for only about 120 days a year, and for 200 days would only eat enough (15 kg) to maintain its resting metabolism. Averaged over the year this represents 14.8 kg day^{-1} or 7.8% of the seal's body weight.

Doidge and Croxall (1985) have analyzed energy requirements and food consumption of the fur seal population at South Georgia. They estimated that krill accounted for 69% of the food biomass taken by the herd, fish 19%, and squid 12%. In summer, the population could consume about 23% of its biomass daily, assuming an assimilation rate of 75%. If there was a higher assimilation rate (say 90%, as has been estimated by Lavigne et al. (1982, 1986), then 19% of the body weight would be required each day. For the northern fur seal *Callorhinus ursinus*, it has been estimated that juveniles need to consume 14% of their body weight to meet existence requirements. A higher rate of 16% (Costa and Gentry quoted in Doidge and Croxall 1985) has recently been calculated. These estimates indicate that fur seals have higher energy demands (e.g., 7% of body weight), than previously assumed (McAlister et al. 1976; Laws 1977b; Payne 1979).

8.6 REPRODUCTION, GROWTH, AND DEVELOPMENT

8.6.1 Annual Reproductive Cycle

Antarctic seals produce their pups in the spring during a short synchronized period which varies according to the species and latitude. The timing of the pupping season of all species is shown in Figure 8.9. This timing seems to be remarkably constant for any one colony and from year to year (Smith and Burton 1970; McCann 1980a, 1980b). The latitudinal changes which occur in this timing are illustrated by the Weddell seal where the peak birth date varies with latitude from September 7 at Signey Island (61°S) and to October 23 at McMurdo Sound (78°S) (Mansfield 1958; Stirling 1969a). Within a population age classes tend to pup or mate at different times, e.g., young elephant seal females pup earlier than old females (Laws 1956; McCann 1980a, 1980b).

Table 8.4 gives details of the approximate duration of the female reproductive cycles. From this table, it can be seen that the lactation period ranges from about 23 days in the elephant seal to 110–115 days in the fur seal; these periods are all much longer in Arctic seals. The growth of the seal pups is rapid due to the quantity and quality of the milk produced by the females. In the elephant seal the fat content of the milk increases from about 12% at birth to over 40% in the second week. In the fur seal, which has a much longer period of lactation, the mean percentage of fat is 26.4%.

Pinnieds as a group exhibit delayed implantation. The blastocyst arrives in the uterus about 6 days after successful mating and the subsequent period until implantation varies from 5 weeks in the leopard seal and Weddell seal to 4 months in the fur seal and elephant seal. From Table 8.4, it can be seen that the period from parturition to conception is inversely proportional to the period from conception to implantation, or parturition to implantation, and directly proportional to the period from implantation to parturition (Laws 1984a). Delayed implantation can be seen as a mechanism that compensates for the varying period from parturition to conception.

8.6.2 Comparison of Mating Systems

As Laws (1984a) points out the feeding behavior and breeding behavior of land-breeding seals occur in completely different habitats from the ice-breeding species. They are adapted anatomically and physiologically to exploit marine food resources, but give birth to their young on land. The gregarious behavior of the land-breeding species has made it

TABLE 8.4
Approximate Duration (Days) of the Stages in the Annual Cycle of the Antarctic Female Seals

Species	Lactation Period	Parturition to Conception	Conception to Implantation	Parturition to Implantation	Implantation to Parturition
Fur	110	8	125	133	232
Elephant	23	19	120	139	226
Crabeater	28	30	80	110	225
Weddell	50	48	48	96	269
Leopard	302	48	48	96	269
Mean	(48)	31	84	115	245
Range	(87)	40	77	43	43
Range as % of mean	(181)	129	92	37	17

Source: From Laws, R.M., in *Antarctic Ecology,* Vol. 2, Academic Press, London, 621, 1984a. With permission.

possible for them to become concentrated in closely packed breeding colonies. In the polygnous species, such as the elephant seal and the fur seal, the males holding territories for the longest periods have opportunities to fertilize more females than other males. Thus in these species the males have evolved to be much larger than the females. Fat stored in the blubber serves as an energy source during fasting and larger animals can go for longer periods without food than smaller ones, because of the more favorable ratio of surface area to metabolic rate. There is also strong selection for male aggressiveness. Larger canines, protective shields of skin or fur, structures used in visual or oral threats, and the capacity for prolonged fasting are all characteristics that contribute to territory maintenance.

In contrast to the land-breeding species, the ice-breeding species have evolved a reversed sexual dimorphism, with the males smaller then the females. In the pack-ice-breeding species the spacing of the females is strongly influenced by the distance between floes and floe size. The unpredictability of floe size and the predominance of floes that will hold only one female group has selected against the development of colonial breeding. Siniff (1982) suggests that predators may have played an important role in the evolution of crabeater reproductive behavior since underwater copulation would probably attract large predators and increase vulnerability. The leopard seal, on the other hand, appears to copulate under water and presumably is able to cope with the only other large predator, the killer whale *O. orca*. Where mating is under water (leopard, Ross, and Weddell seals), the advantage may lie not in the male size, but in agility under water, where smaller size may be an advantage. The Weddell seal is of special interest in that in its breeding areas on the fast ice it is not subject to predation. The predictable annual ice cracks along which the pupping colonies form can be considered a resource required by the females for reproduction. Siniff (1982) suggested that: “Rather than defending the female directly, it is advantageous (for the individual males) to defend sections of the tide crack, since their mating success is thus increased.” In addition, there may be advantages to the male in remaining in the water where energy expenditure may be less than on the surface and opportunities for feeding may occur. If he were defending females on the surface, he would have to fast, like the elephant and fur seals.

8.7 POPULATION DYNAMICS

In common with other large mammals the Antarctic seals have certain characteristics which make them unique but difficult to study (Fowler and Smith 1981). The most common characteristic is their lengthy life span, an attribute which makes it difficult to understand their population dynamics. Since individuals live to 25–30 years long-term population studies are needed and of these there are all too few, the exception being studies on Weddell seals (Stirling 1989a, 1989c, , 1971a; Siniff et al. 1970, 1977b; Hiby 1983; Testa and Siniff 1987) and those on the Fur Seal at Bird Island (Bonner 1981; Croxall et al. 1988b).

Estimation of a number of population parameters is needed for each species if we wish to understand the factors influencing survival, and population trends, i.e., whether the population is increasing or decreasing and at what rate. These factors include reproductive parameters such as age at maturity, percentage pregnant and secondary sex-ratio, age structure, longevity, population density, both during the breeding season and the nonbreeding season, and how these factors may vary with population density and food supply. Changes in population size are probably due to concurrent changes in several parameters.

8.7.1 AGE STRUCTURE, FECUNDITY, AND SURVIVAL

Laws (1960b) constructed what was probably the first life table for a pinniped, the elephant seal, for South Georgia females, exposed only to natural mortality, for males exposed only to natural mortality, and for males exposed to both natural and hunting mortality. These data were used to formulate new management regulations for the elephant sealing industry (see Chapter 18). Since then, commercial sealing operations have stopped (in 1964) and subsequently McCann (1980a) developed revised life tables incorporating additional information, including sightings of known-age branded animals (Carrick and Ingham 1962). The data indicate higher survival but they are approximately close to Law’s values. McCann (1980a) recalculated Law’s (1960b) 82.5% pregnancy rate as 88%, and for the life table construction assumed pregnancy rates of 2% at 3 years, 79% at 4 years, and 85% for 5 years and over. Sex ratio was estimated at 53% males.

Bonner (1968) estimated fur seal survival to age at first pupping at 3 years as 19–56%, whereas Payne (1977) estimated the same parameter at 52%. Payne’s survival curve for the Bird Island population is plotted in Figure 8.15. Doidge and Croxall (1983) investigated density-dependent effects by comparing a high-density breeding site (Bird Island; 170 pups at 1.5 individuals m^{-2}) and a low, but increasing density site (Schlieper Bay; 415 pups at 0.2 individual m^{-2}). Pup mortality at Schlieper Bay was only 5% compared with 25–30% at Bird Island.

Bengston and Laws (1984) aged a sample of 1,304 crabeater seals. The foetal sex ratio was 55% male:45% female, whereas the sex ratio at birth was 51% male:49% female. The observed later (tertiary) sex ratio of 42% male:58% female indicated a substantially higher male mortality after weaning; as the population aged, there was an increasing proportion of females, reaching 63% of the animals older than 20 years. The survival curve for females is shown in Figure 8.15. The data for the construction of this curve included an estimated first-year survival of 56% and an overall survival to first pupping at 4 years of 25%. The average pregnancy rate for all mature females was 90%; for ages 3–25 it was 94%, and 97% for the most fertile years while declining at higher ages.

Much more research has been carried out on Weddell seal populations, both in space and time (Strling 1969a,

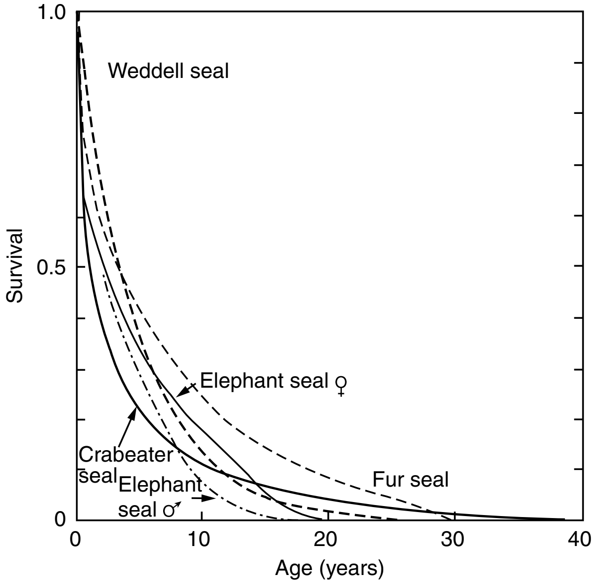


FIGURE 8.15 Equilibrium survival curves for female Antarctic seals and male elephant seals. (From Laws, R.M., in *Antarctic Ecology*, Vol. 2, Academic Press, London, 621, 1984a. With permission.)

1971b; Siniff et al. 1977b; Croxall and Hiby 1983). Human interference, especially the taking of seals for dog food, has affected a number of study populations. For the Signy Island population Croxall and Hiby (1983) estimated that the annual female survival rate from 1970 to 1977 was constant at 0.80. This is in close agreement with rates for McMurdo Sound populations of 0.77 (Siniff et al. 1977b), and the reanalysis of Stirling's (1971a) data gave rates of 0.84 and 0.87. Male survival rates were 0.72, 0.75, and 0.88, depending on the analytical method (Siniff et al. 1977b).

In Figure 8.15 a survival curve for an equilibrium population of Weddell seal females is plotted, based on a survival rate from birth of 0.815. Stirling (1971b) calculated an overall pregnancy rate of 80.5% to age 17 years. However, Siniff et al. (1977b) obtained a fecundity rate of only 62% from 7 to 18 years for 1970–1974, the comparable rate for the same population in 1966–1968 was 83% (Stirling 1971b), and for the Signey Island population it was 90%.

Data on leopard and Ross seal population dynamics are lacking apart from some published pregnancy rates. For leopard seals, the pregnancy rates are 85% (Brown 1957), 93% (Tikhomirov 1975), and as low as 61% (Øritzland 1970a, 1970b). For Ross seals, rates of 88% (Øritzland 1970a, 1970b) and 90% (Tikhomirov 1975) have been recorded.

The survival curves in Figure 8.15 are for females, apart from the curve for elephant seal males. The lower survival rate of the males in this species is probably paralleled, to a greater or lesser extent, in the other Antarctic seal species. Laws (1977a) drew attention to the different shape of the survival curve of crabeater and Weddell seals. The crabeater seal is a solitary breeder in an unstable habitat and it clearly suffers from significant predation, especially from leopard seals, in the first year of life. Subsequently it probably faces fewer hazards and has a higher adult survival rate than Weddell seals. In contrast predation is insignificant in the southerly breeding Weddell seal where breeding takes place on fast ice. As an adult, however, the Weddell seal is subject to mechanical senescence due to the wear of teeth in maintaining breathing holes (Bertram 1940; Stirling 1969b).

Population studies have revealed conspicuous variation in year class strength of Antarctic Peninsula crabeater seals, with peak year classes at mean intervals of 4.67 years (ranging from 4 to 5 years) (Laws 1984a). Strikingly similar fluctuations in the abundance of juvenile leopard seals occur at Macquarie Island (Rounsevell and Eberhard 1980). Peaks occur every 4 or 5 years (mean 4.67). Laws (1984a) lists some possible explanations for these fluctuations.

- In crabeater or leopard seals, or both, recruitment may be directly correlated with krill abundance, pack ice extent and type of weather.
- Year-to-year crabeater recruitment may be dependent on leopard seal predation pressures, perhaps influenced by conditions in the pack ice (e.g., packing of floes).
- Successful leopard seal conception and therefore births may be related to abundance or availability of crabeater pups, promoting improved nutritive status of mating leopard seals.

A similar fluctuation might also exist in the krill-eating fur seal at South Georgia. Payne (1977) analyzed population data which suggested peak year classes at a mean interval of 4.25 years. Moreover, in 1978, a year when krill availability at South Georgia was low, there was the highest ever pup mortality (30%) at Bird Island (Doidge and Croxall 1983); 1979 was also a year in which crabeater recruitment would have been particularly low.

Population trends, i.e., whether seal populations are increasing or decreasing, will be discussed further in Chapter 16.

8.7.2 PERIODIC FLUCTUATIONS IN SEAL POPULATIONS

In phocids, reproductive performance (a measure of the maternal investment) during a given season is a reflection of prey availability over the preceding year and represents the mothers' foraging activity over a much larger and temporal scale than is the case for otarids (Costa 1993; Trillmich and Ono 1993). Thus the weaning mass of a phocid pup is an indicator of their mothers' foraging success over the previous year. The subsequent post-weaning survival of the pup is related to both its weaning mass (energy reserves provided by the mother) and the resources available to the pup after weaning. Variability in the numbers of individuals in ice-seal cohorts provides an index of fluctuations in prey availability that correlate with oceanographic events (Costa and Crocker 1996). However, we know little about the foraging range of female seals prior to parturition and essentially nothing about the foraging range of weaned seal pups. Nevertheless, three of the pack-ice breeding seals exhibit quasi-cyclic fluctuations in population processes. Strong cohorts are evident in the age structure of Crabeater Seals at 4- or 5-year intervals (Bengston and Laws 1985). Leopard seals on Subantarctic Islands exhibit a seasonal cycle in their occurrence which is probably related to the proximity of the pack ice edge (Rounsevell and Eberhard 1980). At Macquarie Island, the largest numbers appear every 4–5 years (Rounsevell 1988). Weddell seals in McMurdo Sound exhibit 4–6-year fluctuations in their reproductive rate (Testa and Siniff 1987). Testa et al. (1991) compared such patterns to the SOI, a measure of the strength of El Nino-southern oscillation events. All three data sets exhibited some level of cyclic behavior with an approximate periodicity of 5 years. Weddell seals were generally in phase with SOI, leopard seals were in phase with the SOI throughout the 1960s, but the Southern Ocean oscillation subsequently preceded the leopard seal pattern by about a quarter cycle. These findings suggest that large-scale oceanographic processes may dramatically impact on population processes and could be an important factor in the regulation of top predator populations in the Southern Ocean (Croxall and Rothery 1991).

9 Whales

CONTENTS

9.1 INTRODUCTION

There is probably no conservation issue that has aroused as much heated debate and controversy as the question of the commercial exploitation of whales. Apart from the ethical question as whether it is right to kill these highly intelligent animals there is also the question whether any species of whales are sufficiently abundant to withstand exploitation. Additionally the question remains whether our state of knowledge of their ecology and population dynamics is sound enough to ensure that their exploitation could take place without endangering their survival and causing irreversible changes in the ecosystem of which they are an integral part.

Prior to their commercial exploitation during this century, the Antarctic whales comprised, at least in biomass, one of the largest mammalian stocks ever to have existed on earth. Within a short time consequent changes in the composition and structure of the Southern Ocean ecosystem decimated these abundant whale stocks. Slijper (1982) and Mackintosh (1965) gave general accounts of the attributes of whales. Subsequent reviews of the whales' ecology include the reviews of Anderson (1969), Gaskin (1976, 1982), Allen (1980) and FAO (1981). More recent reviews of studies on Antarctic whales include those of Brown and Lockyer (1984), Bengston (1985a, 1985b), Gambell (1985), Chapman (1988), Boyd (1993), and Stewardson (1997).

9.2 SPECIES COMPOSITION

Cetacean species occurring in the Southern Ocean are widely distributed, and none are exclusive to the region. Seven species of Mysticete (baleen) whales and twelve species of Odontocete (toothed) whales occur in the Southern Ocean south of the Polar Front. Five of the baleen whale species (blue, fin, sei, minke, and humpback) belong to the family Balaenopteridae (rorquals). All of the six baleen whales and the toothed whales (the sperm and killer whales) are, or were, abundant in Antarctic waters. The Antarctic whaling industry has caught large numbers of all the baleen whales and the sperm whale. Of the toothed whales, the killer whale, the two beaked whales, and the pilot whale have been caught in smaller numbers.

9.2.1 BALEEN WHALES

The baleen or whalebone whales can be recognized by the triangular plates of horny baleen which grow from the upper jaws to form an efficient mechanism for sieving small food particles from the water. Their bodies are streamlined in shape. They have relatively large heads with a pair of blowholes on the top. All species of baleen whales are highly migratory, being seasonally abundant in Antarctic waters and breeding in warm-temperate, subtropical waters in winter and feeding in cold-temperate and polar waters in the summer.

The blue whale (*Balaenoptera musculus*) (Figure 9.1) is the largest of all species of whale and is probably the largest animal that has ever existed. It may measure up to 30 m in length and weigh over 159 tons. The fin whale (*Balaenoptera physalus*) (Figure 9.2) may grow up to 20 m and a weight of 90 tons, the sei whale (*Balaenoptera borealis*) (Figure 9.3) may grow up to 18 m and 30 tons, but the minke whale (*Balaenoptera acutirostratus*) (Figure 9.4) seldom exceeds 11 m in length and 19 tons in weight. The humpback whale (*Megapterus novaeangeliae*) (Figure 9.5) is placed in the same family, the rorquals, as those belonging to the genus *Balanopterus*, but the humpback whale is rather plumper in form, has extraordinarily large flippers, up to a third of its total length, and may reach 16 m, with a maximum weight of 60 tons (Mathews 1937). The right whale (*Eubalaena australis* also known as *Balaena glacialis*) (Figure 9.6) is

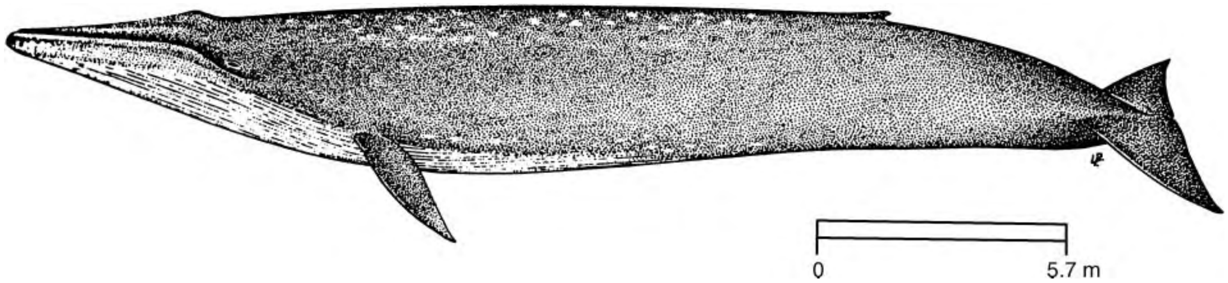


FIGURE 9.1 The blue whale (*B. musculus*). (From FAO, Southern Ocean CCAMLR Convention Area, Fishing Areas 48, 58, and 88. FAO Species Identification Sheets for Fishery Purposes, *Food and Agricultural Organization of the United Nations/Commission for the Conservation of Antarctic Marine Living Resources*, Vol. 2, Rome, 233–471, 1985. With permission.)

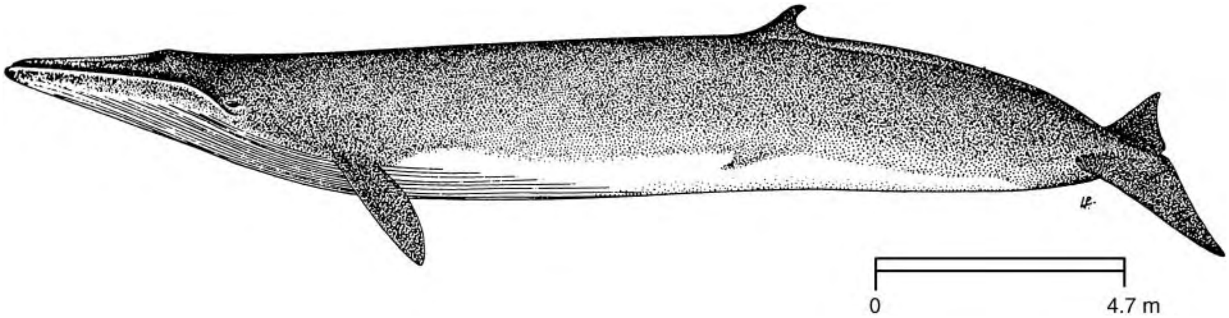


FIGURE 9.2 The fin whale (*B. physalus*). (From FAO, Southern Ocean CCAMLR Convention Area, Fishing Areas 48, 58, and 88. FAO Species Identification Sheets for Fishery Purposes, *Food and Agricultural Organization of the United Nations/Commission for the Conservation of Antarctic Marine Living Resources*, Vol. 2, Rome, 233–471, 1985. With permission.)

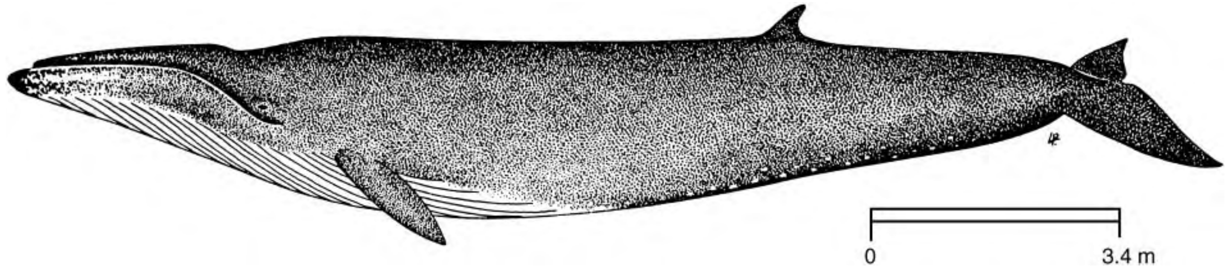


FIGURE 9.3 The sei whale (*B. borealis*). (From FAO, Southern Ocean CCAMLR Convention Area, Fishing Areas 48, 58, and 88. FAO Species Identification Sheets for Fishery Purposes, *Food and Agricultural Organization of the United Nations/Commission for the Conservation of Antarctic Marine Living Resources*, Vol. 2, Rome, 233–471, 1985. With permission.)

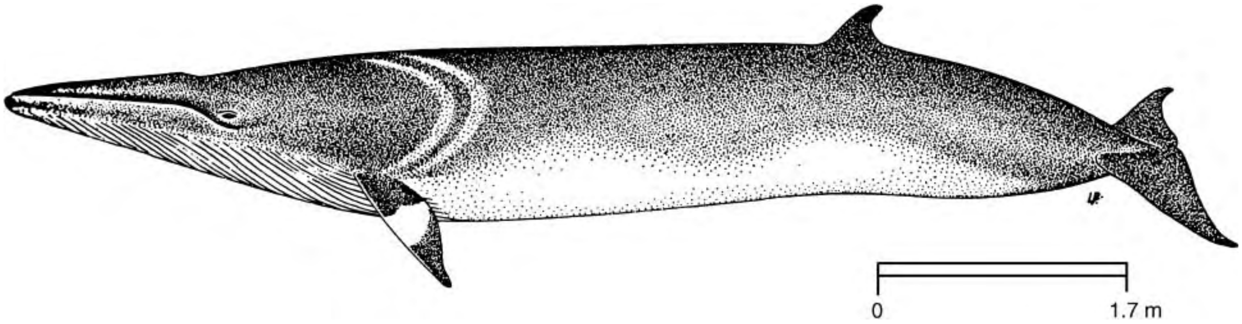


FIGURE 9.4 The minke whale (*B. acutirostrata*). (From FAO, Southern Ocean CCAMLR Convention Area, Fishing Areas 48, 58, and 88. FAO Species Identification Sheets for Fishery Purposes, *Food and Agricultural Organization of the United Nations/Commission for the Conservation of Antarctic Marine Living Resources*, Vol. 2, Rome, 233–471, 1985. With permission.)

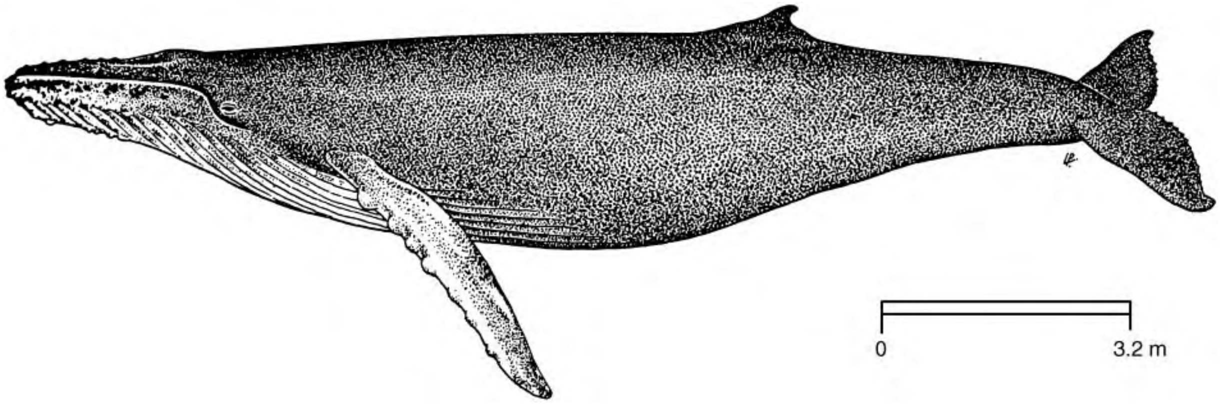


FIGURE 9.5 The humpback whale (*M. novaeangliae*). (From FAO, Southern Ocean CCAMLR Convention Area, Fishing Areas 48, 58, and 88. FAO Species Identification Sheets for Fishery Purposes, *Food and Agricultural Organization of the United Nations/Commission for the Conservation of Antarctic Marine Living Resources*, Vol. 2, Rome, 233–471, 1985. With permission.)

also a plump animal, reaching a weight of 90 tons for an 18 m specimen. This whale is distinguished from the rorquals due to its lack of a dorsal fin and throat grooves.

9.2.2 TOOTHED WHALES

The sperm whale (*Physeter macrocephalus*), also known as *Physeter catadon* (Figure 9.7) is the largest of the toothed whales and shows a marked sexual dimorphism. Only the largest males, which grow to 18 m and 70 tons, penetrate the Antarctic waters. The females, which are less than 11.5 m in length and weigh less than 17 tons, juveniles, and the smaller males remain in temperate and tropical waters. Killer whales (*Orcinus orca*) (Figure 9.8) show a similar difference in size between the sexes—the males reaching 9 m and the females 8 m, with weights of up to 7 or 8 tons. The dorsal fin of

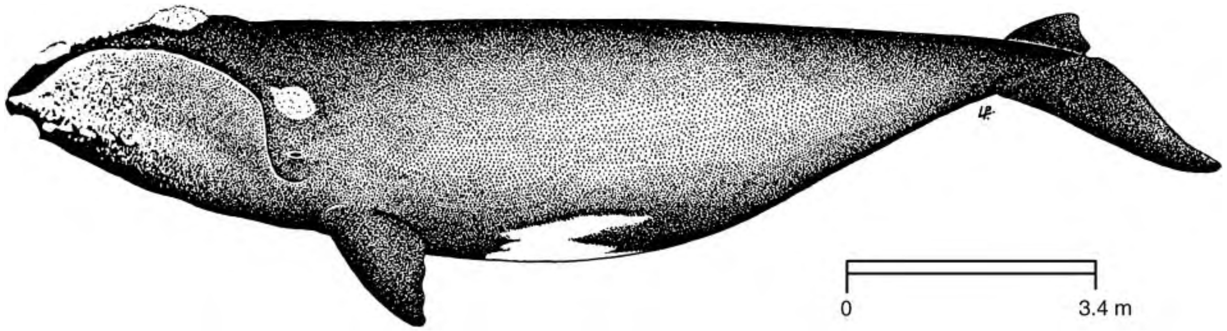


FIGURE 9.6 The right whale (*B. glacialis*). (From FAO, Southern Ocean CCAMLR Convention Area, Fishing Areas 48, 58, and 88. FAO Species Identification Sheets for Fishery Purposes, *Food and Agricultural Organization of the United Nations/Commission for the Conservation of Antarctic Marine Living Resources*, Vol. 2, Rome, 233–471, 1985. With permission.)

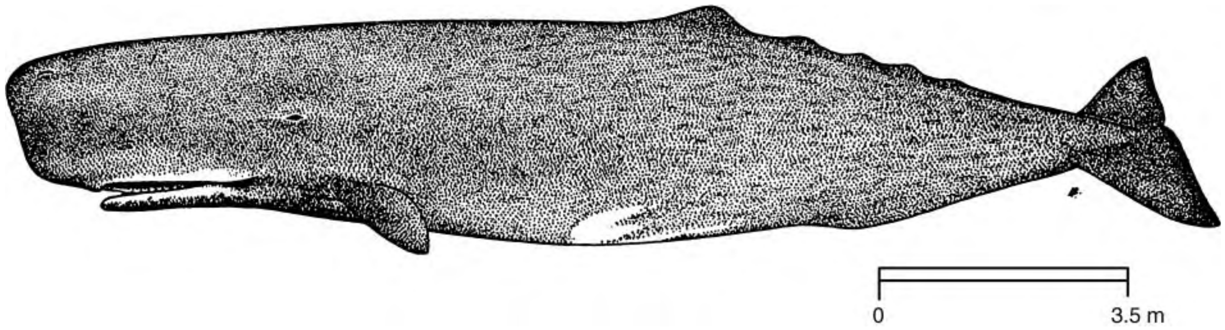


FIGURE 9.7 The sperm whale (*P. catadon*). (From FAO, Southern Ocean CCAMLR Convention Area, Fishing Areas 48, 58, and 88. FAO Species Identification Sheets for Fishery Purposes, *Food and Agricultural Organization of the United Nations/Commission for the Conservation of Antarctic Marine Living Resources*, Vol. 2, Rome, 233–471, 1985. With permission.)

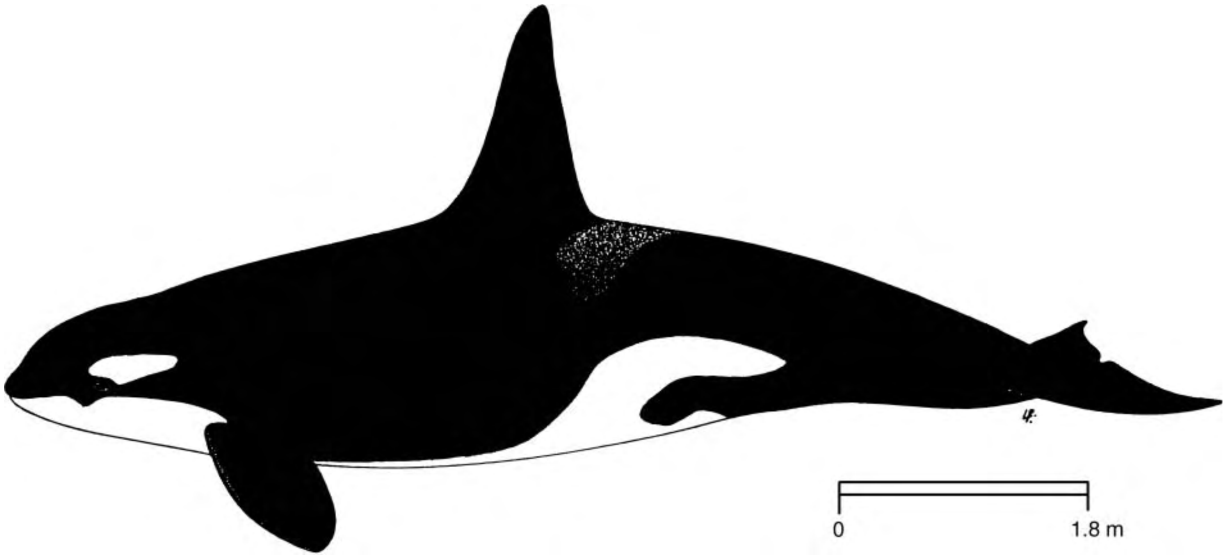


FIGURE 9.8 The killer whale (*O. orca*). (From FAO, Southern Ocean CCAMLR Convention Area, Fishing Areas 48, 58, and 88. FAO Species Identification Sheets for Fishery Purposes, *Food and Agricultural Organization of the United Nations/Commission for the Conservation of Antarctic Marine Living Resources*, Vol. 2, Rome, 233–471, 1985. With permission.)

the adult males can measure up to 1.8 m in length and is twice the size of the dorsal fin of the females.

Toothed whales differ from all other mammals due to having only one nostril, which is normally set in the midline, although two nasal passages are present internally. The blowhole of the sperm whale is sigmoid in shape and is located asymmetrically on the left side of the dorsal surface of the head. The right naris (tubular part of the nostril) forms a wax-filled "case" set on the top of the skull, giving the sperm whale its characteristic blunt head that makes up to a third of the total length of the body. It is thought that the spermaceti wax may have roles both in buoyancy and in sound transmission.

Many of the smaller toothed whales are comparatively rare and poorly known (see Goodall and Galeazzi 1985 for a review of their distribution and ecology). Most are less than 5 m in length. The two largest are the southern bottlenose whale (*Hyperoodon planifrons*), which reaches a length of 7 m and a weight of 3–4 tons, and Arnoux's beaked whale (*Berardius arnuxii*), which attains a maximum length of 10 m and weights of 7–8 tons.

9.3 DISTRIBUTION, GENERAL LIFE HISTORIES, AND MIGRATIONS

No exclusively Antarctic cetaceans exist, and all species occurring south of the Polar Front are distributed more widely. The five balaenopteris species are found in both northern and southern hemispheres. Although they undertake extensive migrations the populations of the two hemispheres remain separate, a gap between the two stocks being maintained at all times. Direct observation of migration and tagging studies has determined migration patterns (Mackintosh 1965; Dawbin 1966; Lockyer and Brown 1981). The adult whales migrate from their winter breeding grounds in subtropical and temperate waters to Antarctic waters for the summer where intensive feeding takes place for periods of up to 6.5 months (Dawbin 1966). Many whales, however, remain in Antarctic waters for a lesser period of up to 5 months. Juvenile whales also migrate, but their timing is slightly different from adult whales' timing. Also their penetration into higher latitudes is not as great (Mackintosh and Wheeler 1929; Kawamura 1974; Lockyer 1981a; Lockyer and Brown 1981). While the sperm whales also undertake annual feeding migrations, the migratory patterns of other Southern odontocetes is poorly known.

Breeding of the large baleen whales takes place in warm tropical and subtropical waters located to the north of the summer feeding grounds. The life cycle of these whales is closely related to the pattern of seasonal migrations between breeding and feeding areas. For the humpback, blue, fin, and sei whales, mating takes place during the winter months, often resulting in conception in many of the females. In the spring, the whales migrate south towards the polar feeding grounds, and as the ice retreats they penetrate further into Antarctic waters to feed on the rich planktonic organisms that comprise their diet. After a period of three to four months of intensive feeding the whales migrate once more in the autumn to temperate or subtropical waters. Gestation takes nearly a year, and the pregnant females give birth in these warmer waters approximately a year after mating. Relatively little feeding appears to take place in the warmer waters because blue, fin, humpback, and sei whales examined at subtropical whaling stations in winter usually have little or no food in their stomachs compared with animals examined on the Antarctic whaling grounds (Mackintosh and Wheeler 1929; Chittleborough 1965; Bannister and Baker 1967; Best 1967). Thus during the winter the whales live largely on reserves of food stored in the blubber and body tissues during the intensive summer feeding period.

The newborn calves accompany their mothers on the following spring migration towards the waters of the Southern Ocean, living on their mother's milk. Six months after birth the calves are weaned and can follow the migration cycle independently. Humpback calves, however, may be dependent on their mother's milk for up to a year. The migration of minke whales follows a somewhat different pattern to that of the larger rorquals because some minke whales are present in temperate waters throughout the year, for example, in the Indian Ocean (Best 1982).

Distribution patterns in the Southern Ocean and other seas are as follows:

1. *Blue Whales*. Blue whales have a circumpolar distribution. A round trip migration between 20 and 65°S may cover 9,000–10,000 km (Lockyer 1981a). Their arrival in Antarctic waters commences in early November, earlier than the arrivals of fin. sei and minke whales. Adults arrive first, followed by juveniles about a month later. Pregnant females are frequently the first to arrive and the last to leave. Lactating cows with calves are usually the latest arrivals (Mackintosh and Wheeler 1929; Lockyer 1981a). Except for pregnant females, the whales depart in the same order as they arrived. Their average stay in Antarctic waters is about four months. Most of the blue whales will have left by March–April.

   Based mainly on evidence from the concentrations of whales reflected in commercial catches and sightings in the Antarctic, Mackintosh (1942) proposed that the distribution of blue whales could be divided into six areas extending through some 60–70° of latitude (shown in Figure 9.9). These feeding concentrations were considered as stocks at least for management purposes and were believed to correspond to biological stocks.
2. *Pygmy Blue Whales*. Pygmy blue whales are found mainly near Marion Island, Isles Crozet and Isles Kerguelen (Ichihara 1966b). Their distribution is mostly Subantarctic, occurring in a restricted zone between 45 and 55°S and 0–80°W (Mackintosh 1965; Ichihara 1966a).
3. *Fin Whales*. Gunther (1949) described a uniform circumpolar distribution of fin whales throughout

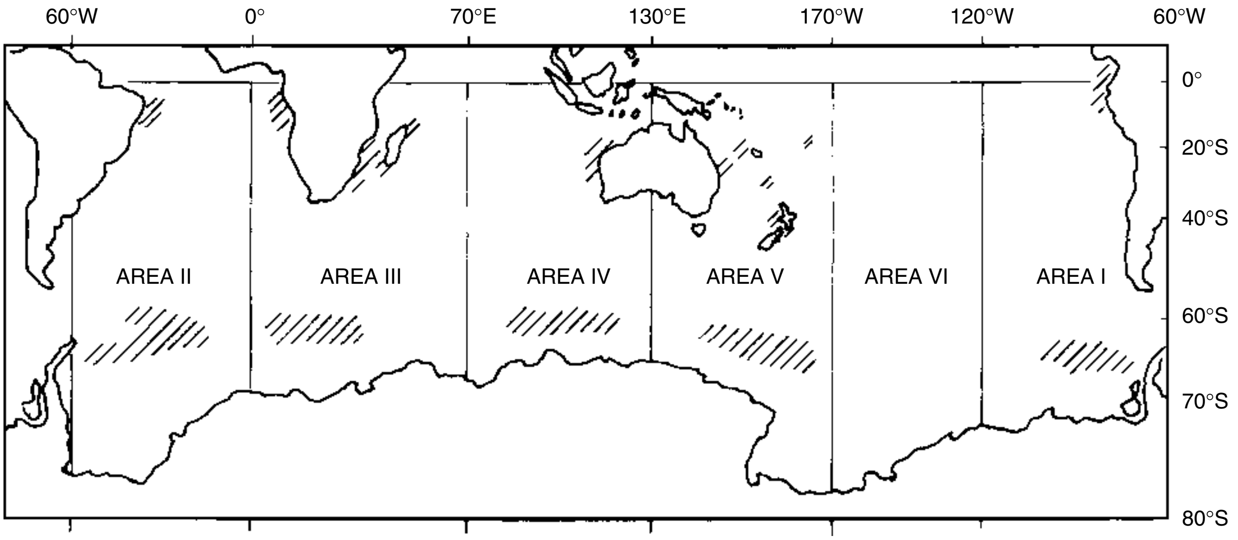


FIGURE 9.9 Blue whale feeding areas in the Antarctic. (From Mackintosh, N.A., *Diac. Rep.*, 197, 1942 with permission.)

their feeding grounds. The densest concentrations are found where Antarctic krill are abundant (Mackintosh 1965, 1973; Lockyer and Brown 1981). Their annual migration patterns thought to be similar to that of blue whales (Lockyer and Brown 1981; Brown and Lockyer 1984). Whale marking has shown that most fin and blue whales return to the same region of the Southern Ocean after their winter sojourn in warmer waters (Brown 1962b), and many may travel hundreds of kilometres east or west of the feeding grounds within one summer (Brown 1962a). Fin whales are considered to have similar stock divisions to those of blue whales, with the addition of the subdivision of the fin whales in the Atlantic and western Indian Ocean sectors into eastern and western groupings to give a total of eight stocks (Gambell 1985).

On the basis of catches made in Antarctic waters it appears that males head the fin whale migrations while the females tend to migrate later (Gambell 1985). Older animals precede the younger. Laws (1981) concluded that the older animals and pregnant females migrated first with sexually immature individuals at the rear of the migration. Although the first fin whale migrants penetrate Antarctic waters from October to November onwards, the peak presence of the species probably occurs two to three weeks later than that of the blue whales (Lockyer 1981a). Most adult fin whales arrive in Antarctic waters about three weeks before the juveniles.

4. *Sei Whales*. Omura (1973) and Budylenko (1978) suggested that there were up to six southern hemisphere populations of sei whales: two (east and west) in each of the Atlantic, Indian, and Pacific Oceans, with possible additional populations in the central Indian and central Pacific Oceans. The general pattern of migration is similar to that of blue and fin whales, although the timing is a little later and they do not penetrate into such high latitudes (Gambell 1985; Brown 1977; Budylenko 1978). Doi et al. (1967) suggested that most sei whales remain south of 50°S year-round. Peak animal numbers occur in January and departures in April (Gambell 1985).
5. *Minke Whales*. Minke whales have a circumpolar distribution and are concentrated in high latitudes close to the ice edge (Ohsumi 1976). Doroshenko (1979) suggests that there are at least four population units—“Brazilian,” “Indian,” “New Zealand,” and “Chile-Peruvian.” The occurrence of minke whales in subtropical waters in the winter and spring (Best 1974a; Williamson 1975) suggest that they migrate into these waters. Kasamatsu et al. (1987) estimated southbound migration speeds at 20 nautical miles per day in waters north of the Subtropical Convergence Zone and 40–60 nautical miles per day in water south of the Convergence.

Minke whale catch data has demonstrated that there is a considerable temporal and spatial segregation of the sexes on the high latitude feeding grounds (Kasamatsu and Ohsumi 1987). Females predominate nearest the ice edge, while males are more abundant away from the edge of the pack ice even though they arrive earlier and stay longer on the feeding grounds than the females. School composition of minke whales is highly variable; groups of 10–25 are not uncommon, and aggregations of up to 90 have been observed (Bengston 1985a). Kasamatsu et al. (1998) investigated the clustering and aggregation of minke whales on the Antarctic feeding grounds based on extensive surveys in the southern Ross Sea, the Weddell Sea, and Prydz Bay. Despite the fact that the distribution patterns showed that minke whales clustered in the Antarctic feeding grounds, they were relatively randomly distributed within the aggregations.

6. *Humpback Whales*. There is more known about the seasonal distribution and migrations of the humpback whales (Dawbin 1966) than for any other species of whale. The reason is because they characteristically stay close to coastlines during their migrations between summer and winter grounds (Chittleborough 1965). Humpback whales breed in tropical coastal waters with a temperature of about 25°C, and at least six southern hemisphere stocks have been identified. In the winter these stocks concentrate in breeding areas on the east and west coasts of South America, Africa, and Australia and among the island groups of the southwest Pacific Ocean. Each stock migrates southwards in the spring to form five areas of concentration: in the southeast Pacific, in the south Atlantic, to the south of South Africa, in the southeast Indian Ocean, and to the south of New Zealand. Although there may be some overlap on the feeding grounds there is good evidence that there is little interchange of individuals between the stocks (Mackintosh 1942).

   The speed of migration is about 15° of latitude per month, and there is very clear segregation of the different classes or categories of humpback whales throughout the seasonal cycle. In the vanguard of the migration and those whales arriving first to the Antarctic feeding grounds are a mixture of females in a sexually resting condition and others in early pregnancy. Following at subsequent intervals of several days are successive groups of immature males, and females in early lactation accompanied by their young calves. Once at the Antarctic feeding grounds the various groups become randomly mixed. However, on the northward migration they once again become segregated. Females at the end of lactation accompanied by weaning yearling calves depart northward first, followed in succession by immature animals, mature males with resting females, and finally females in late pregnancy. Pregnant females therefore spend the greatest amount of time on the feeding grounds south of 60°S (about 6.5 months, late November–May), then lactating females accompanied by their calves (4.5 months, late December–April).

7. *Right Whale*. Much information on the distribution of the southern right whale comes from the records of nineteenth century whaling, during which the species was very much reduced in numbers (Townsend 1935), but recent recovery of the species is providing additional information (Omura et al. 1969; Best 1970b, 1974a; Cawthron 1978;). The Antarctic distribution is virtually circumpolar (Kawamura 1978), with the densest concentrations near land masses. Most of the whaling for right whales occurred between 30 and 50°S, north of the Polar Front. While right whales have been taken off South Georgia, the South Shetland Islands and the Antarctic Peninsula, it is probable that today most remain outside Antarctic waters (Hinton 1925). The migrations of this species are less extensive than in other Balaenopterids.

8. *Sperm Whale*. Sperm whales have a worldwide distribution, but only the larger males penetrate Antarctic waters south of the Polar Front (Best 1974b; Lockyer and Brown 1981). The region of the Subtropical Convergence (approximately 40°S) generally marks the southern limit of the distribution of the females and young males, though this limit extends to 14–50°S in the Indian Ocean and southwest Pacific (Ohsumi and Nasu 1970). Whale marking has provided direct evidence of some extensive north–south movements, and the occurrence of the Antarctic diatom *Cocconereis* which forms a yellowish film on the skin of medium-sized and large males in south temperate waters (Best 1969, 1974b; Bannister 1969), is indicative of northward movements from Antarctic waters, as does the presence of the beaks of Antarctic cephalopods in the stomachs of whales killed off Durban, (Clarke 1972). Evidence for separation of sperm whales in the southern hemisphere into separate stocks is sparse. Nonetheless it is clear that the females occupying the oceanic basins separated by continental land masses must constitute independent breeding units (Gambell 1985).

9. *Other odontocetes*. Brownell (1974) reviewed the state of knowledge of the biology of the smaller odontocetes found in Antarctic waters and plotted records of their occurrence in detail. Additionally Nishiwaki (1977), Goodall and Galeazzi (1985) and Kasamatsu and Joyce (2003) have added information on their distribution and reviewed their food habits.

The southern bottlenose whale and Arnoux's beaked whale both range south to the edge of the pack ice. Killer whales are abundant in Antarctic waters where their distribution is circumpolar and seasonally related to potential prey such as seals and penguins (Voisin 1972, 1976; Condy et al. 1978). Dense seasonal concentrations are found in Antarctic coastal waters and along the off lying islands such as South Georgia.

The long-finned pilot whale appears to be generally distributed throughout the Southern Ocean (Davies 1960), while the hourglass dolphin has a circumpolar distribution in temperate and Antarctic waters. Commerson's dolphin occurs commonly in coastal waters off Argentina and Tierra del Fuego, and around the Falkland Islands (Brownell 1974; Goodall 1978). In Antarctic waters, it also is recorded from South Georgia and Isles Kerguelen, but these may be separate populations (Brown and Lockyer 1984). Information on the distribution of other species is sparse. They are probably more abundant than occasional stranding records would indicate.

Overall, the importance of the smaller cetaceans in the Southern Hemisphere food web has been underestimated.

9.4 SEGREGATION

Changes in the composition of whale catches in Antarctic waters and at lower latitude shore stations indicate that the migrations of the different species are staggered (Dawbin 1966). Peak numbers of baleen whales are present in Antarctic waters in January–April (Mackintosh and Brown 1953) but the various species arrive at different times. Blue whales arrive before fin whales, the former being more abundant in the catches from November to December. The fin whales are more numerous in the latter part of the season from January to March. Humpback whales are most frequent in December and January while sei whales are the latest arrivals with their highest densities occurring in the period January–March (Gambell 1972). Not only do the species vary in the time of arrival, but also the species vary in the extent of their penetration into colder waters of high latitudes. This penetration is correlated with body size. The small minke whale is an exception to this rule and has a more southerly year-round distribution. It penetrates the coldest Antarctic waters and may even winter there (Tayor 1957; Ohsumi et al. 1970). According to Ohsumi et al., the highest densities of sei whales are found in the zone of 40–50°S, fin whales 50–60°S, and minke and blue whales 60–70°S.

Within a particular species, the migration of the different sexes and age classes is also staggered in relation to size and feeding (energy) requirements (Laws 1977a). Larger and older whales tend to penetrate to higher latitudes than smaller and younger animals; pregnant females arrive early and lactating females late (Laws 1960a, 1961; Mackintosh 1965; Dawbin 1966). Laws (1960a) has noted that, in addition to the latitudinal segregation, there is also a longitudinal segregation by size. The larger and older whales arrive first and tend to occupy the preferred feeding grounds. Later arrivals tend to be displaced to the periphery to the east or west. This segregation suggests some form of competition for food.

Matsuoka et al. (2003) investigated the relationship between large whale distributions and the southern boundary of the Antarctic Circumpolar Current. Humpback, southern right, sperm and southern bottlenose whales were concentrated between 80 and 110°E. Here a large meander of the southern boundary of the ACC was identified with large-scale upwelling giving rise to high productivity. Figure 9.10 depicts the segregation of humpback and minke whales between 80 and 110°E. High-density areas of humpbacks were observed along the meander. High densities of minke whales were observed along the ice edge and over the continental slope. Southern right, large male sperm and bottlenose whales also were concentrated in this area but were distributed over the Antarctic continental slope. Matsuoka et al. concluded that the species were segregated from each other by their feeding habits.

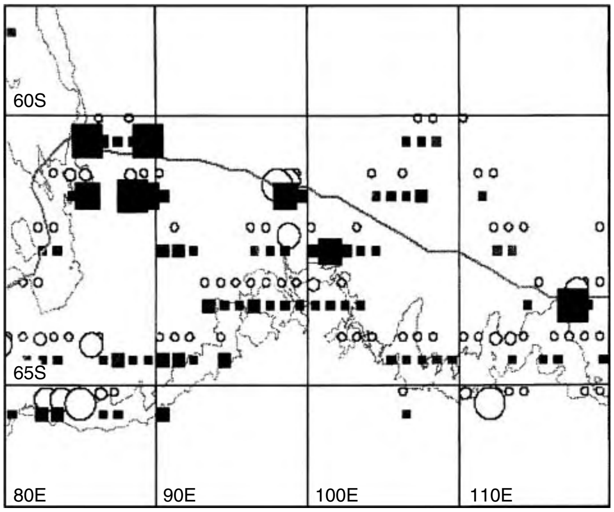


FIGURE 9.10 Humpback and Antarctic minke whales tend to segregate between 80 and 120°E, where the large meander of the southern boundary of the ACC occurs. High-density areas (110–300 whales/100 nautical miles) of humpback whales were observed along the southern boundary of the ACC. On the other hand, high-density areas of Antarctic minke whales were observed along the ice-edge over the continental slope. The thick line shows the southern boundary of the ACC. (From Matsuoka, K., Watanabe, T., Ichii, T., Kishimata, H., Nishiwaki, S., *Antarctic Biology in a Global Context,* Huiskies, A.H.L., et al., Eds., Backhuys Publishers, Leiden, 29, 2003. With permission.)

Matsuoka et al. (2003) investigated the distribution of sperm whales, killer whales, long-finned pilot whales, hourglass dolphins, and members of the family Ziphidae (beaked whales) in surveys carried out in the Antarctic waters of the South Atlantic, Indian, and South Pacific Oceans in 1976/1977 and 1987/1988. Figure 9.11 depicts the latitudinal distribution patterns of these species based on the encounter rate from the ice edge. Killer whales occurred mainly in the very southernmost areas. Sperm whales were found in the southern half of the study area. Beaked whales (mostly southern bottlenose whales) ranged over a wide area, and long-finned pilot whales and hourglass dolphins were manly in the northern regions of Antarctic waters. Abundance estimates for south of the Polar Front in January were sperm whales 28,100, beaked whales 599,300, killer whales 80,400, long-finned pilot whales 200,000, and hourglass dolphins 144,300. Based on this data the biomass of these species were estimated as 0.77 (sperm whales), 2.70 (beaked whales), 0.32 (killer whales), 0.16 (long-finned pilot whales) and 0.01 (hourglass dolphins). Consumption of food (mostly squid) by the Odontocetes was estimated at 14.4 million tonnes with 67% of the total consumed by beaked whales. Indirect consumption of Antarctic krill through predation of squid by beaked whales was estimated to be approximately 24 million tonnes. It was suggested that Odontocetes, especially southern bottlenose whales, have a much greater role in the Antarctic marine ecosystem than previously considered.

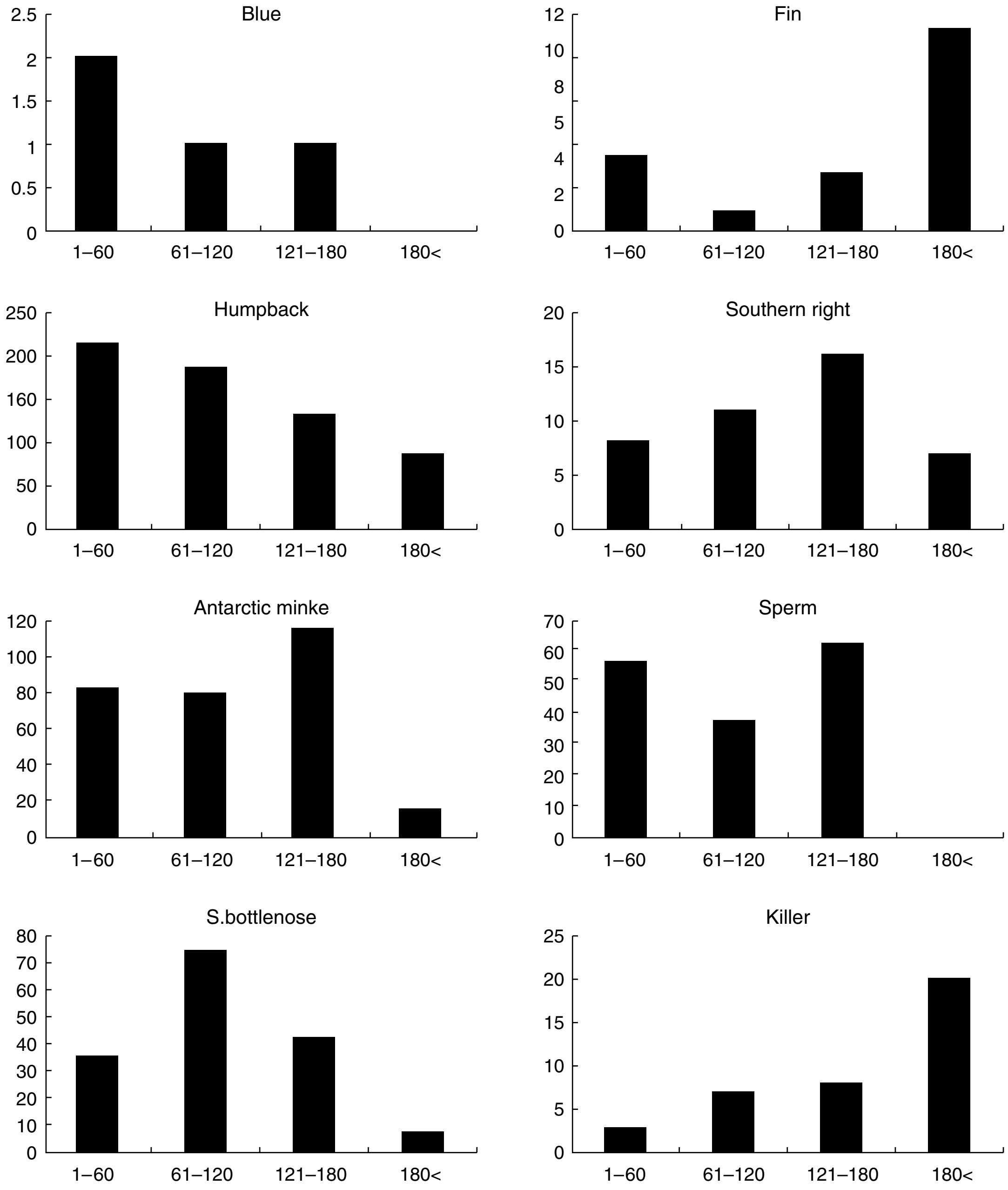


FIGURE 9.11 Histograms of the direct distance between the estimated southern boundary of the Antarctic Circumpolar Current (ACC) and sighting position of each whale species (in nautical miles) between 80 and 110°E where the meandering of the ACC was observed. Humpback whales tended to distribute along the southern boundary of the ACC between 80 and 110°E. Right, and minke and killer whales tended to distribute away from the southern boundary of the ACC between 80 and 110°E. (Redrawn from Matsuoka, K., Watanabe, T., Ichii, T., Kishimata, H., Nishiwaki, S., *Antarctic Biology in a Global Context*, Huiskies, A.H.L., et al., Eds., Backhuys Publishers, Leiden, 29, 2003. With permission.)

Kasamatsu and Joyce (2003) graphed the possible latitudinal segregation of Odontocete species in Antarctic waters based on the encounter rate from the ice edge (Figure 9.12). In general killer whales occurred in the southernmost waters, and sperm whales occurred mostly south of 60°S. Beaked whales ranged over a wide area, and long-finned pilot whales and hourglass dolphins were found mainly in the northern regions of Antarctic waters.

9.5 REPRODUCTION

As discussed earlier the breeding season of baleen whales is well defined with the majority of the conceptions occurring during the time spent in warm water. Of the toothed whales there is only good knowledge of the reproductive cycle of the sperm whale. Strictly speaking, the sperm whale is not a true Antarctic species because only large, sexually mature bulls

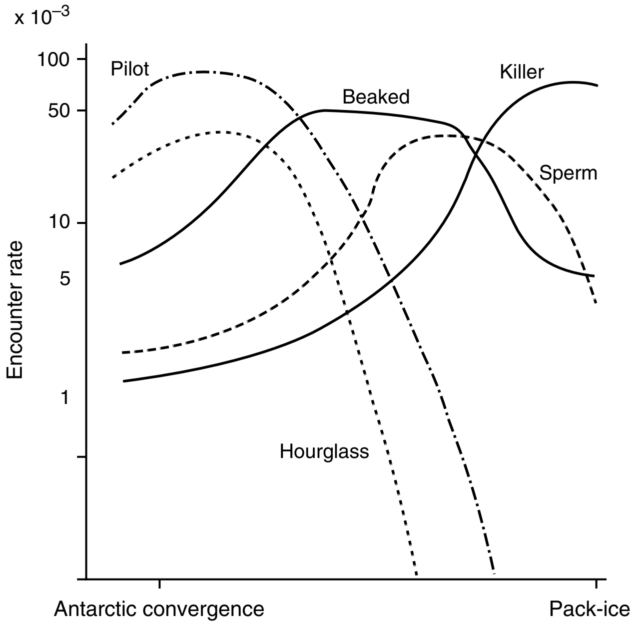


FIGURE 9.12 Outline of the latitudinal occurrence of Odontocetes in Antarctic waters, based on encounter rate from the ice edge. (From Kasamatsu, F., Joyce, G.G., *Ant. Sci.*, 25, 1996. With permission.)

penetrate south of the Polar Front. Little can be reported on the timing of the breeding season of other toothed whales. Table 9.1 gives details of the phenology of reproduction in the larger baleen whales and the sperm whale.

9.5.1 Reproductive Cycle

9.5.1.1 Baleen Whales

A two-year reproductive cycle is common for most of the baleen whales and it is closely tied to the annual migration and feeding cycle (Laws 1961; Chittleborough 1965; Gambell 1968; Donnelly 1969). Birth (which occurs on the warmer water grounds) is not followed normally by another pregnancy even if there has been a post-partum ovulation. With the exception of minke whales one ovulation occurs approximately every 1.5 years. Gestation is approximately one year, and normally a single calf is born. Right whales differ from other species in that they may breed only once every three years (Lockyer 1981a).

The minke whale has an ovulation rate of approximately once per 1.15 years (Ohsumi and Masaki 1975). According to Brown and Lockyer (1984) there is uncertainty as to whether or not the reproductive cycle is one or two years.

TABLE 9.1
Reproductive Cycle of Baleen Whales

Species	Month of Conception	Gestation Period (Months)	Month and Length at Birth (m)	Sucking Period (Months)	Length at Weaning (m)	References
Blue	Jun.–July	11	May 7.0	7	12.8	Mackintosh and Wheeler (1929)
Fin	June–July	11	May 6.4	7	11.5	Laws (1959), Lockyer (1981a)
Sei	July	11–11.5	June 4.5	6.5	8.0	Gambell (1968), Lockyer (1977a)
Minke	August–September	10	May–June 2.8	4	4.5	Williamson (1975), Ivashin and Mikhalev (1978), IWC (1979)
Humpback	August	11.5	July–August	16.5–11.0	8.8	Chittleborough (1958), Dawbin (1966), Matthews (1937)
Southern right	August–October	10	May–July	—	—	Donnelly (1969)

Source: From Brown, S.G., Lockyer, G.H., *Antarctic Ecology*, Laws, R.M., Ed., Academic Press, London, 71, 1984. With permission.

The pregnancy rate has been shown to be higher than that of other species and may reach 86% (IWC 1979). It is likely that minke whales reproduce annually (Masaki 1977), with annual calving in most seasons. Because the minke whales have a shorter calving interval than other baleen whales (annual versus biannual calving), their population may be able to respond more rapidly to changes in the environment than other whales.

9.5.1.2 Age-Specific Reproductive Rates

Age-specific reproductive rates are an important source of information for the analysis of population dynamics. Due to the importance of these rates, reliable methods of age determination are necessary. The most reliable and widely used method of age determination for baleen whales is that of counting growth layers in the ear plugs (Purves 1955, Laws and Purves 1956; Nishiwaki 1957; Nishiwaki et al. 1958; Ohsumi 1976; Ichihara 1966). For fin and sei whales there is evidence that one growth layer forms annually (Roe 1967; Lockyer 1972, 1974). Also in blue and minke whales it has been assumed that one growth layer forms annually. In the humpback whale, however, two growth layers may form annually Chittleborough (1959, 1960, 1962). Physical maturity occurs at an age of about 25–30 years in most baleen whales (Lockyer 1981a). Life spans of some species extends to 90 years.

Various methods have been used to estimate the age of sexual maturity. In general it is determined from: (a) mean age of whales just matured; (b) age at which 50% of the catch is mature; and (c) the transition phase between juvenile widely spaced and/or irregular growth layers and more compact or regular layers (Lockyer 1972, 1974). The age of attainment of sexual maturity has been estimated as approximately 5 years for blue whales (Lockyer 1981a), 5–6 years for the pygmy blue whales (Ichihara 1966b), 6–12 years for fin whales (Lockyer 1972), 9–11 years in sei whales (Lockyer 1972), and approximately 7–14 years in minke whales (Kato 1983), depending on the area and season. Pregnancy rates (the proportion of the females in the catch that are pregnant excluding lactating females) may have fluctuated in relation to exploitation. Evidence for this fluctuation will be discussed later.

9.5.1.3 Toothed Whales

The sperm whale is polygynous (Best 1979), breeding from August to March, with a mid-summer peak in temperate waters (Best 1969; Gambell 1972). Births occur in February or later, gestation being 14.5 months (Best 1969; Gambell 1972). Calves are suckled for approximately two years (Gambell 1972; Best 1974a). Thus a reproductive cycle is four years. Females become sexually mature at 9 years, males at about 19 years (Bannister 1969; Best 1970a; Gambell 1972; Lockyer 1981b).

Little is known of the reproductive cycles of the other odontocetes in Antarctic waters. They are likely to be similar to that of their counterparts in the northern hemisphere.

9.5.2 SOCIAL STRUCTURE

As discussed earlier roquals and humpback whales show segregation of both sexes, sexual classes and ages of whales at different times, especially during migrations.

The number of whales commonly found together on the feeding grounds in Antarctic waters varies considerably; they tend to mingle freely or associate in small groups (Gambell 1972). However, these groupings may reflect more the abundance and distribution of the prey species rather than the social tendencies of the whales themselves (Gambell 1975). Although solitary whales and much larger concentrations are not infrequent, blue, fin, sei, minke, and humpback whales are commonly found in groups of three to five. Aggregations of up to 100 minke whales have been observed on the feeding grounds, and similarly large groups of fin whales have been reported. Little is known of the groupings of right, bottlenose and beaked whales in Antarctic waters.

Sperm whales in the Antarctic consist only of large mature bulls, which tend to be solitary and evenly distributed. However, north of the Polar Front many kinds of schools are found, sometimes being up to several hundreds in number. The composition of such schools is variable. Ohsumi (1971) has described at least six categories of schools: nursery, harem, juvenile, bachelor, and bull schools as well as lone bulls.

Killer, pilot, bottlenose, and Baird's beaked whales are all known to swim in schools, and in the case of pilot whales these schools can be large, sometimes containing several hundred animals. Additionally killer whales exhibit a high degree of group cooperation activities, usually in an extended family pod of five to twenty animals, but sometimes combining into larger groups of 100 or more animals (Tomlin 1967).

9.6 FEEDING ECOLOGY

The baleen whales are terminal predators on a very short food chain (diatoms–krill and other zooplankton–whales) and therefore have a major impact on planktonic secondary production. As filter feeders on planktonic crustacea their morphology and behavior are functionally adapted for feeding on small particles. The toothed whales are predators on squid, fish and other larger animals such as penguins and seals, and are thus terminal predators at the end of a longer food chain.

9.6.1 METHODS OF FEEDING

9.6.1.1 Baleen Whales

Nemoto (1959, 1966, 1970) described three types of feeding categories in baleen whales. These categories were skimming, swallowing, and swallowing and skimming. The various species can be classified as follows:

1. Skimming	Right whale
2. Swallowing	Blue whale Pygmy blue whale Fin whale Minke whale Humpback whale
3. Swallowing and skimming	Sei whale

Swallowing-type feeding occurs when the whale engulfs a mouthful of food and water which then is sieved through the baleen plates by contraction of the previously distended ventral grooves beneath the chin and throat and by raising the tongue in the mouth. The food organisms are retained on the baleen filter and subsequently swallowed (Gaskin 1976). As Mackintosh (1965) pointed out, smaller food organisms necessitate a finer filter; for larger food organisms a coarser filter can be used, with more rapid filtration and a relatively small filtration area. The right whale, which feeds on small copepods, has very fine long baleen—so long that the mouth is enlarged to accommodate it—whereas the baleen of sei, minke, humpback, fin, and blue whales are increasingly coarse (Nemoto 1959).

Humpback whales have been observed to carry out some interesting feeding behaviors. One of these involves circling a swarm of krill, then diving under the surface and coming up vertically with the mouth open to engulf the concentrated food organisms. Another method is that the whale swims in a circle below the surface of the water releasing a trail of air bubbles that arise in a whorl to the surface. The whale then swims up through the centre of the bubble net to engulf the food organisms entrapped in the centre.

The jaw shape and feeding apparatus are very different in the skimmer, like the right whale. The rostral area of the head is also very different due to being very high, arched, and narrow. The actual method of feeding is to swim slowly forward with the jaws agape and usually with the head raised partly out of the water. The water and food are filtered through the baleen plates, and when a quantity of food is accumulated on them the mouth is closed, and the food swallowed. The sei whale feeds by a method somewhat between the two methods described above, according to Nemoto's (1959) study of the anatomy.

9.6.1.2 Toothed Whales

Toothed whales are more likely to use echolocation to detect their food (Gaskin 1976); this is especially true of the sperm whale. A number of observations point to the use of echolocation. Sperm whales are known to make dives of up to a depth of at least 1200 m (Lockyer 1977b); here they may remain for periods of up to an hour. Even at 200 m, the light is negligible so that the prey cannot be detected by sight; thus the sperm whale must feed in total darkness. Recently a sound-stunning behavior has been proposed (Norris and Mohl 1981). The sperm whale is thought to project a beam of sound onto its prey to render it immobile. Although sperm whales have homodont teeth, the maxillary teeth may be interrupted. Juvenile males and females have unerupted teeth yet their diet is similar to that of toothed individuals. Because they feed at such great depths no one has observed sperm whale feeding.

Teeth are probably not used directly in feeding by the bottlenose and beaked whales, which like the sperm whale are known to dive very deeply and for similarly long periods (Tomlin 1967). As their diet is very similar to that of sperm whales (Gaskin 1976), it is likely that they employ similar echolocation feeding methods. Delphinids, on the other hand, are known to actively chase their prey and to use their sharp teeth for seizing and grasping (Gaskin 1982). Killer whales use their powerful teeth for grasping, biting, and tearing. Unlike other odontocetes they will attack large prey such as penguins, seals and even other cetaceans, including some of the larger rorquals (Tomlin 1967; Gaskin 1976). They hunt in large packs or schools (Condy et al. 1978) and appear to coordinate group attacks on large prey (Tarpy 1979). Killer whales are neither deep nor lengthy divers, and most of their prey is taken at the sea surface or even off floes (Condy et al. 1978).

9.6.2 FOOD QUANTITIES AND FOOD PREFERENCES

9.6.2.1 Baleen Whales

When feeding south of the Polar Front, the chief food of all rorquals and the humpback whales is *Euphausia superba* (Nemoto 1959; Marr 1962; Mackintosh 1965; Gaskin 1976; Kawamura 1978). The blue whale tends to feed at high latitudes on first-year krill (20–30 mm); the minke whale feeds on even smaller krill (10–20 mm), thus not competing with the blue whale. The fin whale feeds mainly on second-year krill (30–40 mm) while the chief diet of the sei whale shows a latitudinal succession from north to south of *Calanus tonsus, Calanus simillimus, Depranopus pectinatus, Eucalanus vallentini, Parathemisto gaudichaudii* and *Euphausia superba*. Mackintosh (1974) concluded that whales take the bulk of their food from krill between 27 and 50 mm in length and impose the heaviest mortality on krill in the 15–40-mm range. Blue and minke whales also take the small euphausiid *Euphausia crystallorophias* over the continental shelf. Moreover the finer baleen of the minke whale also enables it to take copepods. Other organisms taken occasionally include fish, especially larvae, of many species, predominantly mycophids.

Thus the baleen whales, especially blue, fin, humpback, sei, and minke whales, appear to be in competition for the same food resource, krill, when feeding south of the Polar Front. However, they tend to have, as discussed above, staggered peaks of arrival in Antarctic waters so that neither different species nor age classes of the same species are in direct competition all of the time. The extent of penetration into polar waters is also an important factor in reducing interspecies competition.

For the blue whale a daily food intake of 30–40 kg (kg of body wt)$^{-1}$ was estimated for a 120 day stay in Antarctic waters (Lockyer 1981a). The first stomach (which is three-chambered) reportedly holds 1000 kg (Zenkovitch 1969), and a daily intake of about 4000 kg for a fully adult blue whale has been estimated (Lockyer 1981a). The quantities of prey consumed by fin whales are somewhat less than those consumed by blue whales, and a daily intake of 2000–2500 kg day^{-1} was estimated by Lockyer (1981a) for adult fin whales. Ohsumi (1979) assumed a feeding rate of about 4% of body weight daily for minke whales in Antarctic waters. He observed that stomachs full of krill weighed on average 136.4 kg. On that basis minke whales would need to consume two meals daily to meet the energy needs. Zenkovitch (1969) estimated that adult humpback whales consumed 2220 kg of krill daily. However, Sergeant (1969) estimated for northern humpback whale populations a 4–4% body weight consumption per day was required to satisfy their energy requirements. On this basis a daily food intake of 1000 kg is more likely.

9.6.2.2 Toothed Whales

Squid forms the greater part of the diet of sperm whales (Berzin 1972; Clarke 1980a, 1980b), and they are also known to be the preferred food of many other odontocetes such as pilot whales (Sergeant 1962). Bottlenose and beaked whales feed almost exclusively on cephalopods (Tomlin 1967).

Many bathypelagic squid are known to exist only from their presence in sperm whale stomachs. Clarke (1956), Tomlin (1967), Berzin (1972) and Clarke (1980a, 1980b) all give accounts of the species of squid and other supplementary items in the diet of sperm whales. Squid and fish are taken in the approximate ratio of 9:1. Some sperm whales taken off Durban, South Africa (30°S), had the beaks of Antarctic squid species in their stomachs. The majority were *Moroteuthis ingens*, *Mesorhynchoteuthis hamiltoni, Gonatus antarcticus*, and an unidentified species of *Moroteuthis*. There was a sudden increase in the incidence of Antarctic squid in the stomachs of whales over 18 years old, and the proportion of stomachs containing Antarctic squid beaks continued to increase with size and age of the whale to over 80%. Fish are apparently taken opportunistically. Large nototheniid fish *Dissostichus mawsoni* and *Dissostichus eleganoides*, up to 170 cm in length and 74 kg in weight, have been reported in the stomachs of sperm whales from Antarctic waters (Koraobnel'nikov 1956; Zemsky 1962; Solyanik 1963; Berzin 1972). Additional fish taken include *Micromestistius australis* and *Ceratus holbochi* as well as large rays and bottom living sharks (Clarke 1972). Feeding rates have been calculated at approximately 3% of body weight daily in whales of 40,000–40,000 kg (Lockyer 1981b). The first stomach would need to be filled three times daily for normal energy intake, whereas a nursing female might need to fill her stomach four to five times daily (Lockyer 1981b).

Because it is based two sources of information: observations of attacks on other animals usually near the surface, and on specimens caught by whalers who tend to concentrate on adult males for higher yields, our knowledge of the diet of killer whales in Antarctic water is biased towards relatively large food items. The diet of killer whales is varied. Squid, fish, cephalopods, birds, seals, and other cetaceans are all attacked and taken. Shevchenko (1975) examined 49 stomachs of specimens caught between 50° and the pack ice. Five were empty while 84% of the others contained remains of minke whales, 45% contained seals, 7% fish, and only 2% squid. Delphinids and phocoeinids both prefer fish but also take squid (Gaskin 1976).

9.7 BIOENERGETICS

9.7.1 INTRODUCTION

In the preceding section the quantities of food consumed by whales in Antarctic waters were considered. The feeding season lasts about four months during the austral summer, when krill and or copepods, fish and cephalopods are consumed in Antarctic waters. In this section the role of consumed food in the bioenergetics of the various species shall be considered.

9.7.2 SEASONAL FATTENING

Because most whales feed intensively only for about one-third of the year and at a reduced rate (and sometimes taking no food for extended periods) for the rest of the year, food energy needs to be stored in the body to meet metabolic needs during periods of reduced feeding or no feeding at all. This energy is stored generally as fat in the tissues of blubber, muscle, viscera, and bone (Brodie 1975; Lockyer 1981a). Lockyer (1981a) has estimated that the total increase in body weight during the summer feeding season is from 30 to 100% of the lean body weight for rorquals such as fin, blue and humpback whales.

9.7.3 METABOLIC ENERGY EXPENDITURE

Direct measurements of metabolic energy output are extremely difficult in cetaceans. Theoretical estimates of metabolism energy requirements for fin and blue whales (Brodie 1975; Kawamura 1975; Lockyer 1981a) give values in the range of 3–8 kcal (kg body wt)$^{-1}$ day^{-1}. For sperm whales, Lockyer (1981a, 1981b) estimated the resting metabolic rate at 5–8.5 kcal (kg body wt)$^{-1}$ day^{-1}. Also Lockyer (1981a) has calculated the relative amounts of energy required for growth and maintenance at various ages. In the Mysticete, the suckling calf was estimated to utilize about 68% of the consumed energy for metabolism; by puberty, 94% is used for this purpose, and near physical maturity nearly all is required for metabolism.

There is evidence that in their annual migrations whales swim continuously not slowing down or ceasing swimming at night (Kawamura 1975). A sei whale marked in the Antarctic was found 10 days later some 335 km distant, having averaged 14.5 km h^{-1} (Brown 1971). Kawamura (1975) considered that a sustained swimming speed equivalent to 18.5 km h^{-1} was possible, and Lockyer (1981a) was of the opinion that for the largest rorquals, such as the blue and fin whales, a speed of 24 km h^{-1} was possible.

A major difference between the Mysticetes and Odontocetes (especially the sperm whale) is that the latter undertake deep, prolonged dives. While this activity must require energy expenditure that is well above resting level, the increase that is needed is unknown.

Reproduction places extra metabolic demands on female whales. Lockyer (1981a) notes that the blubber fat of pregnant female blue and fin whales has been recorded as being about 25% thicker than that of non-breeding females. To accumulate this extra fat pregnant females must remain longer on the southern feeding grounds to consume more food. Nearly all of the extra fat is used in lactation. Lockyer (1978) calculated that the energy cost of lactation was about 12–15 times the cost of foetal development. The energy demands of pregnancy and lactation are less stressful on the female sperm whale than on female baleen whales. Lockyer (1981a) has calculated that in sperm whales the energy cost of pregnancy is negligible until the fifth or sixth month, and this cost would be met by an increase in daily food consumption of only 5–10%. However, the greater energy demands of lactation would require an increase of daily food intake of 32–63%.

9.7.4 ENERGY BUDGETS

Because whales in the past, and possibly in the future, have consumed a major proportion of the annual krill production as well as large quantities of fish and squid, their impact on energy flow through the Southern Ocean marine ecosystem is of considerable interest. An energetics approach to the role of whales in the ecosystem enables the evaluation of this impact in quantitative terms and provides an insight into our understanding of ecosystem stability. The aim of the bioenergetics approach is the preparation of a "balance sheet"to account for the energy inputs and outputs of "typical" individuals at all the critical stages of the life cycle in relation to variations in the environment. The data may then be used to calculate an energy budget for a species population.

In compiling a budget, the following need to be estimated:

1. The calorific value of the food
2. Food intake and feeding rates
3. Metabolism and activity
4. Heat loss
5. Energetic cost of locomotion
6. Energetic cost of growth
7. Energetic cost of reproduction

Lockyer (1975, 1976) has provided separate estimates of projected energy budgets for blue, fin, sei, and sperm whales according to sex and maturity stages. The components of the energy budget for a large cetacean (the sperm whale) based on Lockyer's data have been summarized by Gaskin (1982) (Figure 9.13).

The body weight of a sperm whale at physical maturity may be as much as 50 tonnes in the case of a male but much less, about 10–12 tons, in the case of the female. The stomach capacity of the adult male approaches 2000 l. Current data suggest that food consumption could equal 3% of the body weight per day: about 1500 kg for the male and 450 kg for the female.

Lockyer calculated that the annual food intake of the males might be as much as 550,000 kg but only slightly more than 150,000 kg in the female. The calorific yields of these weights of squid are 43.9×10^{7} kcal (183.8×10^{7} kJ), and 12.2×10^{7} kcal (51.1×10^{7} kJ), respectively. For the purpose of calculating the energy outputs, growth in physically mature adults can be rejected as the annual increment is

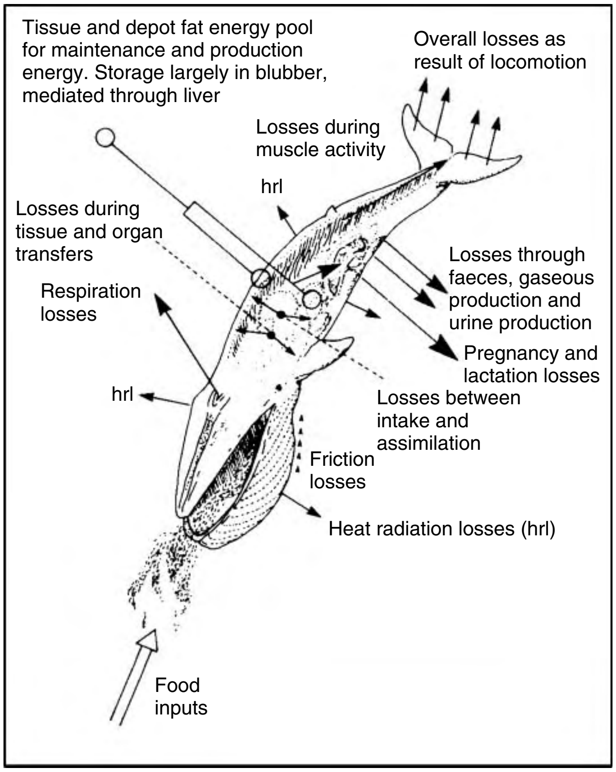


FIGURE 9.13 Schematic diagram to illustrate the balance of energy inputs, storage, and outputs for a whale. White arrows indicate food inputs, which in baleen whales are usually seasonal. Open circles indicate storage, generally in the form of lipids, in fat deposits and the liver. Mobilization of food stores is generally mediated through the liver. Energy losses are indicated by black arrows. These losses occur before the assimilation of food, during transfers from organ to organ and tissue to tissue, through heat radiation, respiration, and through faeces and urine; in the adult female, there is a major loss as a result of pregnancy. Hrl represents heat radiation losses from the body surface. (From Gaskin, D.E., *The Ecology of Whales and Dolphins*, Heineman, London, 1982. With permission.)

negligible. To maintain the theoretical resting metabolism the male needs about 2.52×10^5 kcal (10.5×10^5 kJ) and the female 1.02×10^5 kcal (4.3×10^5 kJ) per year. For active metabolism the equivalent value is 2.02×10^6 kcal (8.5×10^5 kJ) and 8.2×10^5 kcal (34.3×10^5 kJ), respectively. The yearly total expenditure for maintenance and normal activity amount to 31.79×10^7 kcal (133.1×10^7 kJ) for the male and 8.97×10^7 kcal (37.4×10^5 kJ) for the female. The cost of lactation in the female is high, probably adding another 2.8×10^7 kcal (11.7×10^7 kJ). Figure 9.13 illustrates the balance of energy inputs, outputs and storage for the mature sperm whale.

9.8 POPULATION DYNAMICS

9.8.1 INTRODUCTION

For commercially exploited populations it is important to have accurate estimates of the population sizes of the stocks. Considerable effort has gone into research on the population dynamics of whales by the scientists associated with the International Whaling Commission. A number of computer models have been developed to provide information for decision-making in management and conservation. These models have been used to obtain a description of the current characteristics, including, size of a population of whales, or to compare its current characteristics with those of the past, or to forecast its characteristics in the future. The characteristics of such models have been discussed by Allen (1980).

9.8.2 ESTIMATION OF POPULATION SIZE

Allen (1980) and Brown and Lockyer (1984) have reviewed the various methods that have been used to determine the population sizes of the various species of whales. These are:

1. *Direct counts (sightings)*. Here the number of whales sighted within a given area is extrapolated to cover a much larger area occupied by the population.
2. *Mark and recapture*. The proportion of marked animals (numbered metal darts) recovered provides a factor which relates the associated catch to the total population exploited.
3. *Methods based on catch and effort*. These methods rely on accurate catch and effort data from the whale fishery. Essentially, they compare the changes in an observed relation between catch and effort with changes which would occur in a population model. Allowances must be made for natural mortality and recruitment, particularly if they are changing during the period under investigation (Chapman 1968).
4. *Mortality coefficient method*. If in addition to catch and coefficient statistics the age composition of the catch is known, then mortality coefficients can be calculated from linear logarithmic regression of catch on age class after the initial age at full recruitment. Calculations of the natural mortality coefficient at the beginning of the period of fishing enable the fishing mortality to be derived by its subtraction from the total mortality. The ratio between the catch and fishing mortality coefficient gives an estimate of population size.
5. *Least squares method*. This method (Allen 1966, 1968) utilizes catch and age composition data to derive the population of new recruits in all catches, which can then be used to calculate the population size.
6. *Recruitment curve method*. This method depends on the relationship between population size, catch and recruitment, which is a theoretical value based on estimates of reproductive parameters.
7. *Cohort analysis*. This method requires data on age composition of each season's catch, natural mortality coefficient and estimated annual rate of exploitation. The value for exploitation rate is used to calculate population size in each year class.

9.8.3 ESTIMATING MORTALITY AND RECRUITMENT RATES

To construct realistic models of the dynamics of whale populations good data on mortality rates are needed. Mortality is of two basic kinds, that arising from natural causes and that due to catching. Both kinds of mortality vary with age. Most methods of measuring mortality rates require observations of changes in abundance, either with absolute time or with age. For this purpose it is generally necessary to be able to age the animals.

9.8.3.1 Age Determination

For baleen whales three structures have been used in age determination. Baleen plates show ridges, which are probably formed annually, but as they wear with age they are only useful for aging quite young animals. Counts of corpora albicanta in the ovaries provide a record of the number of ovulations. The rate of ovulation must be known to convert the number of ovulations into years. Since the rate of ovulation varies between species of whales, and moreover it is not constant within a species, or even individual animals, this method has been little used in recent years. The most reliable and widely used method is based on counting the growth layers (light and dark bands) in the waxy plugs found in the ears. For fin and sei whales, there is evidence that each pair of light and dark bands form annually (Roe 1967; Lockyer 1972, 1974). It is assumed that this is also true for minke and blue whales.

In Odontocetes age determination is mostly based on tooth structures. The teeth are bisected and the cut surface is etched with 10% formic acid so that the growth layers appear as alternating ridges and troughs. Current evidence (Best 1970a; Gambell 1977) suggests that a ridge and a trough constitute an annual growth layer.

9.8.3.2 Mortality

Three main methods are used for estimating mortality rates. They are based on marking techniques, on changes in the abundance of age groups over time, and on the age structure of the population. However, mortality estimates are complicated by the fact that no good techniques exist for separating accurately the fishing mortality component in the total mortality rate.

9.8.3.3 Recruitment

The rate of recruitment can be expressed in two ways: either as a proportion of the total present population or as a proportion of the current recruited population (IWC 1978). Estimates of age at recruitment, or the age at maturity (i.e., when the individuals become sexually mature) and pregnancy rates are needed for the models used in stock management. In the management of commercially exploited stocks the concept of maximum sustainable yield (MSY) is generally used. In theory, the net recruitment rate (recruitment rate less mortality rate) of an exploited population is believed to increase as the population is reduced. This is brought about by changes in parameters associated with fecundity, growth and mortality so that there is effectively a surplus of recruits to return the population to

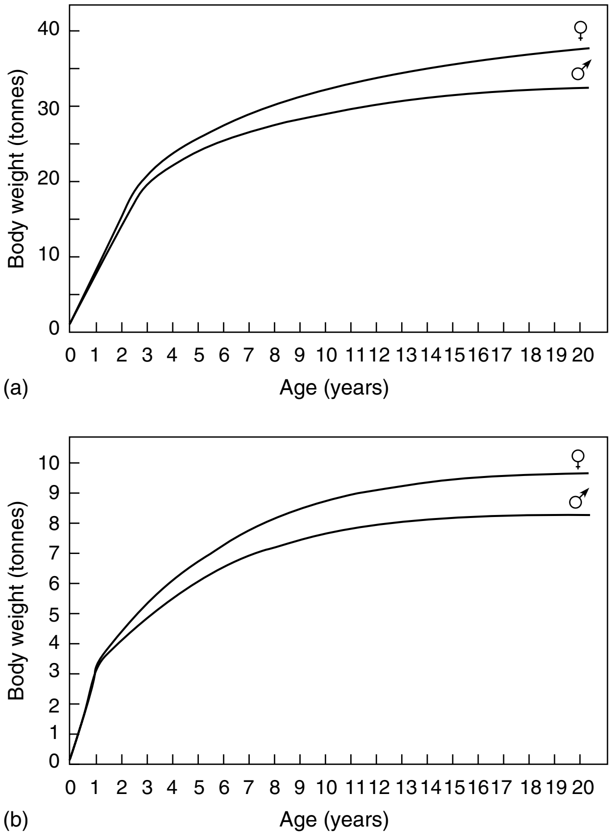


FIGURE 9.14 Average curves of body weight at a given age based on catch data corrected for length bias. A. Humpback Whales. B. Minke Whales. (From Brown, S.G., Lockyer, G.H., *Antarctic Ecology,* Laws, R.M., Ed., Academic Press, London, 71, 1984. With permission.)

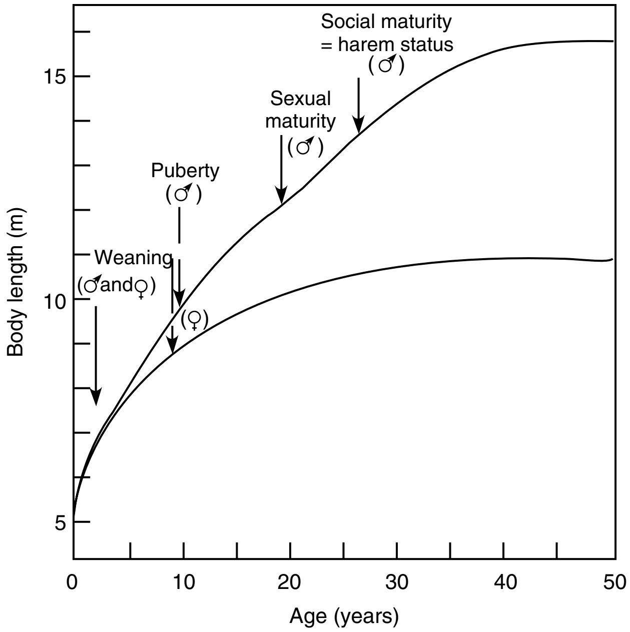


FIGURE 9.15 Predicted average curves of body length at age for sperm whales; based mainly on catch data. (From Brown, S.G., Lockyer, G.H., *Antarctic Ecology*, Laws, R.M., Ed., Academic Press, London, 71, 1984. With permission.)

maximum size. The surplus or replacement yield, can be harvested as a sustainable yield so that after the catch has been taken, the net recruitment rate remains at zero, so maintaining the population at that size. As will be seen in Chapter 16, there have been problems in applying concepts to commercially exploited whale populations.

9.8.4 GROWTH

In baleen whales growth in the first year is very rapid. As puberty is reached the growth rate slows down and then continues at a decreasing rate until physical maturity is reached when the vertebral epiphyses become fused, and further linear growth is not possible (Laws 1961). This stage is generally not reached until an age of 25 years or more in rorquals. In Figure 9.14, simplified average growth curves are shown for humpback and minke whales. However, there is much variability in growth patterns within whale populations and also between populations (Ichihara 1966b; Lockyer 1977b, 1979, 1981a).

The projected average growth in body length for the sperm whale is shown in Figure 9.15. It can be seen that there is a marked sexual dimorphism, with the male attaining a much larger size than the female. The female attains sexual maturity at about 7–12 years when the body length is about 80% of maximum. Physical maturity is reached after 30 years. Puberty in males is a prolonged process. It commences at about 9–11 years at a length of about 12 m. Functional maturity, or social maturity, is attained later corresponding to the attainment of harem bull status at a length of about 13.7 m and an age of about 26 years.

9.9 ROLE IN THE ECOSYSTEM

Whales have played a dominant role in the Southern Ocean ecosystem in determining the relative abundances of both their dominant prey species, *E. superba* and the co-occurring krill consumers. Prior to their exploitation, they were the major consumers of krill. After the reduction of the stocks of the larger baleen whales, the smaller whale species, seals, birds, and fish have had the opportunity of consuming large quantities of krill formerly taken by the larger whales. The degree to which this has occurred and the consequent changes in the demographic parameters of these other krill consumers will be considered in Chapter 16.

The baleen whales, by consuming large quantities of krill, would have had an impact on the abundance and composition of the phytoplankton populations. As discussed in Chapter 15, krill grazing on phytoplankton blooms can alter rapidly the biomass and species composition of the phytoplankton community, changing it from one dominated by microplankton (diatoms) to one dominated by smaller nano- and picophytoplankton.

Odontocetes, particularly sperm whales, must have consumed overall much greater quantities of cephalopods than they now consume. However, the changes which may have occurred can only be guessed at as there are no quantitative data available.

10 Birds

CONTENTS

10.1 INTRODUCTION

Because they are more obvious components of the Southern Ocean than are fish, the seabirds have attracted considerable attention. Due to this and the large colonies of penguins that are found round the margins of the continent and on the surrounding islands, there is the popular view that the Southern Ocean supports extraordinarily abundant and dense populations of a great variety of seabirds. Certainly, large numbers of seabirds congregate in certain areas in the summer for breeding. In the winter, however, few birds are to be seen around the continent and in the pack ice zone, and even in the summer, few birds are encountered in parts of the open ocean. Nevertheless, the seabirds are an important component of the Southern Ocean ecosystem and have a locally significant impact as predators on krill, other zooplankton, and larval fishes.

Three essential features of the Antarctic region are critical to an understanding of Antarctic ornithology:

- The position of the Antarctic continent, centred almost exactly on the South Pole, with most of its land mass below latitude 70°S
- The permanent cover of ice and snow on the continent, with most of its periphery at sea level girdled with glaciers and fast ice with little exposed rock
- Its great isolation from other substantial land masses, due to the wide expanse of the Southern Ocean with its pronounced circumpolar air and water currents (Young 1980). As a consequence, the birds are almost exclusively marine species.

The birds that breed on the Antarctic continent and associated islands, including the penguins, which constitute about 90% of the avian biomass, prey largely on animals whose populations build up rapidly during a short period of concentrated reproduction and growth. The strong summer "pulse" of solar energy is rapidly converted into phytoplankton, which provides abundant food for the zooplankton and larval fishes upon which the birds feed. This food source is available in the summer after the break-up of the pack ice, but is not accessible over the winter, when a large proportion of the sea is frozen over. Consequently, those species breeding on the continent have a short breeding season, after which they disperse northwards.

10.2 SPECIES COMPOSITION AND DISTRIBUTION

A seabird is one which habitually obtains its food either directly or indirectly, as is the case for certain scavengers and predators, from the sea. There are approximately 250 seabird species in the world, of which some 62, including 7 penguins, breed south of a line corresponding roughly to 50°S latitude, but including the Tristan–Gough group of temperate islands. If those species occurring north of the Antarctic Convergence, i.e., those species breeding on one or more of Tristan da Cunha, Gough Island, Marion and Prince Edward Islands, Isles Kerguelen, Macquarie Island and the New Zealand Subantarctic Islands are excluded, then the number of seabird species breeding south of the Antarctic Convergence falls to 36 (Croxall 1984).

The majority of the Southern Ocean's flying seabirds consists of albatrosses and petrels (Procellariiformes) and skuas, gulls, and terns (Charadriiformes). The albatrosses and petrels account for some 40 species (21 south of the Antarctic Convergence), of which most are truly oceanic, avoiding land except when breeding. The order Procellariiformes is represented by members of all four of its families: 6 species of albatross (Diomedeidae), 26 typical petrels, prions, and shearwaters (Procellariidae), 4 storm petrels (Oceanitidae), and 3 diving petrels (Pelecanoidae). The balance of the flying birds consists of two species of gull and three terns (Laridae), two skuas (Stercoriidae), two sheathbills, which are almost exclusively land based (Chionididae), and four cormorants (Phalacrocoracidae), often now regarded as subspecies. Further detailed information on their classification and breeding habits are to be found in Watson et al. (1971) and Croxall (1984).

Penguins, which belong to the order Sphenisciformes, with its single family Spheniscidae, are almost entirely restricted to the Southern Hemisphere. Ten of the 18 species of these flightless birds breed in the area south of 50°S as defined above. Of these, seven species breed south of the Antarctic Convergence. These species, with their breeding distributions, are listed in Table 10.1. Figure 10.1 and Figure 10.2 summarize the distribution of penguins south of the Antarctic Convergence. Only four species, the Emperor, Adélie, Chinstrap, and Gentoo penguins, breed on the Antarctic Continent proper. However, the two latter species are found only on the more northerly parts of the Antarctic Peninsula.

One salient characteristic of the Antarctic avifauna is the uniformity of species across a very large geographic area. Only four species have subspecifically differentiated within the region. The snow petrel is considered to have two forms, with the smaller subspecies *Pagodroma nivea nivea* over most of the continent, and a much larger form *P. n. major* in Adélie Land with the habit of nesting on more open ground. The Blue-eyed Shag is considered to have three subspecies: *Phalacrocorax atriceps gaini* on the Antarctic Peninsula and the Scotia Arc islands, *P. a. nivalis* on Heard Island, and *P. a. georgianus* on South Georgia. Wilson's Storm petrel has one subspecies, *Oceanites oceanicus oceanicus* on Kerguelen and other northern islands, and another, *O. o. exasperatus*, to the south. The penguin *Eudyptes chrysolophus* has two distinct subspecies, *E. c. chrysolophus*, the macaroni penguin, widespread throughout the region, and *E. c. shlegeli*, the royal penguin of Macquarie Island. Apart from these four species, the others are monotypic.

In 1970, Carrick and Ingham summarized the then available information on the distribution of Antarctic seabirds. Important sources of distributional data that have appeared since are Prevost and Mougin (1970), Watson et al. (1971), Barrat and Mougin (1974), Prince and Payne (1979), Prevost (1981), Wilson (1981), Jouventin et al. (1984), Harper et al. (1984), Croxall et al. (1984a), Williams (1984), Woehler (1997), and Woehler et al. (2001).

TABLE 10.1
Breeding Localities of Antarctic Penguins

	Antarctic			Sub-Antarctic	
	Continental	**Maritime**	**Peripheral**	**Cold Temperate**	**Warm Temperate**
Emperor, *Aprenodytes forsteri*	+	—	—	—	—
King, *Aprenodytes putagonicus*	—	—	+	+	—
Adélie, *Pygoscelis adelide*	+	+	—	—	—
Chinstrap, *Pygoscelis antartica*	—	+	+	—	—
Nothern Gentoo, *Pygoscelis papua papua*	—	—	+	+	—
Southern Gentoo, *Pygoscelis papua ellsworthii*	—	+	—	—	—
Macaroni, *Eudyptes chrysolopius*	—	+	+	+	—
Rockhopper, *Eudyptes crestatus*	—	—	+	+	+

Breeding localities are defined as follows: Continental Antartic, Continent and offshore islands to 65°S. Peter I. Oy and Balleney Islands. *Maritime Antarctic*—Penisula south to 65° S, and Islands within the pack ice zone. Peripheral Islands—South Geogia. Heard and MacDonald Islands and Archipel de Kerguelen. Sub Antarctic islands—lie north of the Antarctic-Convergence and within the Subtropical Convergence.

Source: From Stonehouse, B., *Key Environments Antarctica*, Bonner, W.N., Ed., Pergamon Press, Oxford, 266, 1985a.

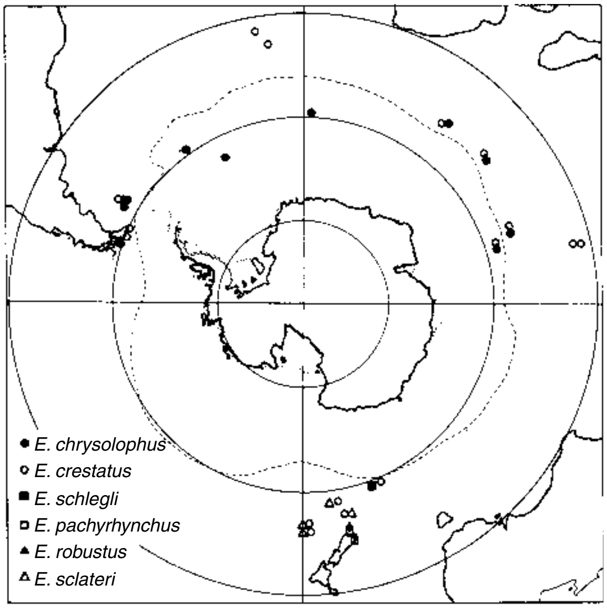


FIGURE 10.1 Breeding distribution of *Eudyptes* species. (From Croxall, J.P., *Antarctic Ecology*, Laws, R.M., Ed., Academic Press, London, 533, 1984. With permission.)

The pelagic marine fauna of the Southern Ocean (Chapter 5) is zonally distributed round the Antarctic continent. These zones tend to be less well-defined for seabirds, which are frequently constrained by the shortage of available breeding areas, but can often compensate by being wide-ranging at sea. Two well-defined zonal boundaries are the Antarctic Convergence and the northern limit of the permanent pack ice zone, marking the limit of the cold Antarctic sub-zone (see Chapter 15 for a discussion of bird distribution in relation to fronts and ice-edge processes). Only one breeding bird species, the Antarctic petrel, is entirely restricted to the latter subzone, but a number of others, e.g., the emperor penguin, Antarctic skua, Adélie penguin, and snow petrel, have their greatest concentration here, though they are also found on the Antarctic Peninsula. The latter area, with its associated island groups, comprises the maritime Antarctic sub-zone, providing a bridge which facilitates the intermingling of Antarctic species and those of more typical Subantarctic islands, along an essentially north-south axis.

One of the most comprehensive analyses of seabird abundance, biomass, and prey consumption is that of Woehler (1997) for the Prydz Bay region. A total of 24 taxa were recorded (Table 10.2) over the 12-year period between 1980/1981 and 1992/1993. The maximum number of species recorded was 22, and the minimum number was 16. The abundance of individual species and the overall abundance varied between years. At the Windmill Islands in Wilkes Land, the total breeding population of Adélie penguins in 1989/1990 was 93,092±9,300 pairs (Woehler et al. 1991). The population had apparently increased by 209% since a survey in the early 1960s. Significant decreases in the observed abundance of five species of seabirds between 1980/1981 and 1992/1993 within Prydz Bay have been detected (Woehler 1995), namely wandering albatross, black-browed albatross, light-mantled sooty albatross, northern giant petrel, and white-chinned petrel (Table 10.2). Formerly one of the most abundant species within Prydz Bay, populations of white-chinned petrel decreased by 86% over the 12-year period. Black-browed albatrosses have not been observed in Prydz Bay since 1984/1985. The percentage decrease of the five species ranged from 62% to 100%.

Estimated mean total abundance of the resident species varied between 1.71 (1980/1981) and 21 kg km^{-2} (mean 6.67±5.21). For the nonresident species, biomass ranged between 0.12 (1985/1986) and 4.89 kg km^{-2} (1980/1981) (mean 1.70±1.64). The overall annual mean biomass of all seabirds was 8.38±4.35 kg km^{-2} (range 5.27–21.13). Total biomass ranged from 6.8 to 27.3 million kg.

Trivelpiece and Fraser (1996) analysed the long-term record of Adélie penguin breeding biology and distribution in the Antarctic Peninsula area and found that this species had discrete subpopulations in the northeastern and south-western regions of the area. These subpopulations are separated by a 400 km gap in their respective distributions, but each is within several hundred metres of predictable pack ice areas in the Weddell and Bellingshausen Seas (Figure 10.3), respectively. These pack ice areas are the over-wintering grounds for each subpopulation, and access to these pack ice areas early in the season, following courtship fasting, is the key to successful breeding. Analysis of colony distribution within each subpopulation found that they were highly clumped, and that they were strongly correlated to physical factors such as bathymetry, currents, and wind direction. The authors proposed that these factors reduce the occurrence of pack ice in the vicinity of the breeding colonies, thereby assuring access to open water in the early season. Snow accumulation, melt water runoff, and solar radiation are factors that impact on the microclimate of the breeding colonies, influencing the selection of breeding sites.

In recent years in the Antarctic Peninsula area, there has been an overall increase in chinstrap penguin populations, with a concomitant decrease in Adélie penguin populations (Croxall and Kirkwood 1979; Woehler 1993). Earlier authors suggested that the increase in chinstrap penguins was related to an increased abundance in their food (krill) brought about by the demise of the world's baleen whale stocks in the region (Conroy et al. 1975; Croxall and Prince 1979; Laws 1985). However, Fraser et al. (1992) challenged this hypothesis, arguing instead that the population changes were related to decreasing winter pack ice cover. In the winter, Adélie penguins frequent the pack ice, while chinstrap penguins are found in the open water. Increased temperatures are correlated with a reduction in the frequency of winter pack ice cover, which in turn negatively affected the pack ice-wintering Adélie penguins while benefiting the pelagic-wintering chinstrap penguins (see also Section 10.21).

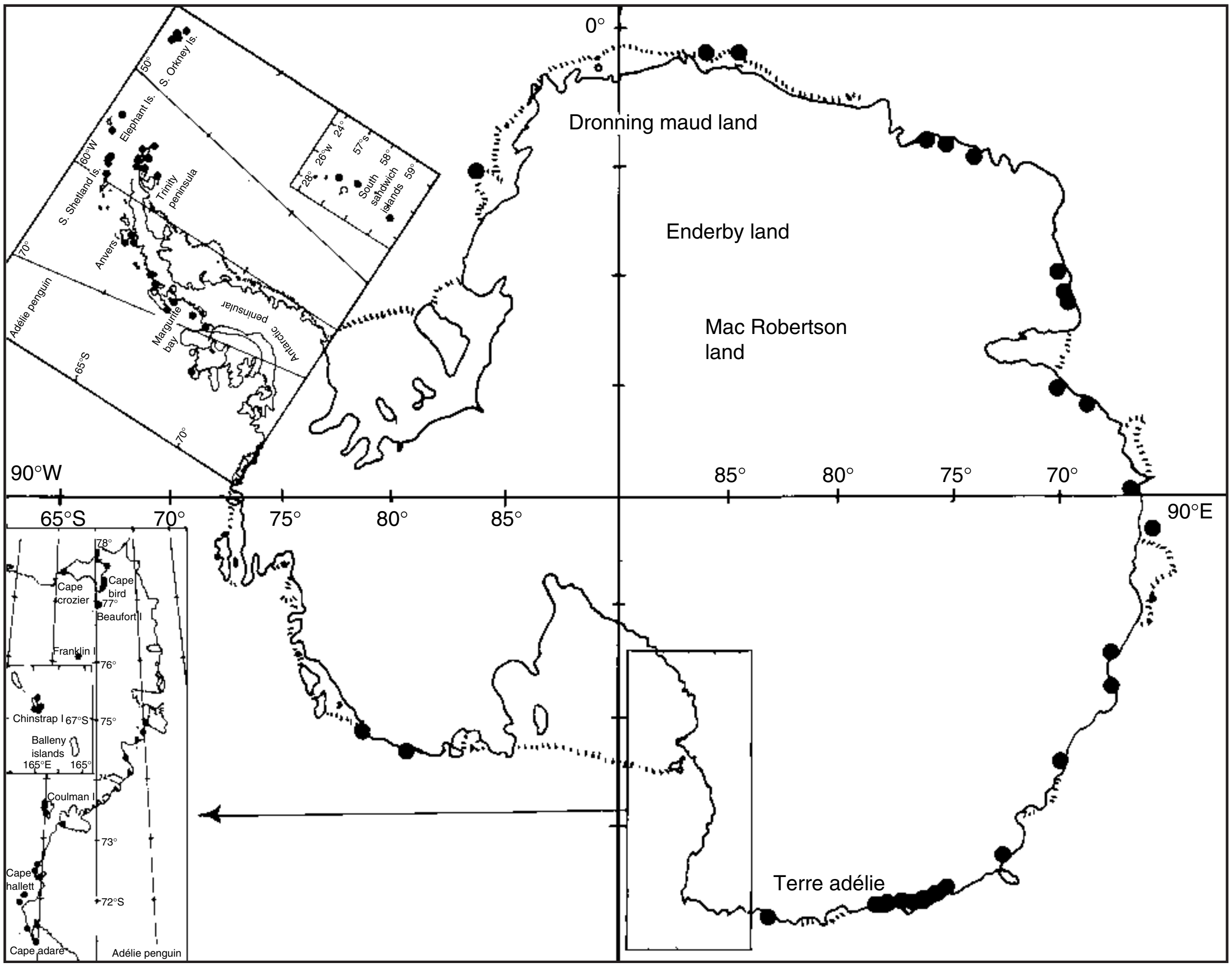


FIGURE 10.2 Breeding distribution of *Aptenodytes* and *Pygoscelis* species. (Based on data in Wilson, G.J., *BIOMASS Scientific Series*, 4, 1983. With permission.)

Whitehouse and Veit (1994) have described the distribution of seabirds near the Antarctic Peninsula in relation to the extent of sea ice and commercial fishing activity. Distinctive seabird assemblages were found in the open water (offshore) and where ice was present (Figure 10.4). Snow petrels were the most abundant species (31% of the survey total). Blue petrels and Antarctic petrels were more abundant in the offshore zone than the inshore zone. Adélie penguins and fur seals were most abundant in the inshore zone.

The most striking aspect of the winter avifauna was its pronounced concentration in the vicinity of fishing trawlers operating on the continental shelf to the north and west of Elephant Island. Five out of the 13 most abundant species observed (Southern fulmar *Fulmaris glacialoides*, Antarctic petrel *Thalassoica antarctica*, cape pigeon *Daption capense*, Kerguelen petrel *Lugensa brevirostris*, and blue petrel *Halobaena caeruleus*) were more abundant near fishing trawlers than elsewhere (Figure 10.5). The trawlers were fishing for finfish, *Notothenia rossi marmorata*, *Notothenia coriiceps neglecta*, *Notothenia larseni*, *Champsocephalus gunnari*, and *Chaenocephalus aceratus*. The fishing activity presented ample opportunities for seabirds to scavenge on offal.

Many species which breed on the Continent and adjacent islands undertake a winter migration before returning to their rookeries to breed. After moulting, Adélie penguins embark on such a migration, which takes them away from their breeding sites for approximately 8 months. Satellite telemetry has enabled the tracking of this species on their migrations. Davis et al. (1996, 2001) monitored the migration of Adélie penguins from Cape Hallett and Cape Bird, Ross Island. A penguin from Cape Hallett travelled 2,792.6 km in 4.4 months, whereas a second penguin travelled northwards up the coast to Victoria Land, keeping within 100 km of the coast, rounded Cape Adare and travelled westwards. When transmission ceased after 2.5 months, it was northeast of the Balleny Islands. This migratory path was confirmed by penguins tracked from Cape Bird. The results of these investigations indicated that: (1) Adélie penguins breeding in the Ross Sea follow a common migratory path; (2)

TABLE 10.2
Body Masses. Estimated FMRs and diet composition for 24 bird taxa observed in Prydz Bay, 1980–1981 to 1992–1993

	Mass (g)	FMR (kJ day^{-1})	%Crustaceans	%Fish	%Cephalopods
Resident species					
Adélie penguin	4.440	3.290	79.3	207	0.1
Antarctic petrel	680	1,051	22.0	78.0	0.1
Cape petrel	425	789	81.5	18.0	0.5
Emperor penguin	32,550	11,173	0.3	96.8	2.7
Snow petrel	270	598	34.0	65.0	0.1
South polar skua	1,000	1,330	0.0	10.0	0.0
Southern fulmar	775	1,139	36.0	63.0	1.0
Southern giant petrel	4,500	3,335	15.2	3.6	16.6
Wilson’s storm petrel	36	175	72.0	28.0	0.0
Nonresident species					
Antarctic tern	105	336	50.0	50.0	0.0
Black-bellied storm petrel	56	229	90.0	10.0	0.0
Black-browed albatross	3,790	3,003	39.9	38.0	20.6
Blue petrel	200	498	91.0	8.0	1.0
Grey-headed albatross	3,790	3,003	3.0	58.0	34.2
Kerguelen petrel	300	638	23.8	6.0	70.2
Light-mantled sooty albatross	2,840	2,518	39.5	10.9	45.5
Mottled petrel	323	667	0.7	0.9	98.4
Northern giant petrel	4,500	3,335	22.6	3.3	2.8
Prion spp.	150	417	98.5	1.0	0.5
Shearwater spp.	600	974	90.0	5.0	5.0
Soft-plumaged petrel	265	591	9.6	1.4	89.0
Wandering albatross	8,730	5,000	0.2	41.5	39.5
White-chinned petrel	1,270	1.540	29.0	24.0	47.0
White-headed petrel	750	1,116	67.0	0.0	33.0

Source: From Woehler, E.J., *Polar Biology*, 17, 383, 1997. With permission.

Adélie penguins breeding in the Ross Sea may travel to a common over-winter ground west and north of the Balleny Islands; and (3) Adélie penguins breeding at 77°S on Ross Island travel nearly twice the distance during their over-winter migration as do those breeding at Cape Hallett and at colonies further north.

Local climatic, oceanographic and topographical conditions influence the composition of the avifauna of the islands in the vicinity of the Antarctic Convergence. South Georgia, Heard Island and Bouvetoya are the only islands well south of the convergence. South Georgia, being larger, with a more varied topography, and closer to a continental land mass, has several additional species more typical of islands at or north of the convergence, such as Macquarie or Kerguelen. Both of the latter, especially Kerguelen, have species derived from islands to their north (Jouventin et al. 1984).

The seabirds of Prince Edward and Crozet, which lie just north of the convergence and close enough for cold Antarctic water to upwell in the lee of the islands (Grinley and David 1985), are essentially similar to those of Kerguelen (Williams 1984). Other islands lying further north of the Antarctic Convergence are the Auckland, Campbell, Antipodes, Bounty, and Falkland Islands. These islands have some species whose presence reflects the islands’ proximity to New Zealand and South America, respectively, but in general they lack some of the colder water species and also some of the warmer water species widespread in the Indian Ocean. However, as discussed in Chapter 18, albatross populations have declined considerably, due to mortality from fishing activity.

Population estimates for the balance of the surface nesting flying species are far less comprehensive and complete, although fair estimates are available for the giant petrels *Macronectes* spp., cormorants, skuas, kelp gulls, and terns. It is unlikely that their populations, in combination, account for more than 500,000 birds. Considerably less is known about the numbers of the southern fulmar *F. glacialoides*, Antarctic petrel *T. antarctica*, cape pigeon *D. capense*, and snow petrel *Pagadroma nivea*, which might total between four and five million birds, according to Mougin and Prevost (1980).

Omitting the two sheathbills, the remaining flying birds include the prions (five species), gadfly petrels (six species),

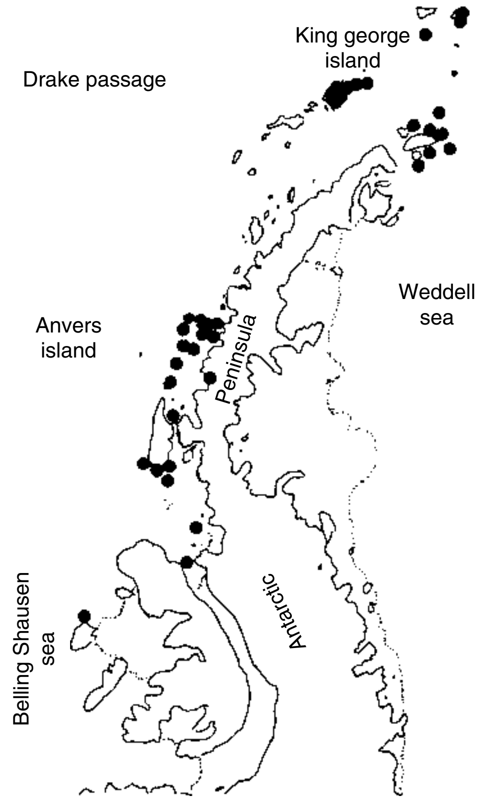


FIGURE 10.3 The distribution of the Adélie penguin population in the Antarctic Peninsula region. There are two distinct populations in the region; one is distributed from Anvers Island southward and winters in the Bellinghausen Sea pack ice, the second is distributed from King George Island and winters in the Waddell Sea pack ice. (From Trivelpiece, W.Z., Fraser, W.R., *Antarctic Research Series*, 70, 283, 1996. With permission.)

shearwaters (four species), and diving petrels (two species). Since these birds tend to nest in burrows, or in crevices and under boulders, and normally visit land only at night, censusing their populations is difficult. Improved field techniques are enabling more accurate estimates to be made, but it will be some time before definite pronouncements can be made on the total abundance of these species. Nevertheless, one recent series of estimates (Mougin and Prevost 1990) yields a grand total of a little short of 150 million birds of these species.

More accurate information is available on the numbers of penguins, since they are concentrated in dense colonies during the breeding season. Population estimates for the region have been summarized by Wilson (1983), and data for specific areas by Croxall et al. (1984a), Harper et al. (1984), Jouventin et al. (1984), and Williams (1984). These population estimates (Table 10.3) are for the number of breeding pairs, and do not include juveniles and nonbreeding adults. Depending on the species, the population estimates would need to be increased by a variable percentage to give estimates of the total population. The total number of breeding pairs in the Southern Ocean (excluding Macquarie Island and the African Subantarctic Islands) is on the order of 20–21 million. The greatest number occurs in the Antarctic Peninsula–Scotia Arc region (about 13 millions). Of the seven species of penguin, the most abundant is the macaroni penguin (approximately 10–11 million), with the chinstrap penguin being the second most abundant (6.5 million). Contrary to popular perception, the Adélie penguin, which is found around the fringes of the Antarctic continent, is not as numerous, with an estimated population of somewhat over 2 million breeding pairs. The two rarest species are the emperor penguin (approximately 135,000–200,000

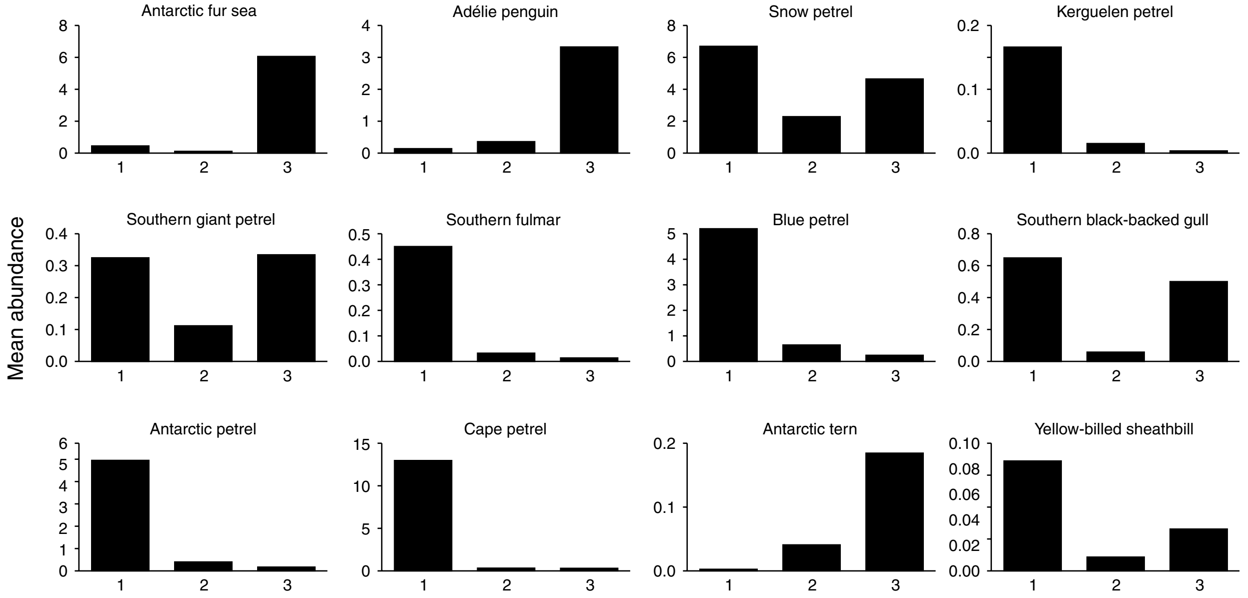


FIGURE 10.4 Mean predator abundance (animals km^{-2}): (1) Elephant Island zone; (2) offshore zone; (3) inshore zone. (From Whitehouse, M., Veit, R.R., *Polar Biology* 14, 328, 1996. With permission.)

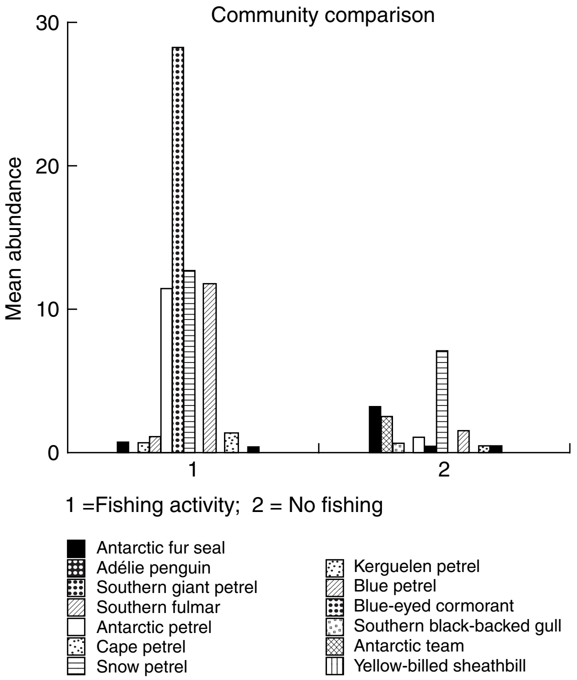


FIGURE 10.5 Predator community comparison: mean abundance (animals km^{-2}) off Elephant Island: (1) during fishing activity; (2) no fishing. (From Whitehouse, M., Veit, B.B., *Polar Biology*, 14, 327, 1996. With permission.)

breeding pairs) and the gentoo penguin (approximately 180,00 breeding pairs). Somewhat more than 1.2 million pairs of penguins breed on Macquarie island, including king, gentoo, southern rockhopper, and royal penguins. The latter relative of the macaroni penguin has a population of over a million.

Woehler (1997) estimated that the total seabird population in the Prydz Bay region exceeded 5.5 million birds in 5 years (1985/1986, 1986/1987, 1988/1989, 1989/1990 and 1990/1991), and was below 2.0 million birds in the other 7 years of the 12-year study (between 1980/1981 and 1992/1993). Estimates of population densities of seabirds based on shipboard observations or aerial surveys have yielded conflicting results. For example, Cooper and Woehler (1994) estimated the total abundance of resident species to be 3.3 times that estimated by Woehler (1997), and the nonresident species at 7.6 times greater. Such differences between studies can be attributed primarily to differences in analytical methodologies and the data sets examined. Various studies have used alternative methodologies such as longer or shorter survey periods, radial surveys, or transects on both sides of the vessels, e.g., Joris (1991) and Plotz et al. (1991).

For the resident and nonresident birds of the Prydz Bay region, Woehler (1997) estimated the mean abundance at 3.75 and 1.81 birds km^{-2}, respectively. Comparable data from the Ross Sea (Ainley et al. 1984) indicated a total abundance of 16.32 birds km^{-2}, due primarily to the high abundance of penguins. In the southern Drake Passage and Bransfield Strait region, Hunt et al. (1990) reported a total abundance of 5.67 birds km^{-2}. Van Frankel (1992) estimated a total abundance of 11.36 birds km^{-2} from the Weddell Sea–Scotia Sea confluence. The results for the seabird community in the Prydz Bay region (5.56 birds km^{-2}) are similar to estimates for most of the other regions of the Southern Ocean. While slightly lower, the results from the Prydz Bay region are of the same magnitude as those obtained elsewhere, with the exception of the Ross Sea.

TABLE 10.3
Percentage Composition by Weight of the Diet of Antarctic Penguins

	Main Prey Classes			Crustacean Prey			Locality	Source
Species	Squid	Fish	Crustacean	Euphausiids	Amphipods	Copepods		
Adélie	+	39	61	98[a]	2	+	Cape Crozier	Emison (1968)
Adélie		+	100	100	+		S. Shetland Is.	Volkman et al. (1980)
Chinstrap		+	96	100	+		S. Shetland Is.	Croxall and Furse (1980)
Chinstrap		+	100	100	+		S. Shetland Is.	Volkman et al. (1980)
Gentoo		15	85	100	+		S. Shetland Is.	Volkman et al. (1980)
Gentoo		33	68	100	+		South Georgia	Croxall and Prince (1980a)
Macaroni		3	98	100	+		South Georgia	Croxall and Prince (1980a)
Macaroni		25	75	75[b]	+		S. Shetland Is.	Croxall and Furse (1980)

+, present in small quantities. Euphausiids all *Euphausia superbu*.

[a] *E. crystallorophias*.

[b] 50% *Thysanoessu macruru*.

Source: From Croxall, J.P., Prince, P.A., *Biol. J. Linn. Soc.*, 14, 103, 1980a. With permission.

10.3 BREEDING BIOLOGY

10.3.1 Breeding Location and Habitat

Reviews of breeding dispersion, colony size, and preferred habitat for Antarctic seabirds generally (Carrick and Ingham 1967) and for South Georgia (Croxall and Prince 1980a) have revealed some species-characteristic patterns. In general, seabirds are colonial; the only exceptions are the Light-mantled sooty albatross and the charadriform species (skuas, gulls, and terns). These latter species defend isolated nest territories and, in the case of some skuas, feeding territories based on parts of penguin colonies (Young 1963a, 1963b; Muller-Schwarze and Muller-Schwarze 1977; Trillmich 1978; Trivelpiece et al. 1980). Sheathbills, which also scavenge on colonies, are similar in this respect (Burger 1979), and nest in solitary colonies.

The burrow-dwelling habit which is confined to the smaller and medium-sized petrels is best developed on the Subantarctic islands, where large areas of peaty grassland are found. Other habitats suitable for burrow excavation include screes, moraine debris, and mossbanks; these are used principally by storm and diving petrels. Crevice nesters include storm petrels, prions, and the snow petrel, cape pigeon, Antarctic fulmar, and Antarctic petrel. The latter, with their preference for nesting on sheltered ledges, provide a link between the crevice-nesting snow petrel and the giant petrel, which prefers sheltered open sites.

The colonial surface-nesting habit is virtually restricted to the larger seabirds, such as albatrosses and penguins. Most albatrosses tend to nest in compact colonies on tussock slopes and cliffs, although the wandering albatross is usually found in dispersed groups on flatter areas. Penguins generally breed on flattish sites of exposed rock, beaches, moraines, or tussock. The emperor penguin is unique in that it breeds on fast sea ice. Although distinct habitats are often attributed to pygoscelid penguins (e.g., White and Conroy 1975), it has been shown that they are by no means consistent between sites (Volkman and Trivelpiece 1981), and it is likely that Adélie and chinstrap penguins have broadly overlapping requirements. The gentoo penguin, while preferring flat sites, has catholic tastes, being found on beaches, tussock, and even boulder areas.

There has been speculation that the availability of suitable terrain has the potential to influence the number and distribution of breeding Antarctic seabirds. However, as Croxall (1984) points out, it is unlikely that its role in limiting breeding numbers is of overriding importance, since adequate breeding sites would appear to be superabundant for most species in most parts of the Antarctic. On a broader basis, however, the nature of available habitat, e.g., suitable terrain for burrowing, presence of grassland, availability of crevices, etc., does limit the number of breeding birds in specific localities. Climate, however, is perhaps a more significant factor in determining distributions and breeding success.

10.3.2 Timing of the Breeding Season

The duration of the breeding season, from egg laying to chick fledging, for species for which adequate data is available, is shown in Figure 10.6. Croxall (1984) has synthesized the available information on the breeding cycles of Antarctic seabirds, and the following account relies heavily on this review.

A number of points arise from a consideration of the overall patterns. First, there are differences in the time of the onset of breeding activities at various sites. Characteristically, the more northerly populations of most species breed 2 or 3 weeks earlier than the more southerly ones (Stonehouse

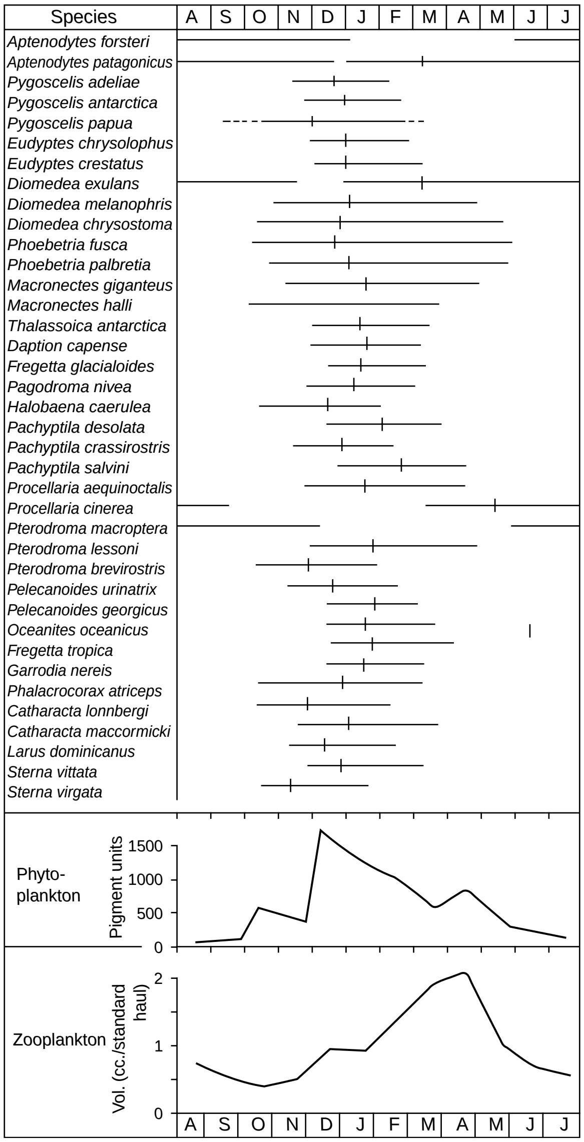


FIGURE 10.6 Timing of the breeding season in Antarctic seabirds. Vertical bars represent hatching dates. Phytoplankton data from Hart (1942) and Foxton (1956), respectively. (From Croxall, J.P., *Antarctic Ecology*, Vol. 2, Laws, R.M., Ed., Academic Press, London, 533, 1984. With permission.)

1964, 1967, 1970; Watson et al. 1971). This is particularly evident between Subantarctic islands and the Antarctic Continent and Peninsula. In some species, there is also a difference in timing between sites at the same latitude, e.g., the royal penguin, which breeds 2 weeks earlier at Macquarie than at Heard Island (Carrick and Ingham 1967). Gentoo penguins show the greatest variation in timing.

Second, even in a single general area, a few species exhibit poor synchrony of breeding, with eggs being laid over two or more months. This is in contrast to most species, in which the breeding is highly synchronized with the eggs being laid over a period of generally less than 3 weeks. This is attributable to the relatively short period of favourable conditions and to the predominantly colonial breeding habit. Exceptions are some medium-sized petrels in lower latitudes (Barratt 1974; Mougin 1975), storm petrels (*O. oceanus* and *F. tropica*) at some sites on Signy Island (Beck 1970), the brown skua, southern black-backed gull (*Larus dominicanus*), and the Antarctic tern (*Sterna vittata*), which are essentially solitary species, and the king and gentoo penguins. King penguins have an unusual breeding cycle involving maintaining chicks in winter and late breeding by parents that have successfully fledged a chick in spring. While the reasons for the well-documented lack of synchrony in gentoo penguins are less clear, Croxall and Prince (1980a) have suggested that as an inshore feeding species with a relatively small foraging range, this may be an adaptation to reduce interspecific competition, especially during chick rearing and adult premoult fattening periods.

Third, there are season to season variations in laying dates at a single site or colony. These are often caused by climatic factors such as the late breakout of sea ice, or snow and ice blocking burrows. However, the variation is seldom more than a week or two, and for some species, colony or population mean laying dates are relatively consistent over long periods of time.

It appears that most species begin breeding as early in the season as practicable, so that the principal demand for food (during rapid chick growth and once the chick has fledged) can coincide with the availability of food. There are, however, a number of species that are winter breeders. The most celebrated of these is the emperor penguin. Winter breeding in the wandering albatross and certain petrels (grey petrel and great-winged petrel) is probably an adaptation to take advantage of the reduced competition for food resources in the winter where climatic conditions are suitable, e.g., in the Subantarctic islands. Such a strategy seems possible only for large species adapted for catching squid, and possibly fishes, as crustaceans are usually not available in sufficient quantities in winter.

10.3.3 BREEDING CYCLES

The basic pattern of events during the breeding season is very similar for most Procellariiformes and penguins. Potential breeding birds arrive at the colonies some weeks before egg laying (males often before females), and a period of courtship behaviour, pair bond formation (or re-establishment) and burrow prospecting (or modification of the burrow/nest of the previous season) ensues. The duration of this period is usually about 20–30% of the time from egg laying to chick fledging (Mougin 1975). After copulation, the female generally departs for the sea for a period often lasting 2–3 weeks, and returns immediately before egg laying. Egg laying quickly follows the female's return and she departs after a short incubation shift.

Large birds lay heavier eggs, but the eggs of smaller birds are proportionately larger in relation to body weight. All procellariform species lay one egg. Most penguins (except *Aptenodytes* spp.), however, lay more than one egg, usually two. Incubation duties are shared between the parents until the chick hatches, and (except for *Eudyptes* spp.) they can often rear more than one chick. Chicks hatch asynchronously and often only the older one survives.

Incubation duties are shared between the parents until the chick hatches, with a tendency for the shift, or shifts, prior to hatching being shorter, ensuring that on hatching the chick receives a meal quickly. This tendency is most marked in large birds with long incubation shifts (e.g., albatrosses) where shift length decreases from about the midpoint of incubation. In penguins the pattern of incubation is extremely variable, ranging from the usual daily changeovers in the gentoo penguin to stints of over a month in eudyptid species. Figure 10.7 gives a simplified diagram of the duration of periods ashore and at sea for both sexes throughout the breeding season for selected species. Of the pygoscelid species the gentoo is not illustrated, as once incubation commences it has a pattern of daily changeovers. Desperin (1972), however, recorded mean shifts of 2.8 days for females and 3.3 days for males at Isles Crozet. Gentoos maintain a similar pattern throughout the chick rearing period. There is insufficient information to construct a diagram for the chinstrap penguin, although it has been suggested (Conroy et al. 1975) that its incubation shifts are shorter (mean 2–8 days), and visits to the chicks more frequent than in the Adélie penguin. In the Adélie the female sometimes takes the first shift, which is then short (6 days), but this is followed by a normal length (15 days) male shift (Spurr 1975).

In the procellariformes, the chick is brooded after hatching for a varying period in alternating shifts by one parent, while the other feeds the chick. Subsequently, both parents feed the chick, which gains weight rapidly, accumulating substantial fat reserves, to reach a peak weight normally substantially in excess of adult weight. Thereafter, it continues to be fed, often with gradually decreasing frequency while the body tissue, muscles, feathers, etc., grow. Weight decreases until fledging as the reserves are used up. Penguins follow a similar pattern, but in most species chicks do not fledge until the moult is completed. In penguins, the mean fledging period varies from 50 days in the Adélie penguin to 350 days in the king penguin; in the chinstrap, the period is 54 days, and in the other species the period ranges from 62 to 90 days. In albatrosses, the period is generally in the order of 120–140 days, with the exception of

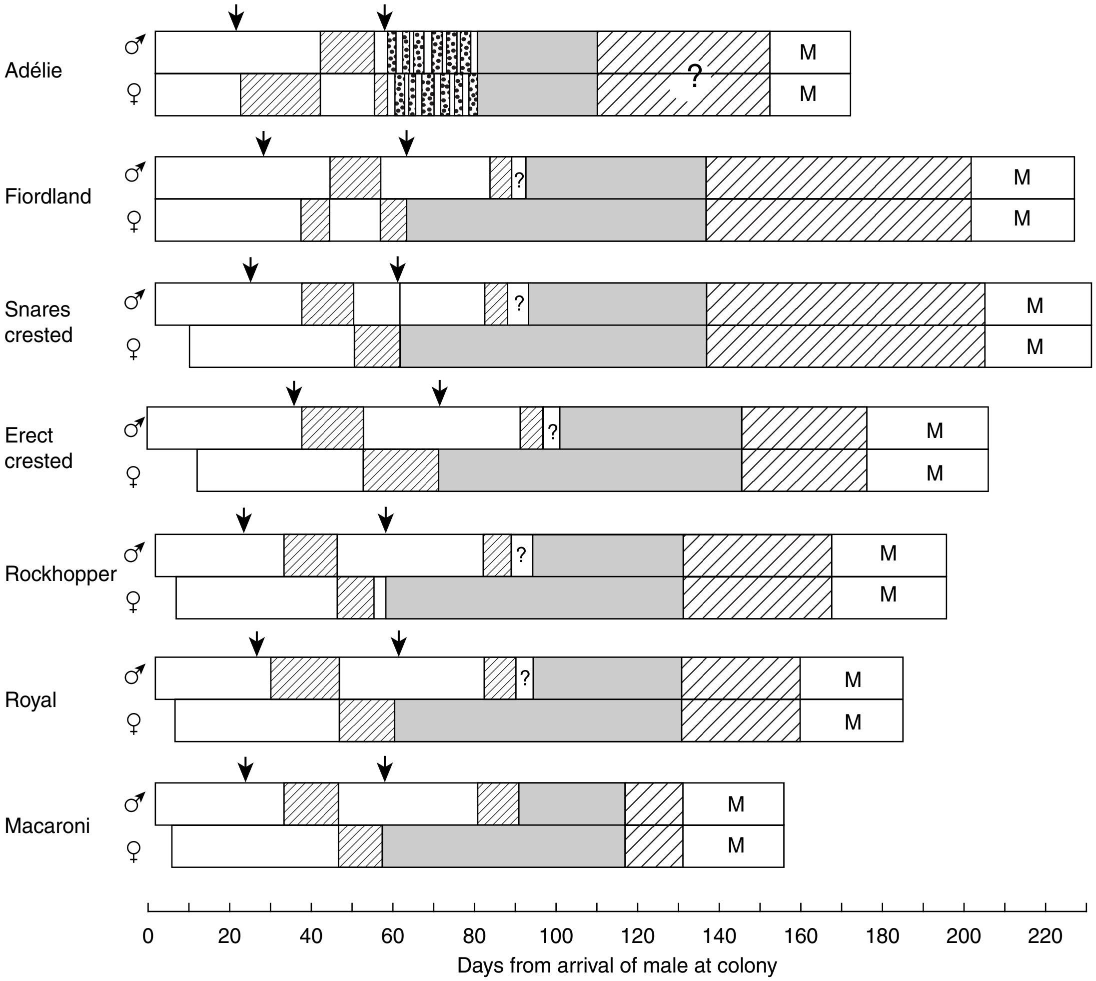


FIGURE 10.7 Duration and timing of breeding season events in some Antarctic penguins (data from in turn: Taylor 1962; Warham 1963, 1971b, 1972b, 1974b; Spurr 1975; Croxall 1984). First arrow, mean laying of second egg; second arrow, mean hatching date; cross-hatched, at sea; stippled, feeding chicks; blank, in colony; M, moult. Periods of unknown duration indicated by ? (From Croxall, J.P., *Antarctic Biology*, Vol. 2, Laws, R.M., Ed., Academic Press, London, 533, 1984. With permission.)

the wandering albatross, where it is 278 days. In the petrels, the fledging periods range from 42 (Antarctic petrel) to 125 (grey-faced petrel).

As a winter breeder, the emperor penguin breeds under the most extreme environmental conditions of any bird. If it were to lay eggs in the spring, the chicks would be unable to fledge before winter; consequently, laying takes place in late summer, with the adults in peak condition, and the chick is reared throughout the winter. It fledges in midsummer at only 60% of the adult body weight (Prevost 1961), the lowest proportion of any penguin. In coping with the problems of incubation and brooding fasts, the adults lose up to 40% of their body mass (Prevost 1961) in temperatures that may drop as low as −49°C. The Emperor shows a number of adaptations: its ambient critical temperature (below which metabolic rate must be increased to maintain body temperature at a constant level) of −10°C (Le Maho et al. 1976); its appendages (flipper and bill) are about 25% smaller in proportion to body size than in other penguins (Stonehouse 1967); its flippers and feet have extremely well-developed vascular counter-current heat exchangers (reducing heat expenditure in cold air); heat loss is minimized in the nasal passages (Murrish 1973); and the behavioural adaptation of huddling, which may involve up to 5,000 birds at 19 m^{-2} (calculated to reduce the theoretical heat loss of body weight by 25–50% (Prevost 1961)).

10.3.4 BREEDING SUCCESS

Data on the proportion of eggs hatched and chicks fledged (summarized by Mougin 1975; Berruti 1979; Croxall and Prince 1979) suggests that it is rare for chicks to fledge from more than half of the eggs laid. Albatrosses and petrels normally have greater (and more consistent) breeding success than penguins. Although direct natural predation is rare, skuas and giant petrels, sheathbills, and gulls take eggs, and more rarely, chicks. Environmental conditions affect breeding success, especially in penguins. Jouventain (1975) and Yeates (1968, 1975) found a direct relationship between the severity of environmental conditions and egg and chick loss in the emperor and Adélie penguins, respectively. The importance of the timing of the sea-ice breakout, which influences the distance that the birds have to travel for food, has been demonstrated for the latter species; early breakout is correlated with high breeding success at Cape Crozier (Ainley and Le Resche 1973) and Cape Royds (Stonehouse 1963; Yeates 1968).

Packice conditions, iceblanketed burrows, or snow-covered nest sites may delay the onset of breeding and may result in chicks fledging at less than optimum weights and time. The relationship between breeding success and colony size (better in larger colonies, Oelke 1975) and nest position (better in central than peripheral birds, Spurr 1975; Tenaza 1971) has been studied in Adélie penguins. This reflects the tendency for the younger birds, which lay fewer (Tenaza 1971) and smaller (Yeates 1968) eggs to breed at the periphery of the colony. Age affects laying date, clutch size, incubation routine (but not incubation period), egg fertilization, and hatching and fledging success (Ainley et al. 1983). The older birds are the most successful breeders.

Buer et al. (2004) investigated the breeding success and chick provisioning in Wilson's storm petrels (*Oceanites oceanicus*) over a 7-year period. The overall success of breeding pairs was low, ranging from 0% to 34%. Snow storms and wind conditions depressed breeding success. In addition, the distribution of wind directions was found to strongly influence the availability of krill to the storm petrels.

10.4 NONBREEDING BIOLOGY

10.4.1 MOULT

Apart from the penguins, information is sparse on the timing and duration of moult in Antarctic seabirds. In petrels, moult usually begins during the incubation period, but primary feather moult takes place after the chicks have fledged. In the cape pigeon (Beck 1969) and possibly the snow petrel (Maher 1962), however, the primary moult commences shortly before the chicks fledge, and as it lasts about 85 days in the cape pigeon, it is completed in May, before the start of winter. An early start to the moult appears to be a characteristic of the larger petrels in high latitudes. Penguins come ashore for a complete moult during a relatively brief and well-defined period (see Figure 10.6). Prior to this, they accumulate considerable fat reserves which are lost during the moult fast.

10.4.2 DISPERSION AND MIGRATIONS

In recent years, there have been numerous papers summarizing the results of the recording of bird sightings at sea. Under the stimulus of the BIOMASS Bird Ecology Working Group, the making of such observations has been standardized so that data from various regions of the Southern Ocean can be compared. Typical of the information that can be obtained from such studies is that of Ainley and his coworkers in the Ross Sea region (Ainley and Jacobs 1981; Ainley et al. 1983; Ainley 1985). During December and January, they recorded a total 9.733,00 birds at an average density of 16.3 birds km^{-2} and a biomass of 0.04 g m^{-2}. Nine species were recorded during the census period, with the dominant species by numbers being the Antarctic petrel (55%) and by biomass the emperor penguin and Adélie penguin (42.8% and 39.3%, respectively). Bird biomass was concentrated over the slope front and in the pack ice of the southwestern Ross Sea. The Antarctic Slope Front described by Ainley and Jacobs (1981) lies over the Ross Sea continental slope and is characterized by steep gradients in physical properties. Biggs (1982) reported peaks in zooplankton biomass over this slope front.

In a similar manner, Abrams (1985a, 1985b) has studied the pelagic distribution of seabirds, excluding penguins, in the African Sector of the Southern Ocean over the period 1979–1981. Seabird density estimates were calculated for four frontal zones and five zones between the fronts and South Africa and the Antarctic Continent (see Figure 10.8). The distribution of the birds in relation to food supply is discussed below. During the nonbreeding season, the procellariform birds disperse widely. The larger albatrosses, especially the wandering albatross, follow the air currents of the westerly winds and may circumnavigate the Southern Ocean. Wilson's storm petrels (Roberts 1940), some Antarctic skuas (Voous 1965), as far north as Greenland (Parmelee 1976), and several Subantarctic species such as the sooty shearwater (Richdale 1963), great shearwater, and mottled petrel (Seventy 1957) are transequatorial migrants. Most other Antarctic seabirds also tend to move northwards in the winter. Those that breed at high latitudes, except the emperor penguin, need to move at least to the packice edge in order to feed.

Related species often show different degrees of winter movement. For example, while Snow and Antarctic petrels maintain a high Antarctic distribution the other fulmarine petrels range much further north, even into the Humboldt and Benguela cold surfacewater currents off South America and South Africa, respectively. Black-browed albatross populations move well to the north in the winter, whereas grey-headed albatrosses remain in high latitudes (Tickell 1967; Prince 1980b). Among the penguins, the gentoo is much more sedentary than the other species.

10.5 FOOD AND FEEDING ECOLOGY

10.5.1 FOOD

Most of the early studies of the nature of the food of Antarctic seabirds were based chiefly on observed stomach contents analysed on the basis of the frequency of occurrence of the main food types (see Carrick and Ingham 1967; Mougin 1975 for reviews). Such studies can be misleading, as they emphasize the presence of indigestible remains, especially squid beaks (Ashmole and Ashmole 1967).

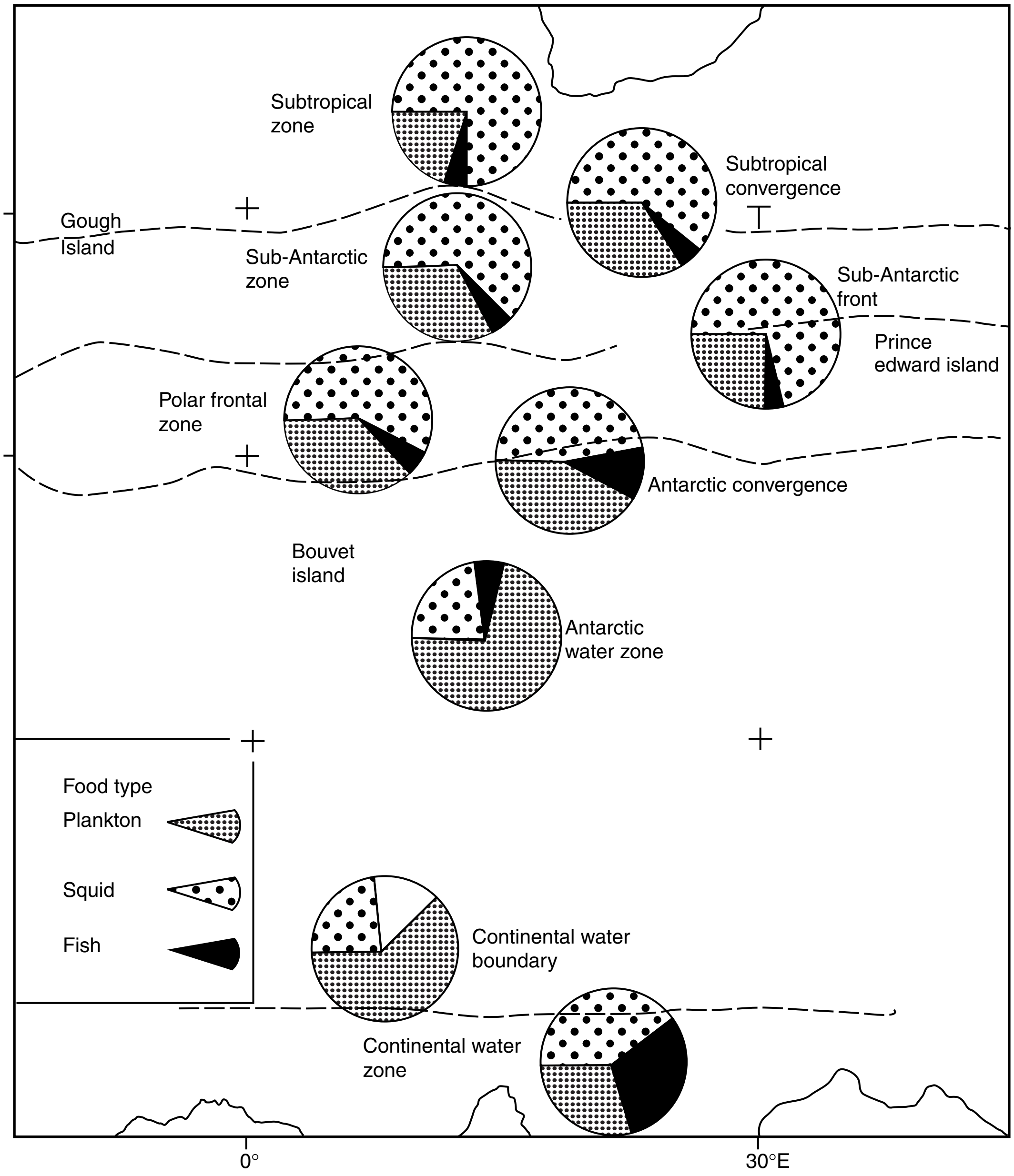


FIGURE 10.8 Proportionate distribution of amount of seabird food types based on diet and carbon requirements (g C m^{-2} per year) of seabird populations in different zones of the African Sector of the Southern Ocean. (From Abrams, R.W., *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., 466, 1985. With permission.)

More recent work (e.g., Emison 1968; Croxall and Furse 1980; Croxall and Prince 1980a, 1980b; Prince 1980a, 1980b; Thomas 1982; Hunter 1983; Montague 1984; Croxall et al. 1984b, 1985; Lishman 1985; Offredo et al. 1985; Klages 1989; Arnould and Whitehead 1991) has provided information on the number of individuals and total weight of each prey class; this has enabled estimates of total consumption to be made.

Croxall (1984) has proposed the following greatly simplified classification of Antarctic seabird's principal natural dietary preferences:

Crustacea. *Eudyptes* spp., *Pygoscelis* spp., *D. melanophris*, *Phoebretia* spp., *Daption*, *Pagodroma*, *Thallassoica*, *Fulmarus*, *Halobaena*, *Pachyptila* spp., Pelecanoides, storm petrels.

Squid. *Aptenodytes* spp., *Diomedia* spp (except *D. melanophris*), *Phoebretia* spp., *Macronectes* spp. (at some localities), *Fulmarus*, *Procellaria* spp., *Pterodroma* spp., *Puffinus* spp.

Fish. *Aptenodytes fosteri*, *Pygoscelis papua*, *P. adeliae* (continent), some *Diomedia* spp., *Halobaena*, *Phalacrocorax* spp. (some squid), *S. vittata* (and crustacea?).

Other. *Macronectes* spp. (carrion), *Catharacta* spp. (eggs, chicks, small petrels, also fish and crustacea in *C. maccormicki*), *Larus* (beach invertebrates), *Sterna virgata* (insects, etc.).

In his study of seabird distribution and feeding in the African sector, Abrams (1985a, 1985b) found that the proportions of plankton, fish, and squid eaters changed from north to south (Figure 10.8). Squid was predominant in the diets in the Subtropical Zone (STZ) north of the Subtropical Convergence (STC) and in the Subantarctic Zone (SAZ). The percentage of plankton in the diet increased at the Antarctic Convergence (Antarctic Polar Front, APF), reaching a maximum in the Antarctic Water Zone.

In a subsequent investigation, Pakhomov and McQuaid (1996) investigated surface zooplankton and seabird densities in the Atlantic between Cape Town and SANAE Base on the Antarctic Continent, and in the Pacific between New Zealand and the southern Ross Sea. The macroscale positions of the zooplankton communities were associated with specific water masses and hydrographic features. A homogeneous "Subantarctic" zooplankton community was identified both south of Africa between the STC and the APF and south of New Zealand between the SAF and APF. The dominant species were the hyperiid amphipod *Thermisto gaudichaudi* and the euhausiid *Euphausia tricantha* (in the Pacific sector only). South of the APF, as far south as 60–65°S in both sectors, a community dominated by *Salpa thompsoni* was identified. Among the other dominants were *Euphausia superba* in the Atlantic sector and *E. tricantha* in the Pacific. From Figure 10.8 it can be seen that the diets of the seabirds differed in the various zooplankton communities. North of the APF, squid dominated the seabird diet, while south of the APF, a mixed diet of copepods, amphipods, and euphausiids dominated.

Ainley et al. (1992) posed the question: "Does prey preference affect habitat choice in Antarctic seabirds?" They investigated the pack ice and open water seabird assemblages in the confluence zone of the Weddell and Scotia Seas. Diet samples were obtained from three habitats: open water, sparse concentrations of ice, and heavy ice cover. Cluster analysis showed broad overlap in seabird diet regardless of species, habitat (ice/water mass), or year. Seabirds exploited prey largely according to ranked availability, although they appeared to choose the larger fish and crustaceans over smaller crustaceans. Not surprising was the prevalence of fish in the diets of snow petrels (Ainley et al. 1984; Klages et al. 1990), of squid and fish in the diet of white-chinned petrels, of squid and fish (*Notolepis coatsi*) in the diets of emperor penguins (Gales et al. 1990), and the diverse diets of the remaining species: Antarctic fulmar, cape petrel, and Wilson's storm petrel (Figure 10.9). Kerguelen petrels were found to eat large decapods.

One surprise was the great importance of myctophids to the avian predators. It was concluded that in the Weddell Sea, myctophids, especially *Electrona antarctica*, formed the basis of the avian diet, with krill as the secondary component. The authors considered that the importance of krill to top trophic level predators in the Southern Ocean appears to have been over-emphasized. Their observations on the importance of myctophids have been supported by studies that have considered the year-round diet of the predators (see Adams and Klages 1987; Croxall and North 1988; Gartshore et al. 1988; Adams and Brown 1989; Cooper et al. 1990; Klages et al. 1990).

Plankton-feeding species account for approximately 55% of the total abundance of pelagic seabirds (excluding penguins). Most are prions and petrels which feed on the surface of the sea on crustaceans, e.g., the Antarctic petrels at Prydz Bay, which feed exclusively on *E. superba* (Montague 1984). Arnould and Whitehead (1991) studied the breeding season diet of the three surface-nesting petrel species (the cape pigeon, the Antarctic petrel, and the southern fulmar) at Prydz Bay. The pelagic fish *Pleurogramma antarcticum* and krill (*E. superba*) dominated the diets of all species. By mass, they constituted 78% and 22% of the Antarctic petrel diet, 63% and 36% of the southern fulmar diet, and 14 and 85% of the cape petrel diet, respectively. This group of birds tends to be most abundant south of the Antarctic Convergence. Squid eating species, comprising approximately 20% of the pelagic avifauna, dominate north of the Antarctic Convergence (Siegfried 1985). These are the larger birds, including the albatrosses and the larger petrels. At South Georgia, squid constituted 49% of the diet by weight of the grey-headed albatross (Prince 1980) and 47% in the light-mantled sooty albatross (Thomas 1982). The third group consists of fish-eating species. Except in the vicinity of land and the Antarctic ice shelves, these birds account for an almost negligible proportion of the avian abundance, probably reflecting the comparative rarity of pelagic fishes in the Southern Ocean. Fish, however, do constitute a substantial percentage of the diets of some species, e.g., 35% by weight in the grey-headed albatross and 37% in the black-browed albatross at South Georgia (Prince 1980b, 1985), and 24% in the white-chinned petrel at the same locality. Few species, except some of the plankton feeders, feed exclusively on one category of prey. Most have a mixed diet, with one of the main diet categories being predominant. Some species, the mixed-diet group, have a more varied diet. Such species constitute about 20% of the avian abundance.

Although the plankton-eaters predominate in the total avian numbers of the Southern Ocean, they probably account for less than 25% of the total avian biomass. The larger albatrosses, in contrast, help to boost the squid-eating group to approximately 50% of the total avian biomass (excluding penguins) (Siegfried 1985). In an 11-year study of the diet of the wandering albatross, *Diomedia exulans*, Xavier et al. (2003) found that the cephalopod component of the diet was relatively stable over the period of the study (Figure 10.10). By number of lower beaks, three species predominated in the cephalopod component of the diet: *Kondakovia longimana* (29.5%), *Taonius* sp. (20.4%), and *Histioteuthis* sp. B (19.5%). Figure 10.8 depicts the proportion of "Antarctic", "Subantarctic," and "Subtropical" taxa in the diet over the period of the study. The "Antarctic" cephalopod component

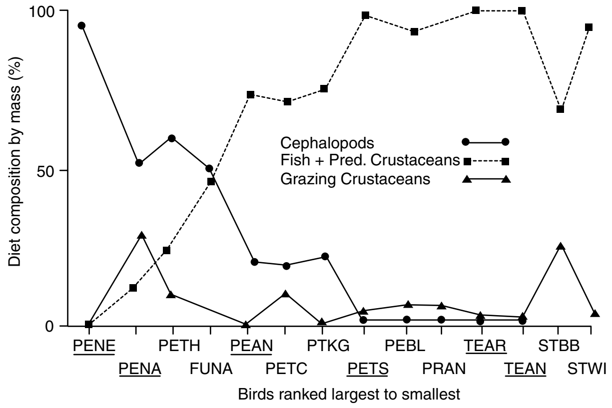


FIGURE 10.9 The proportion of squid, fish (plus large predatory crustaceans) and small crustaceans in seabird diets as a function of predator size and ranked largest to smallest. Underlining indicates pack ice species. (From Ainley, D.G., Ribic, C.A., Fraser, W.R., *Marine Ecology Progress Series*, 214, 1992. With permission.)

dominated, suggesting that Antarctic waters were an important foraging area for the albatrosses.

In a review of nocturnality in seabirds, Brooke and Prince (1991) consider that squid-eating Procellariiformes generally feed at night. Bioluminescence and diel vertical migration (Imber 1976; Clarke et al. 1981) of the cephalopods have been invoked to substantiate the argument that these birds feed at night. This belief has been challenged by Weimerskirch and Wilson (1992), who fitted stomach sensors to five wandering albatrosses. The results of this study showed that 89% of all prey were caught during the day.

Data on the percentage composition by weight of the diet of Antarctic penguins for which adequate data is available is given in Table 10.4. Crustacea are the predominant item in the diets, ranging from 61 to 100% by weight. At the South Shetland Islands, Adélie and chinstrap penguins feed exclusively on *E. superba*. At Cape Crozier, *E. superba* is replaced in the diet of Adélie penguins by the smaller *E. crystallorophias* (Emerson 1968). Penguins take other crustaceans occasionally, especially hyperiid amphipods. Depending on the location, fish, especially larvae, may be an important secondary component of the diet, e.g., at Cape Crozier, where they constituted 39% by weight of the diet of Adélie penguins. The fish consumed are mostly larval or juvenile specimens, especially those of the pelagic species *P. antarcticum*.

Over the last 15 years, there have been numerous papers on the diet, feeding methods, and foraging ranges of Antarctic penguins, particularly Adélie penguins. In the southern Ross Sea, the pelagic fish *P. antarcticum* is the most important item in the diet of Adélie penguins, especially during years or periods when little pack ice was present. Juvenile *Euphausia crystallorophias* predominated in years of heavy pack ice cover; more *E. superba* were consumed when pack ice was sparse. In Lutzow-Holm Bay in East Antarctica, Endo et al. (2000) found that euphausiids accounted for 75% of total wet weight of stomach contents, and fish 27%. Among the euphausiida, *E. superba* accounted for 83%, and *E. crystallorophias* 17%.

In an investigation of extinct Adélie penguin colonies in Marguerite Bay, Antarctic Peninsula, covering a span of 6,000 years, Emslie and McDaniel (2002) found that two species, the Antarctic silverfish (*P. antarcticum*) and the squid *Psychroteuthis glacialis*, were commonly represented

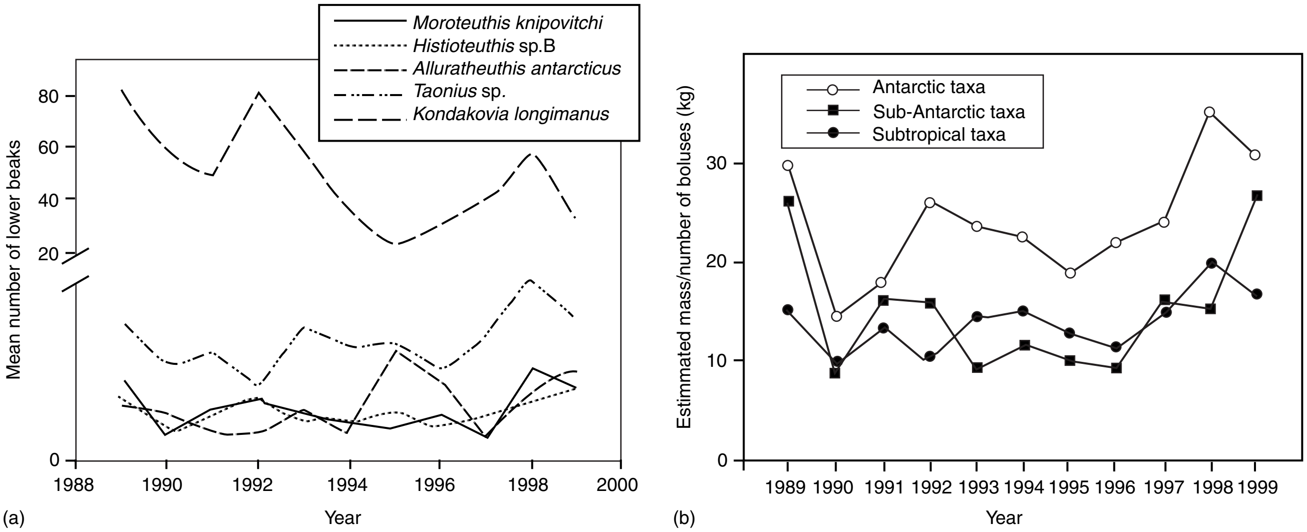


FIGURE 10.10 Cephalopod consumption by seabirds at Bird Island, South Georgia. (a) Inter-annual variation in estimated mass of the most important cephalopod species present in the boluses from wandering albatross chicks at Bird Island, South Georgia between 1989 and 1999 (only *K. longimana* contributed greater than 5 kg to the diet). (b) Inter-annual variation in the mean number of lower beaks from "Antarctic," "Subantarctic," and "Subtropical" cephalopods present in boluses from wandering albatross chicks at Bird Island, South Georgia between 1989 and 1999. (From Xavier, J.C., Croxall, J.P., Tratham, P.N., Rodhouse, G.P., *Marine Biology*, 142, 617, 2003. With permission.)

TABLE 10.4
Feeding Methods and Foraging Range of South Georgia Seabirds

	Methods							
Species	**Pursuit**	**Plunge**	**Dive**	**Surface Seize**	**Dip**	**Filter**	**Scavenge**	**Maximum Foraging Range (km)**
King penguin	XXX							*c.* 500
Chinstrap penguin	XXX							
Gentoo penguin	XXX							31.5
Macroni Penguin	XXX							115
Wandering albatross				XXX			XX	2650
Black-browed albatross		X	X	XXX			XX	925
Grey-headed albatross		X	X	XXX			X	950
Light-mantled sooty Albatross		X	?	XXX			X	1250
Southern giant petrel				XXX			XXX	*c.* 330
Northern giant petrel				XXX			XXX	*c.* 350
Cape pigeon				XXX			XX	
Snow petrel				XXX			X	
Dove prion				XX			XXX	300
Blue petrel			XX	XX	XX			600
White-chinned petrel			XXX	XXX				1650
Common diving petrel	XXX	XX	XX	XX				360
South Georgia diving Petrel	XXX	XX	XX	XX				330
Wilson’ storm petrel		X			XXX		X	250
Black-bellied storm petrel		XX			XXX		X	
Grey-backed storm petrel		XX			XXX			
Blue-eyed shag	XXX							
Brown shua							XXX	
Southern bluck-backed Gull				XXX			XX	
Antarctic tern		XXX			XXX			

XXX, common; XX, occasional; X, rare. Foraging range estimate based on (a) interval between successive feeds to chick by the same parent and (b) calculated flight and swimming speeds.

Source: From Croxall, J.P., Prince P.A., *Biol. J. Linnean. Soc.*, 14, 103–134, 1980a. With permission.

in the sediments; dating suggested that silverfish may have been exploited more during cool climatic intervals, and squid in warm climatic intervals.

Adélie (*Pygoscelis adeliae*) and chinstrap penguins (*P. antarctica*) are morphologically and ecologically very similar, have a similar diet, and breed sympatrically in the Scotia Arc from the South Sandwich Islands to the Antarctic Peninsula. Lynnes et al. (2002) used satellite tracking data from Adélie and chinstrap penguins to compare foraging distributions during the breeding seasons of 2000 and 2001. In both years, the diet of both species was exclusively *E. superba* of the same size range. In a year of low prey availability (2000), there was a statistically significant segregation of foraging areas between the two species. However, in a year of normal resource availability (2001), there was no such segregation. There was a significant difference in the foraging areas used by Adélie penguins between years; this was not true for chinstrap penguins. Adélie penguins foraged significantly further north (mean 100 km) from the colony than chinstrap penguins (mean 58 km) in 2000, but not in 2001 (mean 58 and 35 km, respectively). In 2000, the breeding success of Adélie penguins was 51% lower than the long-term mean, compared to 15% lower in chinstrap penguins. Both species achieved above average breeding success in 2001. The changes in foraging distribution and breeding success suggest that in years of low resource availability, chinstrap penguins may be able to competitively exclude Adélie penguins from potential inshore foraging areas.

Information on the food of emperor penguins (*A. fosteri*) originally was rather sparse. However, there has been a significant increase in investigations of the diets of emperor penguins in the last decade. Offredo and Ridoux (1985) studied the diet of emperors in Adélie Land and found that the birds were largely fisheaters, fish constituting 65% of the stomach contents by weight. The diet of emperor penguins in the Weddell Sea in October and November was mainly krill, the Antarctic silverfish *P. antarcticum*, and the squid *P. glacialis* (Klages 1989).

Studies on the diet of emperor penguins in the Ross Sea region (Offredo and Ridoux 1986; Klages 1989; Gales et al. 1990; Robertson et al. 1994; Putz 1995; Kirkwood and Robertson 1997) indicated that penguins nurturing their chicks feed on fishes, squid, and crustaceans, with the silverfish *P. antarcticum* always a major component of the diet. At Cape Washington, Cherel and Kooyman (1998) found that penguins feeding chicks consistently preyed on fishes (89–95% by mass) and crustaceans (5–11%). *P. antarcticum* constituted 89% of the fish prey; the remainder of the fish prey were mainly unidentified juveniles of different species of channichthyid fishes. Three species dominated the crustacean part of the diet: the gammarid amphipods *Abyssochomene rossi plebs* (30% of the crustcean prey) and *Eusirus microps* (22%), together with the euphausiid *E. crystallorophias*. At Coulman Island and Cape Roget, fish, mainly *P. antarcticum*, formed the bulk of the food (88% and 93% by mass, respectively); crustaceans were minor prey (2.5% and 0.4%, respectively), and the squid *P. glacialis* accounted for a small but significant part of the food (3.5% and 0.8%, respectively).

In studies of emperor penguins at the Auster and Taylor Glaciers on the Mawson Coast, Kirkwood and Robertson (1997) found that the stomach contents of females returning to feed their chicks were dominated by pelagic prey species, Antarctic krill (*E. superba*, 70% by mass) and Antarctic silverfish (*P. antarcticum*, 13% by mass). At the Auster colony, Weinecke and Robertson (1997) found that the diet of females comprised 72% fish (by mass), 16% squid, and 12% krill, whereas that of the males comprised 53% fish, 2% squid, and 43% krill. While in all studies silverfish were a major dietary component, the composition appears to be determined by the availability of other prey species.

Diets of the smaller flying birds in the Southern Ocean have not been as intensively investigated as those of the larger species. Prions are conspicuous members of the avifauna of the South Atlantic, with a breeding population on the order of 20 million at South Georgia (Croxall and Prince 1987). They feed predominantly on zooplankton. Prince (1980a) found that 80% of the food of *Pachyptila desolata* was made up of crustaceans; over 50% by weight was krill, nearly one-third large copepods and the remainder amphipods, other euphausiids and mysids. Goss et al. (1997) found that the concentrations of feeding prions off Bird Island coincided with peaks in zooplankton numbers.

The importance of the smaller species of seabirds in the ecology of the Southern Ocean can be seen when their large populations on the islands of the Subantarctic region are considered. For example, at Kerguelen, 35 bird species, including 24 species of Procellariiformes, number 6.5–10.9 million breeding pairs each year (Woehler et al. 2001). Five species of small burrowing petrels account for about 66% of the total number of birds of the archipelago, South Georgian (*Pelecanoides georgicus*) and common (*P. urinatrix*) diving petrels, thin-billed (*Pachyptila belcheri*) and Antarctic (*P. desolata*) prions, and blue petrels (*Halobaena caerulea*). It was estimated that the five species together consume 0.6 million tonnes of marine resources annually (Guinet et al. 1996). At South Georgia, the prey species of the two species of *Pachyptila* is dominated by crustaceans, in particular euphausiids (mainly *E. superba* and some *Thysanoessa*), which contribute 47–76% of the biomass of crustaceans in the diet, and copepods, which contributed 71% of the biomass of crustaceans in the diet of *P. urinatrix* (Reid et al. 1997). *Calanoides acutus* was the most numerous copepod in the diet of both species; however, *Rhincalanus gigas* was more common in *P. urinatrix* than in *P. georgicus*. The dominant amphipod in the diet of *P. georgicus*, *Primno macropa*, was absent from the diet of *P. urinatrix*, in which *T. gaudichaudii* (rare in *P. georgicus*) dominated. Information on the prey species and on the diving abilities and foraging habitats of these petrel species suggests that at South Georgia, *P. urinatrix* feeds closer inshore and dives deeper than *P. georgicus*. At Isles Kerguelen, Bocher et al. (2000) found that the two species fed consistently on different prey, the diet of *P. georgicus* being dominated by the euphausiid *Tjysanoessa* sp. (50% in number of prey and 81% of reconstructed mass) and the copepod *C. acutus* (45% and 10%, respectively), and that of *P. urinatrix* by the hyperiid *T. gaudichaudii* (61% and 91%, respectively) and the copepod *Paraeuchaeta antarctica* (21% and 9%, respectively). This dietary separation, together with observations of the birds at sea, showed a complete horizontal spatial separation between the two species of diving petrels, with *P. urinatrix* foraging in coastal waters in the close vicinity of their colonies, and *P. georgicus* in more distant offshore waters.

The bulk of the crustaceans consumed by Antarctic seabirds are krill (*E. superba*), except near the continent, where krill are replaced by *E. crystallorophias*. Other groups of crustaceans may be important, e.g., copepods in the diet of the Broad-billed and Dove Prions (and possibly *Pachyptila salvini*), diving petrels, and possibly storm petrels. Amphipods, especially the hyperiid, *Parathermisto gaudichaudii*, may be important to *P. belcheri* (Harper 1972; Strange 1980), and significant differences have been noted in the proportions of amphipod species common to the diets of both taken by blue petrels and dove prions (Prince 1980a).

Very little is known about the winter diets of most of the bird species of the Southern Ocean. Krill may not be as accessible to the birds due to the extensive ice cover, and alternative species may be taken. Those species that feed on fish and squid in the summer would doubtless continue to do so.

10.5.2 FEEDING METHODS

The main feeding methods of Antarctic seabirds are shown in Table 10.5. There are two principal feeding techniques,

TABLE 10.5
Feeding Zone of Antarctic Seabirds

	Inshore	Intermediate	Offshore	Intermediate	Pelagic
Diving	Gentoo penguin Shags Diving petrels	Chinstrap penguin	Macaroni penguin Adélie penguin	King penguin	
Surface feeding	Storm petrels Diving petrels Giant petrels Antarctic skua Antarctic tern	Prions	Black-browed albaross Grey-headed albaross Snow petrel Antarctic fulmar Cape pigeon	Blue petrel Antarctic petrel	Wandering albatross Sooty albatross White-chinned petrel Grey-faced petrel Grey petrel Kerguelen petrel White-headed petrel

Source: From Croxall, J.P., *Antarctic Ecology*, Laws, R.M., Ed., 533, 1984. With permission.

pursuit diving and surface feeding (Croxall and Prince 1980a). The former technique is particularly characteristic of penguins, which are preeminently adapted for life as aquatic pursuit divers. Diving depth is one aspect of penguin feeding behaviour that has been investigated recently in some detail (Croxall et al. 1988b; Croxall and Davis 1990). Multiple depth recorders, logging the number of dives within set depth ranges, have been deployed on King (Kooyman et al. 1982), Adélie (Wilson 1989), chinstrap (Lishman and Croxall 1983), and gentoo penguins (Wilson 1989). The large *Aptenodytes* spp. (feeding on fish and squid) dive to depths of 236–265 m (Kooyman et al. 1982, 1986), whereas the krill-eating chinstrap penguins' dives do not exceed 70 m, with 40% of the dives found to be shallower than 10 m (Lishman and Croxall 1983). A gentoo penguin has been caught in a net at 100 m (Conroy and Twelves 1972). A blue-eyed shag has been caught in a net at 25 m (Conroy and Twelves 1972), and although diving times of up to 2.5 min have been recorded (Kooyman 1975), comparable to those of the smaller penguins, it is doubtful whether they have the capacity for controlled diving. The diving petrels are also specialized for diving and swimming underwater, chiefly by a reduction in wing length, attaining a "paddle-like" condition for underwater propulsion (Kuroda 1967). However, they are certainly not deep divers, and feed in the top few metres.

An animal's feeding behaviour is constrained by its morphological and physiological specializations for feeding. Within these limits, many species show considerable plasticity in response to both abiotic and biotic conditions, or to changes in their energetic needs or the different stages of the annual life cycle (reproduction, migration, moult). The diving patterns of penguins during their foraging for food vary according to light (Wilson et al. 1993), the presence of sea ice (Watanuki et al. 1997), prey abundance and availability (Watanuki et al. 1993), breeding stage and energy demands (Charrassin et al. 1998), and seasons and years (Clarke et al. 1998).

Penguins are generally believed to be pelagic feeders. However, Subantarctic penguins, in particular, have evolved different feeding strategies, ranging from pelagic feeders like king and macaroni penguins (*Aptenoytes patagonicus* and *Eudyptes chrysolophua*) to inshore benthic feeders like gentoo, rockhopper and chinstrap penguins (*P. papua*, *E. chrysocome* and *P. antarctica*, e.g., Adams and Klages 1989; Robinson and Hindell 1996; Tremblay and Cherel 2000). Together with Imperial Cormorants (*Phalocrocorax atriceps*), Gentoo penguins are the main avian benthic consumers of the Subantarctic. The diet of the gentoo penguin varies greatly with locality, consisting mainly of krill at Antarctic localities, whereas fish are more important at Subantarctic localities. At the Kerguelen Islands, the diet is composed mainly of neretic fish and crustaceans. Fish dominate in the diet at localities facing the open sea, while crustaceans dominate in the more protected seas. Fish are more abundant in the winter diet, and the euphausiid, *Euphausis vallentini*, is more abundant in the summer diet of rockhopper penguins *Eudyptes chrysocome* (Tremblay and Cherel 2000). Yellow-eyed penguins *Megadyptes antipodes* (Seddon and Van Heezik 1990) and emperor penguins *Apenodytes fosteri* (Robertson et al. 1994) are known to include a substantial proportion of benthic/benthopelagic organisms in their diet.

In the coastal waters of Isles Kerguelen, Tremblay, and Cherel (2000) investigated the diving patterns and dive profiles of the southern rockhopper penguin *E. chrysocome*. They found that they performed typical pelagic dives as well as a series of consecutive square-wave benthic dives. The penguins maximized bottom time (i.e., feeding time) of benthic dives through an increase in both descent and ascent rates, thus minimizing transit time between the sea surface and the bottom. Bathymetry and dive depths indicated that the penguins were able to reach about 80% of the sea floor surrounding the colony. Dietary analyses showed that rockhopper penguins fed upon benthic prey (a few fish and the mysid *Mysidetes morbihanensis*) and pelagic organisms, the major item being *Euphausia vallentini*.

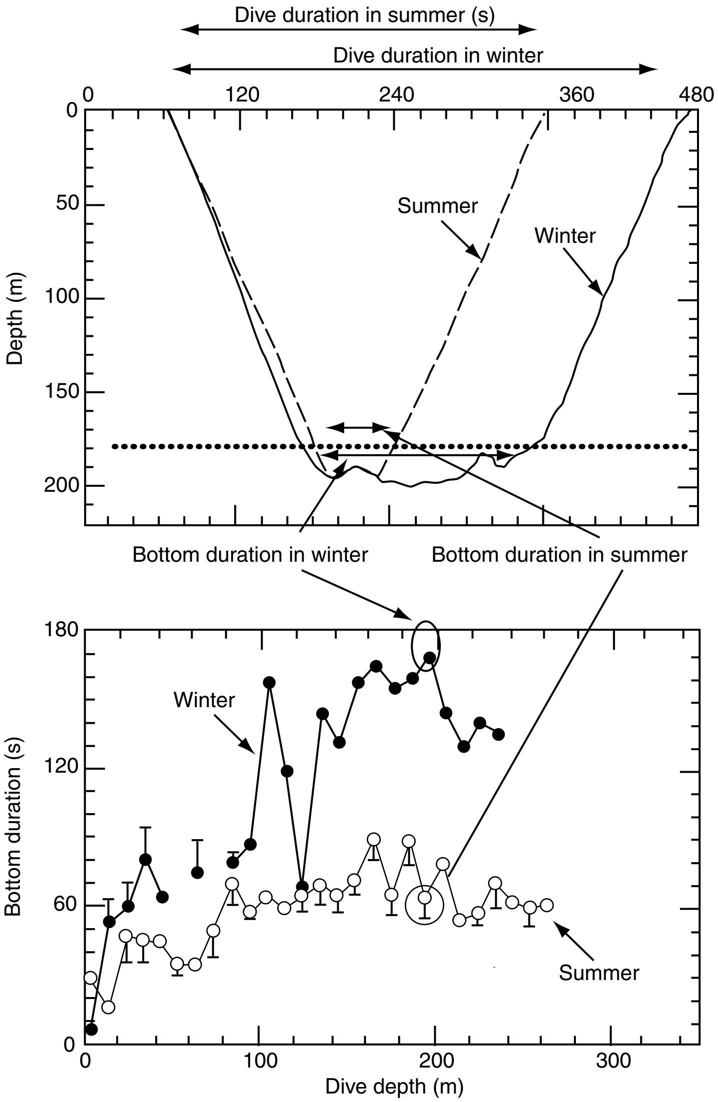


FIGURE 10.11 *Aptenodytes patagonicus*. Typical profiles of dives to 200 m executed in summer and in winter by two king penguins at the Crozet Islands, showing the drastic increase of bottom duration and dive duration over the season (upper panel). This increase in winter occurs over the whole range of dive depths, as shown by the bottom duration plotted against dive depths for the same birds (lower panel). (From Charrassin, J.B., et al., *Oecologia*, 114, 586, 2002. With permission.)

Charrassin et al. (2002) investigated seasonal changes in the diving parameters of the king penguin *Aptenodytes* at Possession Island, Crozet Archipelago. The time spent at the bottom of the dives, which probably represents a substantial part of the feeding time, was much longer in winter (2.5 min per dive for dives over the 120–210 m layer than during other seasons (1.0–1.4 min) (Figure 10.11). The large increase in bottom and dive duration from spring to winter was inversely related to the seasonal prey density, with the penguins spending more time searching for prey. Recent studies based on the accurate detection of prey ingestion by oesophagus temperatures have shown that at least 40 and 70% of feeding events occur during the bottom phase of dives in king and Adélie penguins, respectively (Charrissin et al. 2001; Ropert-Coudert et al. 2001).

Nearly all the albatrosses and petrels take prey at the surface. Following Ashmole (1971), the surface-feeding methods can be subdivided into several categories. There are a few species which mainly detect prey while in flight and either execute a shallow plunge to catch it (Antarctic tern), or stop to secure it during flight. Plunging is occasionally recorded in albatrosses, but is more common in some petrels. Dipping is characteristic of the storm petrels, which patter near the surface, and the gadfly petrels (*Pterodroma* spp.) and blue petrels that swoop down from a height. Surface diving is most prevalent amongst the petrels, especially *Puffinis* and *Procellaria* species, but is also used by albatrosses and diving petrels. The most specialized technique is that of certain prions (*P. desolata*, *P. salvini*, and *P. vittata*) that have broad deep bills with a comb-like lamella forming a fringe on the inside of the upper mandible, through which they expel water and filter out small prey organisms.

Most seabirds are opportunistic scavengers, but some species obtain most of their food in this way, either at sea or on land. Preeminent carrion feeders are the giant petrels (Johnstone 1977, 1979; Hunter 1983, 1985). Hunter (1985) estimated a total world breeding population of about 8,600 pairs for *Macronectes halli* and 3,800 pairs for *M. giganteus*, with a total nonbreeding population of about 26,000 and 113,000, respectively. He calculated that they consume 1,328.4 tonnes of seals, 12.947.5 tonnes of penguins, and 1,200 tonnes of small birds annually. They also take other prey, including an estimated 3,049 tonnes of crustaceans (principally euphausiids), 661.6 tonnes of squid, and 253.9 tonnes of fish. Skuas also scavenge, particularly the brown skua (and southern black-backed gull). Detailed studies of the role of skuas and their effect on penguin colonies have been made by Young (1963a), MullerSchwarze and MullerSchwarze (1977), Trivelpiece et al. (1980) and Trivelpiece and Volkman (1982). Young (1963a) showed that some Antarctic skuas, particularly those that do not have territories which include portions of penguin colonies, sustain themselves by catching fish (mainly *P. antarcticum*) and even crustaceans at sea.

10.5.3 FORAGING RANGE

Species with similar breeding seasons, diets, and foraging methods may still be ecologically separated if there are sufficient differences in their feeding zones and feeding depths. For breeding birds, the length of the incubation shifts, and particularly the time between successive visits to feed a chick, can be an indication of the potential foraging range. Using information from a variety of sources, Croxall and Prince (1980a, 1980b) provided estimates of the times between successive feeds by the same parent for South Georgia penguins and petrels. These varied between at least twice daily (giant petrel) to every 5–6 days (wandering albatross). Imber (1976) gives a parental absence period of 8 days for grey-faced petrels. Such information was used by Croxall (1984) to classify birds into inshore (at least one feed by each parent per day), offshore (each parent visits at about 2 day intervals), and pelagic (interval of at least 3 days) (Table 10.5; Figure 10.12).

The maximum distance travelled by birds on their foraging trips can be calculated from estimates of reasonable swimming and flight speeds (see Croxall and Prince 1980a and Figure 10.13 for details). It should be emphasized that these estimates are far from accurate, especially for inshore species, since they assume a straight direct path and no stops for feeding (Williams and Siegfried 1980).

The development of new radiotelemetry techniques in which radio transmitters are attached to penguins to monitor their behaviour at sea can now provide more accurate information on foraging behaviour. Penguin swim speeds measured with autoradiography range from 1.6 to 2.4 m s^{-1} (average 2.1 m s^{-1}), while transit speeds estimated from radiotelemetry are in the range 1.2–1.3 m s^{-1} (Croxall and Davis 1990). Using this technique with gentoo and chinstrap penguins, Trivelpiece et al. (1986) were able to distinguish five foraging behaviours: porpoising, underwater swimming, horizontal diving, vertical diving, and resting or bathing. Gentoo penguins spent a significantly greater proportion of their foraging trips engaged in feeding behaviours than did chinstraps, which spent significantly more time travelling. The study provided new insights into the feeding ecology of the two species. Gentoos had significantly longer feeding dives than chinstraps (128 vs. 91 s) and significantly higher divepause ratios (3.4 vs. 2.6 s). Trivelpiece et al. (1986) concluded from their observations that travelling speeds of penguins at sea may be considerably lower than the 7.2 km h^{-1} speeds reported for Adélie penguins (Kooyman 1975), and that penguin foraging ranges based on swimming speeds (see Table 10.5) may have been overestimated (Croxall and Prince 1980b; Croxall et al.1984b). They estimated maximum overall swimming speeds of 5.5 km h^{-1}. Gentoo penguins require significantly more krill to rear their chicks to fledging than do chinstraps (118 vs. 73 kg per breeding pair; Trivelpiece et al. 1986), and have significantly shorter nest relief intervals during chick rearing (12.5 vs. 16.7 h; Volkman et al. 1980). Foraging ranges based on nest relief intervals, feeding times and travelling times were estimated as within 17 km of the rookery for gentoos and within 27 km for chinstraps (Trivelpiece et al. 1986). Thus, gentoos, which require more krill per day, can acquire this food from a more restricted foraging range because of their greater diving ability. There is therefore less overlap in the feeding niches of the two species than would appear at first sight.

At Esperanza on the Antarctic Peninsula, Wilson et al. (1991) found that foraging Adélie penguins with eggs and with brooded and creching chicks spent mean periods away from the nest of 96, 36, and 21 h, respectively, during which time means of 29.0 h (30%), 11.2 h (31%), and 2.7 h (13%), respectively, were spent under water at depths of greater than 5 m. Maximum depth reached was 170 m, but the birds spent most time at shallow depths. The principal prey was krill, caught at a mean rate of 7.2 g min^{-1} spent under water.

The breeding success of penguins is dictated by the distribution, abundance, and availability of prey. However, there is a dearth of information on the location of feeding areas relative to penguin breeding sites, apart from the pioneering studies of Trivelpiece et al. (1986) discussed above. Using radiotelemetry, Sadlier and Ley (1990) found that Adélie penguins at Cape Bird, McMurdo Sound generally foraged close inshore, and within 15 km of the rookery.

Lynnes et al. (2002) list the maximum foraging distance from colonies of Adélie and chinstrap penguins from 11 studies. For Adélie penguins, the maximum foraging distance ranged from 50 to 174.4 km (mean 133.4), while for chinstrap penguins it ranged from 24.2 to 132 km (mean 66.5). In the migrations of these penguins from Signy Island, it was found that in a year of low prey (*E. superba)*

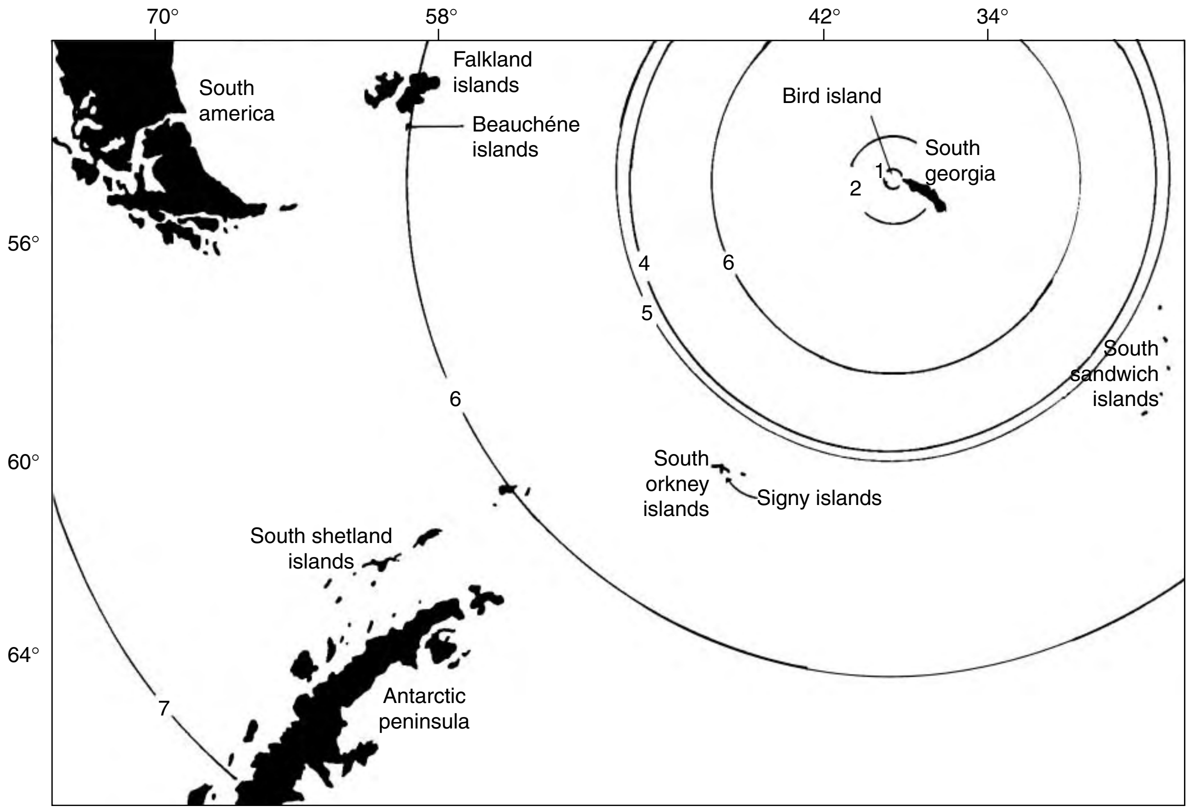


FIGURE 10.12 The maximum estimated foraging range of seven species of South Georgia birds during chick rearing. Estimated from swimming/flying speeds and duration of feeding trips at sea. (From Croxall, J.P., Prince, P.A., *Oceanus*, 26, 18, 1983. With permission.)

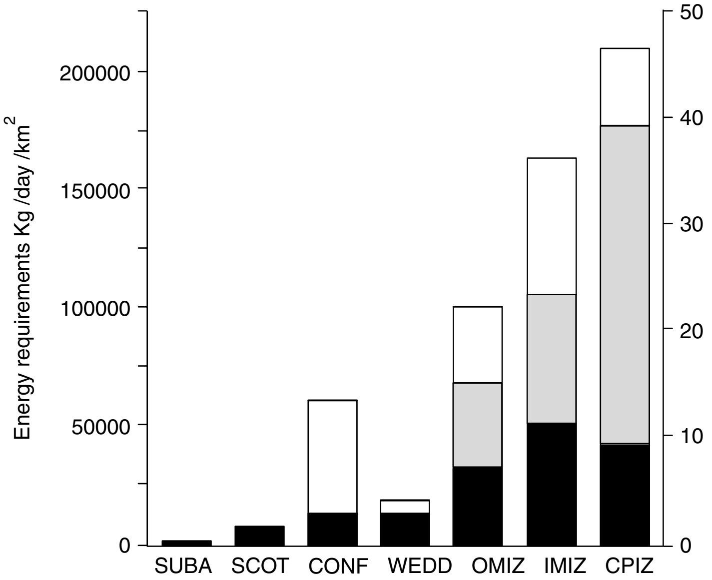


FIGURE 10.13 Energy and food requirements of top predators in different zones of the Southern Ocean. EPOS Leg 2, all counts ($n = 704$). The zones are: SUBA, Subantarctic Waters; SCOT, Scotia Sea Water; CONF, Scotia–Weddell Confluence; WEDD, Weddell Sea Gyre; OMIZ, Outer Marginal Ice Zone; IMIZ, Inner Marginal Ice Zone; CPIZ, Closed Pack Ice Zone. Birds: White; Seals: Stripeel; Whales: Black. (From van Frankel, J.A., *Polar Biology*, 12, 100, 1992. With permission.)

availability, Adélie penguins foraged significantly further (mean 100 km) than chinstrap penguins (mean 58 km), but not in a year of normal resource availability (means 58 and 35 km, respectively). The changes in foraging distribution and breeding success suggested that in years of low resource availability chinstrap penguins may be able to competitively exclude Adélie penguins from particular inshore foraging areas.

The foraging range of many species varies over the year as a consequence of the stage of the breeding cycle and the availability of food resources. Charrissin and Bost (2001) and Charrissin et al. (2002) investigated seasonal changes in the foraging behaviour of king penguins at the Crozet Archipelago. By studying the birds over an annual cycle with satellite tracking and temperature–depth sensors, they observed a drastic increase in the foraging distances over the seasons. In summer birds foraged ~400 km south of the colony, while in the autumn and winter they travelled down to the pack ice area ~1,600 km away. Dive depth simultaneously increased from ~160 m in summer to ~200 m in winter (Charrassin and Bost 2001). This change is associated with the availability of their prey, primarily mycophid fishes.

Stahl et al. (1985) have studied the foraging ranges of the birds which breed on Crozet in the southwestern Indian Ocean. They found that four species were restricted to the immediate vicinity of the islands: the imperial cormorant (*Phalacrocorax atriceps*), the southern black-backed gull (*L. dominicanus*), and the terns *S. vittata* and *S. virgata*. A second group, typified by the king penguin (*Aptenodytes patagonicus*), the macaroni penguin (*E. chrysolophus*), and the black-browed albatross (*Diomedia melanophris*), foraged principally over the shelf and slope areas. The remaining species, such as the blue petrel, thin-billed prion, white-chinned petrel, yellow-nosed albatross, white-headed petrel, and Kerguelen petrel, foraged regularly over pelagic waters. In general, the birds were concentrated over the productive shelf areas and frontal zones.

Obst (1985) has examined the relationships between krill and seabirds off the Antarctic Peninsula. Mean avian density was 2.6 times greater in waters where krill schools were present than in waters without krill schools. While seabird density was a good predictor of the presence of krill it did not correlate with krill density or krill school depth. However, two species, the Southern fulmar *F. glacialoides* and Wilson's storm petrel *O. oceanicus*, were associated with krill significantly more often than expected by chance alone. Where penguin densities were high (>30 penguins km^{-2}) krill schools were always present.

The species which travel the greatest distances during their foraging trips are the albatrosses. In these excursions they may travel several thousands of kilometres. The wandering albatross, *D. exulans*, breeds bianually on several Subantarctic Islands around Antarctica, in the South Atlantic, southern Indian, and South Pacific Oceans (Tickell 2000). While rearing chicks at Bird Island, South Georgia, wandering albatrosses forage as far north as southern Brazil (28°S) and as far south as the Antarctic Peninsula (67°S). They also forage eastwards to Tristan da Cuhna (17°W) and westwards to Chile (75°W).

Catry et al. (2004) investigated foraging of the grey-headed albatross (*Thalassarche chrysostoma*) at Bird Island. The albatrosses foraged mostly over oceanic waters, probably associated with the Polar Front north of South Georgia and also overshelf-slope waters around the Antarctic Peninsula. While at sea, the birds spent most (81%) of the day flying, and most (94%) of the night resting on the water. A considerable proportion (26% by mass) of prey was consumed during darkness. Many ingestion events (up to 27% of the overall food intake) showed temperature signatures characteristic of fluids, suggesting that albatrosses may feed on gelatinous and rapidly digested prey (e.g., salps and jellyfish) much more often than previously suspected. Diet samples delivered to the chicks comprised mostly squid (particularly *Martialia hyadesi*) and Antarctic krill *E. superba*.

Using satellite telemetry, Waugh et al. (1999) analysed the marine habitat exploited by two sympatric albatross species, the black-browed albatross, *Diomedia melanophrys*, and the grey-headed albatross, *D. chrysostoma*, which breed on Campbell Island south of New Zealand. Black-browed albatrosses spent 55% of their time on the Campbell Plateau, but also made long foraging trips to the Polar Frontal Zone and the Antarctic Zone at a distance of over 2,000 km. Grey-headed albatrosses spent 71% of their time foraging over the deep waters of the Polar Frontal Zone.

It is clear that the differing abilities of species to feed at different distances from a breeding colony is important in reducing direct competition (Croxall and Prince 1980a). This, combined with dietary and feeding method differences, and differences in the timing of the breeding season may, as has been emphasized by Croxall and Prince (1979) for South Georgia, well provide adequate ecological isolating mechanisms to ensure that in normal circumstances direct competition for food is avoided, at least in the summer.

10.5.4 QUANTITIES OF FOOD EATEN

Various estimates have been made of the overall food consumption of seabirds in the Southern Ocean. Such global figures, however, while they indicate the order of magnitude of consumption, are subject to considerable uncertainty due to the inadequacy of the information on the populations of many species, and their food intake and energetics.

Some of the most reliable data on the levels of food consumption by seabirds is for the Scotia Arc region, which has been the site of the most detailed quantitative studies on diets (e.g., Croxall and Prince 1980a) and studies of bioenergetics (e.g., Croxall 1982a, 1984). In a series of papers, Croxall and his coworkers (Croxall and Prince 1971, 1980a; Croxall et al. 1984, 1985) have summarized the available information on seabird population estimates, sex-specific weights, the nature and timing of the activities of each sex throughout the annual cycle, mortality rates, caloric contents of prey, and bioenergetics. The seabirds breeding at South Georgia and the Scotia Arc were estimated to consume $6{,}720\times10^3$ tonnes of krill, 600×10^3 tonnes of squid, 400×10^3 tonnes of fish, $1{,}010\times10^3$ tonnes of copepods, and 262×10^3 tonnes of amphipods annually. It is thus clear that they have a major impact on the food resources, especially krill.

One of the most comprehensive studies of food consumption by Antarctic seabirds for a specific region is that of Woehler (1997) for the Prydz Bay region. Total prey consumption of the resident and nonresident species was estimated to be between 471,000 and 1.1 million tonnes, or between 2.02 and 4.53 kg km^{-2} per day. Consumption of resident species exceeded that of nonresident species in all summers except three (1980/1981, 1981/1982, and 1984/1985). Proportionally, resident species consumed approximately $65.2\pm26.0\%$ of the estimated total consumption within Prydz Bay (range 25.7% in 1980/1981 to 97.0% in 1990/1991). Together, Antarctic petrels (24.6%), Adélie penguins (19.3%), southern fulmars (11.9%), and snow petrels (11.1%) ate 66.8% of the total consumed by resident species, and 45.6% of the total summer prey consumption within Prydz Bay. White-chinned petrels (38.8%), light-mantled sooty albatrosses (18.5%), prions (18.1%), and shearwaters (10.4%) ate 85.8% of the prey consumed by nonresident species, and 31.0% of the total prey consumed. In total, these eight species accounted for 76.6% of the total summer prey consumption.

Woehler and Green (1992) estimated the consumption of marine resources by seals and seabirds (king, gentoo, rockhopper, and macaroni penguins, back-browed and light-mantled sooty albatrosses, giant petrels, Antarctic and fulmar prions, Wilson's storm petrels, South Georgia and common petrels, Heard Island cormorants, and Antarctic terns) at Heard Island and the McDonald Islands. The total annual consumption of marine resources was estimated to be approximately 521,000 tonnes of fish, 41,600 tonnes of squid and 312,000 tonnes of crustaceans. The annual energy flux to this seabird and seal community was estimated to be 2.17×10^{12} kJ, and approximately 56,000 tonnes of carbon are consumed annually (Table 10.6).

Estimates of the overall consumption of food by the seabirds of the Southern Ocean are given in Table 10.7.

10.6 ENERGETICS

10.6.1 SPECIES REQUIREMENTS

Croxall (1984) reviewed the then-available information on metabolic rates in birds, with special reference to the seabirds of the Southern ocean. He pointed out that the relationship between basal metabolic (BMR) and resting and active metabolic rates is imperfectly understood, e.g., flapping flight has been assessed at six times the resting metabolic rate. Kooyman et al. (1976) showed that for Adélie penguins immersed (but not swimming) in water at 5°C, the metabolic rate was 3.6 times that of resting in air. This response to cold ambient temperatures is probably an additional energy cost to Antarctic seabirds.

The energy budgets of active adult birds are difficult to assess. The use of labelled isotopes to estimate total energy costs over a known period shows promise. However, it is difficult to obtain a breakdown of activity (e.g., the time spent flapping, gliding, resting, feeding, etc.) over time. Preliminary information for king, macaroni, and gentoo penguins suggests that the daily cost of foraging during chick rearing is about 2.5–3.5 times the BMR (Kooyman et al. 1982; Davis et al. 1983; Davis and Kooyman 1984).

During the breeding season, and, in the case of penguins, also during the moult, most birds spend long periods ashore, and they suffer considerable weight loss at these times. It had been assumed that the bulk of the loss comprised fat, but Groscolas and Clement (1976) obtained values of 55.5% fat, 9.2% protein for fishing emperor penguins, while Williams et al. (1977) obtained values of 38.0% fat, and 12.0% protein for moulting, fasting rockhopper and macaroni penguins, the residue being water. In reviewing available data on fasting weight loss and energy requirements in petrels and penguins, Croxall (1982a) concluded that fat is unlikely to comprise more than 50% of weight loss. Average daily costs of incubation in petrels were assessed as 1.3 times BMR (range 0.8–2.0), of incubation in penguins as 1.4 times BMR (range 1.0–1.6) and of moulting in penguins as 2.0 times BMR (range 1.6–2.4).

TABLE 10.6
Biomass and Energy Consumption of Antarctic Seabirds

	Sub-Antarctic		Antarctic		Total	
	Biomass (1×10^{12})	Energy Consumption (kcal $\times10^{12}$ y^{-1})	Biomass (1×10^{12})	Energy Consumption (kcal $\times10^{12}$ y^{-1})	Biomass (1×10^{12})	Energy Consumption (kcal $\times10^{12}$ y^{-1})
Penguins	410	22.3	198	14.1	608	36.4
Other species	53	5.1	3	0.5	56	5.6
Total	463	27.4	201	14.6	664	42.0

Source: From Croxall, J.P., *Antarctic Ecology*, Laws, R.M., Ed., 533, 1984. With permission.

TABLE 10.7
Body Weight and Individual Daily Energy and Food Requirements of main top Predators in EPOS Leg 2. (Species Occurring in Density Higher than 0.1 km^{-2} in Any of the Marine Zones; except for whales)

Species	Body Weight (g)	Energy Required (kJ day^{-1})	Food Required (g day^{-1})	
Birds				
Adélie penguin	4,400	3,911	869	*Pygoscelis adeliae*
Chinstrap penguin	4,150	3,754	834	*Pygoscelis antartica*
Unidentified penguin	4,275	3,833	852	*Pygoscelis sp.*
Black-browed albatross	3,790	3,521	782	*Diomedea melanophris*
Grey-headed albatross	3,790	3,521	782	*Diomedea chrysostoma*
Cape petrel	425	755	168	*Daption capense*
Southern fulmar	775	1,152	256	*Fulmarus glacialoides*
Antarctic petrel	680	1,051	234	*Thalassoica antarctica*
Snow petrel	373	688	153	*Pagodroma nivea*
Antarctic prion	162	383	85	*Pachyptila desolata*
White-chinned petrel	1,250	1,631	362	*Procellaria aequinoctialis*
Black-bellied storm petrel	56	181	40	*Fregetta tropica*
Wilson's storm petrel	36	133	30	*Oceanites oceanicus*
Antarctic tern	120	310	69	*Sterna sp.*
Mammals	(kg)	(kJ/day)	(kJ/day)	
Crabeater Seal (adult)	193	75,937	16.9	*Lobodon carcinophagus*
Leopard Seal (adult)	272	98,899	22.0	*Hydrurga leptonyx*
Minke Whale	6,500	1,138,983	253.1	*Balaenoptera acutorostrata*
Large unid. whale	35,000	4,163,957	925.3	
Medium unid. whale	15,000	2,168,524	481.9	
Small unid. whale	4,000	783,718	174.2	
Fin Whale	40,000	4,614,876	1,025.5	*Balaenoptera physalus*
S. Bottlenose Whale	3,600	722,648	160.6	*Hyperoodon planifrons*

Source: From van Frankel, J.A., *Polar Biology*, 12, 94, 1992. With permission.

10.6.2 Population Requirements

Estimates of the overall energy consumption of Antarctic seabirds vary widely (e.g., Mougin and Prevost 1980; Williams et al. 1979). Croxall (1984) has modified the estimates of Mougin and Prevost (1980) on the basis of data in Croxall and Kirkwood (1979), Croxall and Prince (1979, 1980a), the references cited in Williams et al. (1979), and some unpublished information, and has come up with some very approximate figures for Southern Ocean bird biomass and energy requirements (Table 10.7). The data in this table emphasizes the preeminent role of penguins. In terms of biomass and consumption, all the seabirds of the Antarctic region are effectively penguins, and two-thirds of these are Adélie penguins; in the Subantarctic region, 80% of the birds are penguins, and of these 50% are macaroni penguins.

Van Frankel (1992) estimated the energy and food requirements of the top predators (birds, seals, and whales) in the various water masses of the confluence and marginal ice zones of the Weddell and Scotia Seas (see Figure 10.13 for the nomenclature of the various zones). Table 10.7 lists the daily energy and food requirements of the seabirds encountered during the second cruise of the European Polarstern Study (EPOS Leg 2). From Figure 10.13 it can be seen that the energy and food requirements of the bird component were low in the Subantarctic Zone, the Scotia Sea water and the Weddell Sea water, but higher in the Scotia–Weddell Confluence and the Pack Ice Zone. In the Pack Ice Zone, the combined energy requirements of the top predators amounted to about 2,000 kJ day^{-1} per km^{-2}. In open water, the daily energy and food requirements of seabirds were low.

In Prydz Bay, Woehler (1997) calculated that the daily energy flux to the seabird community was between 8.3×10^3 and 18.99×10^3 kJ km^{-2}, and the mean carbon flux was 0.000297 ± 0.000070 g C m^{-2} per day. Approximately 65% of the carbon flux within Prydz Bay went to the resident species.

10.7 POPULATION STRUCTURE AND DYNAMICS

Seabirds are known to be long-lived (i.e., having low annual mortality, especially as adults) and to delay breeding until they are several years old (Carrick 1972; Ainley and DeMaster 1980). The age of onset of breeding is variable, from 2 years in the common diving petrel to 10 years in the sooty albatross. For most species, it takes several years from the time when breeding is first recorded for half that year-group to be breeding.

Annual survival may reach 95% per annum. However, diving petrels seem to be a notable exception, and penguins, apart from emperor penguins, have a lower adult survival rate of 82–87%. As adults, many species do not have important natural predators. Skuas take numerous storm petrels, diving petrels and prions at night when they arrive on their nesting sites to feed their chicks, while some leopard and fur seals take penguins as they come and go from their nesting sites; giant petrels and skuas take penguin chicks and recently fledged individuals.

In terms of mean life expectancy, the smaller petrels may reach 10–15 years of age, and the albatrosses and giant petrels at least 25 years. Many of the larger birds live longer; wandering petrels and snow petrels over 35-year-old were still breeding at South Georgia and Signy Island in 1984 (Croxall 1984). There is a field record of a 16-year-old Adélie penguin (Ainley and DeMaster 1980).

The bulk of mortality probably occurs in the first year after fledging, and it has been estimated that perhaps only a third of the birds fledged survive this period (Croxall 1984). Subsequently, the survival of prebreeding birds is high until they commence breeding, when mortality becomes high again until the survivors become established. Mean annual survival rates vary from 96% in the wandering albatross (Tickell 1968; Croxall 1982b), and 95% in the snow petrel (Hudson 1966), the sooty albatross (Weimerskirch 1982), the grey-headed albatross (Croxall 1984) and emperor penguin, to 82% for the king penguin (Barrat 1976; Jouventin and Mougin 1981) and to 61–70% for the Adélie penguin (Ainley and DeMaster 1980). Adélie penguins have the poorest survival both as juveniles and adults of any of the penguin species (Ainley and DeMaster 1980).

10.8 CURRENT STATUS AND POPULATION TRENDS IN ANTARCTIC SEABIRDS

In 1983 (Wilson 1983) authored a report in the BIOMASS Scientific Series on the distribution and abundance of Antarctic and Subantarctic seabirds. Since the 1980s, the Scientific Committee on Antarctic Research (SCAR), through the Bird Biology Subcommittee (BBS) of the Working Group on Biology (WGB), has provided advice and information on the status and trends of Southern Ocean seabird populations to the Scientific Commission for the Conservation of Antarctic Marine Living Resources (SC-CCAMLR) (SCAR Bird Biology Subcommittee 1988; SCAR 1992; and Woehler and Croxall 1997). In response to a request in 1998 from SC-CCAMLR for a statistical assessment of the available population data, the SCAR BBS organized a Southern Ocean Seabird Population Workshop to examine statistically long-term population data for Southern Ocean seabirds. The report prepared by the Workshop was submitted to CCAMLR in 2001 (Woehler et al. 2001).

A summary of the species assessments follows:

- Emperor penguin *Aptenodytea forsteri*. The population at Pointe Geologie decreased (0.9% per annum) until 1978, then halved within 5 years and decreased since 1984 (1.2% annually). At the Auster and Taylor Glacier colonies, the population was stable from 1988 to 1999.
- King penguin *A. patagonicus*. All colonies at Ile de Possession, apart from one that was disturbed by the establishment of a base, increased significantly. Three undisturbed colonies showed linear increases of +15.0, +6.9 and +4.8%. Colonies on Iles Crozet and on the eastern part of Isles Kerguelen showed similar trends. The king penguin population at Heard Island increased linearly between 1949 and 1993 from under 800 pairs to nearly 2,000 pairs. These population increases are sustained by the enhanced availability of their myctophid prey.
- Adélie penguin *P. adeliae*. All East Antarctic colonies showed persistent long-term statistically significant linear increases; at Mawson, the population increased by 176% between 1973 and 1999, at Point Geologie 63% between 1982 and 1998, at Syowa 62% between 1982 and 1998, while there was also a linear increase at Whitney Point. Within the Antarctic Peninsula area, the Admiralty Bay (King George Island) Adélie penguin population decreased significantly over the period 1978–1998, as did that at Palmer Station. At Signy Island, there was a period of increase from 1979 to 1989 (5% at an annual rate of about 0.6%) followed by a subsequent decrease of about 18%. At Cape Bird, Ross Island, the population increased significantly up to 1984, and subsequently decreased. A similar trend was observed at Cape Crozier, whereas the population at Cape Royds increased linearly from 1989 to 1999. There were strikingly different trends in the various regional populations.
- Gentoo penguin *P. papua*. Antarctic Peninsula and Marion Island populations showed significant linear increases since the 1980s. On the other hand, the population at Admiralty Bay showed an overall significant decrease, while at Signy Island, there was a significant linear increase of 173% at an annual rate of 5% over a 20-year period. At Marion Island, populations showed an overall increase up to 1995, followed by a decrease.
- Chinstrap penguin *Pygoscelis antarctica*. At Admiralty Bay, the population showed a significant decrease over the 1978–1999 period. At Palmer Station, the pattern from 1975 to 1998 showed a statistically significant increase. At Signy Island, there was an overall significant linear decrease from 1979 to 1998. Populations in the Antarctic Peninsula region exhibited varying trends.
- Macaroni penguins *E. chrysolophus*. Populations on Marion Island showed different trends. One did not

show a significant trend, while two others showed a linear decrease. The Bird Island study population increased from 200 pairs in 1958 to a maximum of 1,400 pairs in 1983 (an average annual rate of increase of 9.7%). A much larger colony has decreased by 60% since 1977. At Isles Kerguelen, several large colonies showed a slight increase.

- Northern rockhopper penguin *Eudyptes chrysocome moseleyi*. The population at Ile Asterdam decreased significantly from 1972 to 1994, whereas that on Ile St Paul increased significantly.
- Eastern rockhopper penguin *Eudyptes chrysocome filholi*. The Marion Island population showed an overall linear decrease of 4.3% per annum over the period 1986–1999.
- Wandering albatross *D. exulans*. At Bird Island, the population decreased significantly (15.3% at 1% per annum) from 1972 to 1998. At Iles Kerguelen, the population decreased from 1972 to 1990 by 54%, at 5.8% per annum, subsequently increasing by 29%, at 2.9% per annum. At Marion Island, data suggested that there was a probable decrease until about 1991, followed by an increase. At Ile Possession, there was a rapid population decrease of about 57%, at 3.1% per annum from the 1960s to the mid-1980s, followed by a period of consistent increase thereafter. Long-line fisheries in the Southern Ocean are inferred to be the primary cause of the observed long-term decreases.
- Black-browed albatross *Thalassarche melanophris*. The main study colony at Bird Island showed a significant linear decrease (66% at an annual rate of 4.5%) from 1976 to 1999. At Iles Kerguelen, there was no significant overall trend. As with the wandering albatross, long-line fisheries are inferred to be the primary cause of the decrease.
- Grey-headed albatross *Thalassarche carteri*. At one colony on Bird Island, the linear decrease was significant, while at the main Bird Island colony, the population showed a significant linear population decrease (37% at 2% per annum) from 1976 to 1999. On Marion Island, a significant linear increase was detected over the period from 1977 to 1999. While both the Bird Island and Campbell Island populations are decreasing, that on Marion Island is increasing.
- Sooty Island albatross *Phoebetria fusca*. Populations at Ile de la Possession and Iles Crozet have shown a linear decrease through the period 1981–1999, at an annual rate of 5.1%. Again, long-line fishing is implicated in this decline.

10.9 ROLE IN THE ECOSYSTEM

The seabirds of the Southern Ocean have an important role in the marine ecosystem. Although our knowledge of their distribution, abundance, biomass, and energetics is far from complete, even rough estimates of their biomass and prey consumption indicate that their impact as predators is important in structuring the pelagic communities, especially in the vicinity of breeding colonies. As we have seen, annual krill consumption by seabirds in the Scotia Arc region may be in excess of 16 million tonnes per annum, while the total consumption throughout the Southern Ocean may be as much as 115 million tonnes per annum. This is considerably more than the annual amount consumed by present whale stocks, and nearly two-thirds of the estimated annual krill consumption by seals.

The birds also have a considerable impact on the terrestrial ecosystems of their breeding areas. As a consequence of the relatively long-lasting incubation and chick-rearing phase of many Procellariiformes, the birds play an important role in the functioning of the terrestrial ecosystems of the islands of the Southern Ocean, especially in the Subantarctic. As Siegfried (1986) points out, their land-based activities have three important consequences: first, the birds are on land for long enough to support populations of avian scavengers, such as black-backed gulls and sheathbills, and predators, such as skuas; second, the birds deposit considerable amounts of organic products in the form of excreta, eggs, carcasses and feathers; finally, they modify the physical nature of the terrain, chiefly by burrowing into the ground and by trampling the vegetation. Considerable progress has been made by South African scientists in quantifying these impacts (Smith 1977; Siegfried 1985).

The amounts of avian products deposited annually by the surface-nesting birds on Marion Island in the 100 km of coastal lowland are impressive: 3,200 tonnes of fresh guano (Burger et al. 1978), 500 tonnes of feathers (Williams et al. 1978), and 200 tonnes of eggs (Siegfried et al. 1978). Moreover, these figures take no account of the contributions of thousands of burrow-nesting petrels. The egg shells contain predominantly calcium that is duly returned to the ecosystem to be taken up by the plants. Calcium is an important element limiting primary production on the islands. The Marion Island soils are essentially deficient in nitrogen, and the contribution of the birds via their guano could be essential for the growth of the vegetation. Much of the avian-derived guano is penguin guano, which is washed straight into the sea, fertilizing the inshore waters and enhancing their production. Similar enrichment occurs off penguin colonies on the continent. However, at least 100 tonnes, representing 90% of all the nitrogen introduced annually into the Marion Island terrestrial ecosystem, reaches the plants (Smith 1978).

The seabirds thus transport considerable quantities of nutrients from the sea to the land, a process that is crucial to the production of the terrestrial vegetation. Little of the vegetation is consumed by herbivores, and it is essentially recycled through the detritus pathway. Populations of macroinvertebrates, such as earthworms, snails, and mites are enhanced; they are important food for sheathbills and black-backed gulls (Burger 1985).

11 Benthic Communities

CONTENTS

11.1 INTRODUCTION

Since the Belgian Antarctic Expedition (1897–1899) to the South Shetland Islands and the Antarctic Peninsula when the *Belgica* made the first systematic collection of benthic animals, naturalists and others on Antarctic expeditions have been continually fascinated by the unique fauna of the Southern Ocean. Early expeditions used remote sampling methods, a variety of grabs, dredges, trawls, etc., to sample the benthos and consequently they provided limited information on the quantitative composition and biomass of the fauna. It was not until the establishment of permanently occupied research stations during and following the International Geophysical Year that progress was made in understanding the dynamics of the inshore benthic communities in particular, and the life history strategies and physiology of the component species. At the same time more quantitative techniques were being used to study the benthic faunas of the continental shelf and deeper waters.

In addition to the benthic studies around the Antarctic Continent and in deeper waters of the Southern Ocean, there has been considerable research on the ecology of the intertidal and shallow littoral benthos of the Subantarctic islands, commencing with the pioneer work of Skottsberg on the marine algae of the Subantarctic islands, especially the Falklands and South Georgia (1941). Contributions to our understanding of the benthic ecology of these islands have been made by Kenny and Hayson (1962) and Simpson (1967a, 1976b, 1977) on Macquarie Island; Smith and Simpson (1985) on Heard Island; Delepine and Hureau (1968), Desbruyeres and Guille (1973), Arnaud (1974), Desbruyeres (1977) and Bellido (1982) on Iles Kerguelen; De Villiers (1976) on Marion and Prince Edward Islands; and Knox (1963, 1975, 1979) and Hay et al. (1985) on the New Zealand Subantarctic Islands.

The history of research on the Antarctic benthos is summarized and the bulk of the early literature is cited in Dell's comprehensive review of Antarctic benthos (1972). In addition, the reviews of Hedgpeth (1969, 1970, 1971), Arnaud (1970, 1974, 1977), Knox and Lowry (1977), White (1977, 1984), Clarke (1979, 1983, 1996), Picken (1980, 1985a, 1985b), Dayton (1990), Antz et al. (1994, 1997), and Clarke and Johnston (2002) provide much information on the principal characteristics of the Antarctic benthos.

11.2 THE ANTARCTIC BENTHIC ENVIRONMENT

The Antarctic continental shelf is generally narrow, varying in width from 64 to 240 km. Ice moving off the continent carries a large quantity of debris gouged from the underlying land surface, and this is deposited on the seabed when icebergs break up and melt. An estimated 500 million tonnes of material are transported out to sea every year, the equivalent of depositing 135 tonnes on each square kilometer. Hough (1956) found that the northern limit of the glacial deposits coincided with the average maximum northern extension of pack ice. The northern boundary of these glacial deposits is a junction with a wide belt (100–2000 km) of diatom ooze, consisting mainly of diatom frustules that have settled out from the surface waters.

Thus the sedimentary history of the Antarctic shelf and slope is similar around the continent. As Brodie points out, the glacial deposits on these areas are derived from a continent on which subaerial chemical weathering of the rocks is effectively nonexistent, and where the total seaward transport of rock fragments is by ice (1965). There is thus no river or windborne organic or inorganic deposits added to the shelf sediments. The marine sediments that result are poorly sorted and include muds, fine and coarse sands, pebbles, and large and small rocks. Large areas of the shelf are covered with coarse, poorly sorted deposits, interspersed with boulders of various sizes and gravel transported by icebergs (Usachov 1963).

A number of papers (e.g., Dayton 1990) have stressed the relative constancy instead of the "stability" of physical conditions in the Southern Ocean (except light, which varies in a strongly seasonal and predictable manner).

Compared to other marine systems, the relatively constant conditions of benthic environments are:

1. *Low but Stable Temperatures*. The benthic environment is characterized by low stable temperatures. The greatest seasonal variation occurs in surface waters, especially in the more northern localities, but even here the extreme range is only from +4.0 to 1.9°C. Near the seabed at a depth of 10 m off Signy Island, the temperature range is from 1.8 to 0.4°C (Picken 1985a). Further south and in deeper waters, the annual temperature range is even smaller; at 585 m in McMurdo Sound, the range is only 0.07°C around an average of −1.89°C (Littlepage 1965). Generally both the mean annual temperature and the range of annual variation increase from the Antarctic Continent out towards the Antarctic Convergence, but there are exceptions due to the inflow of warm deep water (Dunbar et al. 1985; Antz et al. 1992) or cold deep water (Dayton 1990) moving up onto the shelf. At Signy Island temperatures may vary by 0.5°C (Clarke 1988), whereas at 17 m in Arthur Harbour they vary between −1.8°C in winter and +1.0°C in summer (Ayala and Valentine 1978). In Admiralty Bay (King George Island) summer temperatures are around +1.76°C (max +3.4°C) at the surface and around −0.18°C in deeper waters (Wagle and Buto 1990).
2. *Low Fluctuations in Salinity*. The normal range in the benthic environment is 34.6–34.9 (Lipps and Hickman 1982; Clarke et al. 1988a). Exceptions are shallow water and intertidal areas where melt water inflow, tide, and currents can cause substantial variations in salinity (Barry 1988).
3. *Low Input of Terrestrial Sediments*. Sediment input from melt water is minimal since there are no major river inflows (Dunbar et al. 1985).
4. *Isolation by Deep sea, Circumantarctic Currents, and the Antarctic Convergence*. These all contribute to the constancy of conditions in the Southern Ocean benthos (White 1984).

On the other hand, other conditions fluctuate intensely:

1. *Light Regime*. This is highly seasonal. Coupled with this is the seasonality of primary production and organic matter flux to the benthos.

2. *Sea Ice Cover*. Ice is a major factor influencing the distribution of Antarctic benthos. In its various forms ice affects water temperature, levels of transmitted light, ocean currents, salinity, the composition and stability of benthic sediments and of littoral and sublittoral communities (Picken 1985a). Shorelines, both rock and gravel, or sand, are abraded by fast ice, pack ice, brash ice and push ice (floes driven ashore and piled upon each other by storms). The impact of such ice may scour the littoral and sublittoral areas to a depth of 15 m. Sea ice impacts on primary production in the water column and the flux of organic matter to the benthos (Spindler and Dieckman 1991). It can also impact the light available for the photosynthesis of benthic microalgae and macroalgae in shallow waters.
3. *Anchor Ice*. Anchor ice is a major source of physical variation is shallow water communities. Dayton has shown that to some extent it is responsible for the zonation of the benthic fauna down to about 30 m (Dayton et al. 1969, 1974; Dayton 1990). It does not generally occur at depths greater than 33 m except in some cases where Deep Cold Water moves up the shelf (Dayton 1990). Anchor ice can entrap plants and animals and lift them up off the substrate; it is capable of lifting up to 25 kg (Picken 1985a).
4. *Iceberg Scours*. Icebergs which float with about 80% of their bulk submerged can have a considerable impact on the benthos. A berg with a height of 30 m above the water will therefore ground in a water depth of 150 m. When driven by ocean currents, bergs can plough furrows in the bottom, thus disturbing benthic communities (Galeron et al. 1992; Peck et al. 1999; Gutt 2001; Knust et al. 2003).
5. *Ice Shelves*. Where these are grounded they can suppress the development of a benthic fauna. Further from these seaward edges where they float on seawater of variable depth, they may limit the development of a macrobenthic community. However, Knox has shown that a substantial and varied benthic community can be found 20 km from the edge of the McMurdo Ice Shelf (1986).
6. *Variation in Currents and Circulation Patterns*. Bottom current intensity determines sediment grain size, organic particle flux, and resuspension of surface sediments (Dunbar et al. 1985). Fildes Strait (King George Island), with turbulent tidal currents of velocities up to 2.5 m $\sec^{-1}$, seems to be favourable for a greater number of species as compared to the adjacent Maxwell Bay that is characterized by quiet water. For example, 103 amphipod species have been recorded from Fildes Strait, whereas only 55 species have been found in Maxwell Bay (Rauchet 1991).

   Circulation patterns are also responsible for dramatic differences in productivity in eastern McMurdo Sound as compared to the western Sound (see Chapter 12). The western Sound is oligotrophic whereas the eastern Sound is highly productive (Barry 1988; Barry and Dayton 1988; Knox 1990). This oligotrophic-to-euphotic shift is accompanied by marked differences in the density of the benthic epifaunal and infaunal communities (Dayton and Oliver 1977; Dayton et al. 1986).
7. *Impact of the El Nino Southern Oscillation*. Barry and Dayton have discussed the modification of circulation patterns in McMurdo Sound during the 1982–1983 El Nino event that caused a heavy ice year after a decade of low ice years (1988).
8. *Volcanic Eruptions*. Volcanic eruptions at Deception Island resulted in local benthic mortality (Gallardo and Castilla 1970; Gallardo 1988). In recent years a number of benthic volcanic vents have been found. These will result in the development of a unique associated fauna.

Picken (1985a) has characterized the Antarctic benthic environment as follows: "Conditions in the Antarctic benthos are therefore unique. A deep shelf and abyssal plain are littered with hard substrates. Water temperature is constantly low, and the impact of primary production is large, shortlived and generally regular every year. Ice constantly invades the littoral and shallow sublittoral regions. Despite the apparent harshness of the environment many invertebrate taxa thrive here although their communities are very different from those found in other continental shelf assemblages."

11.3 LITTORAL COMMUNITIES

11.3.1 Introduction

Castellanos and Perez have given an account of the animals in a series of tide pools at Cape Spring on the Antarctic Peninsula (1963). Delepine and Hureau (1968) have discussed the zonation of marine plants down to 50 m at Isles Petrels and on the coast of Terre Adélie, while Arnaud (1965) has briefly discussed the zonation of plants and animals on the same coast and Delepine (1966) has reported on the vegetation of the Melchoir Peninsula. More recently Arnaud (1974) has compared in greater detail the Antarctic littoral communities of Adélie Land with those of Subantarctic Kerguelen, while Castilla and Rozbaczylo (1985) have described the rocky intertidal assemblages of the South Shetland Islands. The intertidal zone near Palmer Station was examined by a number of ecologists in the late 1960s and early 1970s (Hedgpeth 1969; Shabica 1972; Stout and Shabica 1970; Stockton 1973, 1990; Moe and DeLaca 1976). More recently, Barnes (1995a, 1995b) has described the littoral zonation patterns on Signey Island and Kim (2001) has described that of King George Island.

The Subantarctic Islands are much better known, beginning with the pioneer study by Kenny and Haysom (1962) on the littoral ecology of Macquarie Island, which was followed by further studies by Simpson (1967a, 1976b, 1977). Grua (1971), Arnaud (1974), and Bellido (1982) have described aspects of the littoral ecology of Iles Kerguelen. More recently Smith and Simpson (1985) have described biotic zonation patterns on the littoral shores of Heard Island, while De Villiers (1976) has given an account of the littoral ecology of Marion and Prince Edwards Islands. In a series of papers, Knox (1960, 1963, 1975) has reviewed information on the littoral ecology of the Subantarctic region.

The most striking feature of Antarctic shores is the almost complete absence of an intertidal flora and fauna over a large part of the coast. In 1960 (Knox 1960), I remarked that in Antarctica a littoral fauna is "generally absent"; where algae are found, they exist in sheltered nooks and do not usually form the bands so characteristic of cold-temperate and Subantarctic areas. The sessile marine invertebrates found widely in the intertidal zones elsewhere, such as mussels and balanoid barnacles, are completely absent, although some molluscs can be found in the summer (for example, the limpet *Nacella concinna*, and a variety of small gastropods and bivalves). In spite of the work that has been carried out since then, the basic picture is that described above.

11.3.2 DISTRIBUTION PATTERNS OF THE BIOTA

Ice abrasion and snow cover severely limit the extent and composition of the intertidal communities of the shores of the Antarctic Continent and the offlying islands. In many areas the formation of winter fast ice, and the subsequent tidal movement of this ice usually leads to a build up of ice around the upper intertidal zone (Figure 11.1), often referred to as *the ice foot* (Barnes 1995a). While some longer-lived sessile organisms (e.g., small bivalves) may survive in sheltered crevices, the flora and fauna of the ice foot zone is eliminated in the winter.

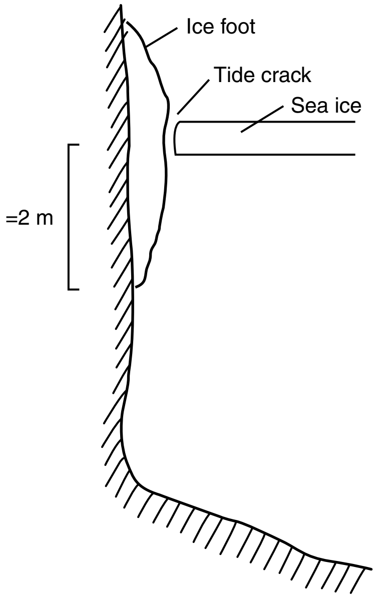


FIGURE 11.1 Diagram illustrating vertical rock face at Signy Island with the ice foot associated with the fast ice. Tidal water movement creates a gap between the ice foot and the fast ice forming the: tide crack. (From Barnes, D. K. A., *Mar. Biol.,* 121, 556, 1995a. With permission.)

The zonation pattern described by Castilla and Rozbaczylo (1985) at Robert Island, South Shetland Islands, where ice action is not as severe as on the continental mainland further south, will be used as a starting point to describe the distribution patterns of the biota. The upper eulittoral is characterized by a belt of the red alga *Porphyra endiviifolium*, the greens *Urospora penicilliformis* (mixed with *Ulothrix* sp.) and *Enteromorpha bulbosa* and a yellow lichen. In the mideulittoral there is a well developed belt of the red alga *Iridaea obvata* and a less conspicuous belt of the brown *Adenocyctis utricularis*. Lithothamnioid algae cover the bottom of tidal pools and patches of the dark encrusting red alga *Hildenbrandia* and black lichens are relatively abundant. The small gastropod *Laevilittorina antarctica* is present throughout this zone. The lower eulittoral has dense concentrations of the limpet *Nacella concinna*, and abundant crusts of lithothamnioid alga. Along the upper fringe of the sublittoral, large algae such as *Desmarestia ligulata* and *Ascoseira mirabilis* are abundant.

During the summer months at Palmer Station there develops a well-defined band of filamentous green algae, including species of *Enteromorpha, Ulothrix, Urospora*, and *Caldophora* (Stockton 1973, 1990). In the more sheltered cracks and crevices there are small thalli of red algae including *Leptosomia simplex, Curdiea racowitzae*, and *Iridaea obvata*. During the winter, all of these disapperar (Shabica 1977) and the flora must recruit afresh to the intertidal zone next season. The fauna is sparse with the most conspicuous species being the limpet *Nacella concinna*. There are also bivalves (*Lasaea rubra, Kidderia bicolor*) as well as several gastropods, polychaetes, hydroids, nemertines, and amphipods. In some areas there are conspicuous patches of the crustose red alga *Hildenbrandia,* the upper limit of which can form a strait line (Hedgpeth 1969; Stockton 1990).

Kim (2001) has described zonation patterns at King George Island. Three major zones were recognized. *The upper intertidal* was characterized by the absence of grazing molluscs and the presence of a zone occupied by the red alga *Porphyra endiviifolium* with filamentous algae, such as *Urospora penicilliformis, Ulothrix* sp. and *Bangia atropurpurea,* whose distribution extended down into the middle intertidal. In the *middle intertidal* filamentous algae occurred in spring but disappeared in the summer. The red alga *Palmaria decipiens* inhabited rock pools. In the lower part of the middle intertidal, thalli of *Adenocystis utricularia* and *Iridaea cordata* grew in rock crevices and pools. The microalgal grazer, *Nacella concinna,* migrated into this zone. In addition, numerous small gastropods, (e.g., *Naecilittorina* sp.) inhabited crevices and depressions with tutbellarians under boulders. *The lower intertidal* was characterized by the presence of the limpet *Nacella concinna* and the algae *Adenocystis urticularis* and *Iridaea cordata* throughout the year. The annual green algae *Monostroma hariotii* occurred

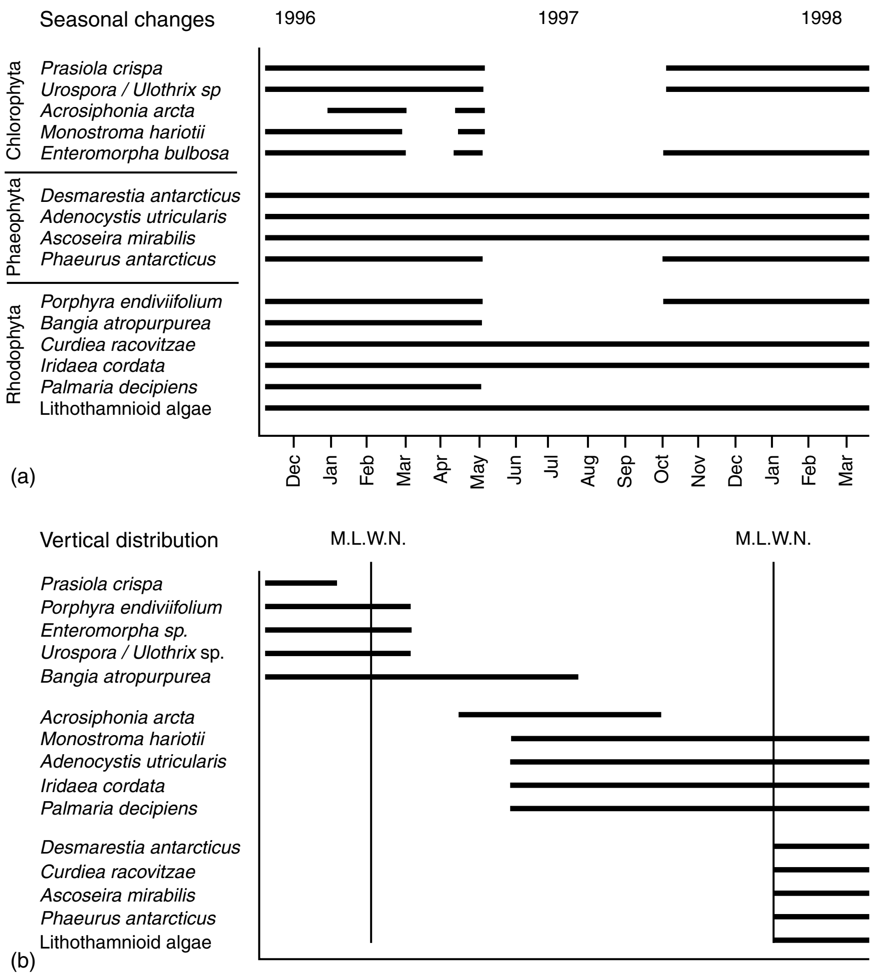


FIGURE 11.2 Seasonal changes (a) and vertical distribution (b) of intertidal algae in Potter Cove, King George Island. (From Kim, D., *Ber. Polarforsch*., 397, 20, 2001. With permission.)

occasionally in the summer. In the lower part of the intertidal, the macroalgae *Ascoseira mirabilis, Gigartina skottsbergii, Phaeurus antarcticus*, and *Desmarestia* sp. occurred in rock pools and extended down into the sublittoral. Figure 11.2 depicts the vertical limits of the marine algae in the intertidal zone. *Nacella concinna* entirely disappeared from the intertidal zone in the winter and recolonized again in the summer. The mean density in the intertidal varied from 0 in July to 47 ± 3.2 ind. m^{-2} in February (Figure 11.3). The maximum mean density was 129 ± 49.5 ind. m^{-2}.

Table 11.1 is a generalized diagram of the zonation pattern of the shores of the Antarctic Continent. This basic zonation pattern shows regional variations influenced to a large extent by the amount of ice and snow present. The littoral fringe is characterized by seasonal growths of the dark green alga *Prasiola crispa* and a number of lichen species. The upper eulittoral has seasonal growths of the filamentous greens *Ulothrix australis* and *Urospora penicilliformis*. A "bare zone" is characteristic of the mid eulittoral, which, however, is colonized in the summer by a dense felt of diatoms. In the lower eulittoral, annual algae such as the reds *Monostroma harioti, Leptosomia simplex* and the green *Chaetomorpha* develop. These species also extend into the sublittoral. The fringe of the upper sublittoral is marked by encrusting growths of the coralline algae *Lithophyllum aequable* and *Lithothamnion granuliferum*. These species extend up into the lower and mid littoral zones where rock crevices and pools are present. In the lower eulittoral, the black obligate marine lichen *Verrucaria serpuloides* is usually present extending down to 9 m below mean low water. Seasonal growths of the brown alga *Adenocystis utricularis* may occur in the lower part of the eulittoral. Other algae that have been recorded from the lower eulittoral, especially in rock pools, include *Porphyra* sp., *Iridaea obvata, Phaerus antarcticus, Curdiea racovitzae, Monostroma hariotii*, and *Phyllophora antarctica*. In the summer a thick diatom felt covers the bottom of many of the rock pools.

The dominant animal is the 3–4-cm long Antarctic limpet *Nacella concinna,* which grazes freely on the diatom felt and encrusting algae when submerged. The extent of the penetration of this species into the intertidal varies

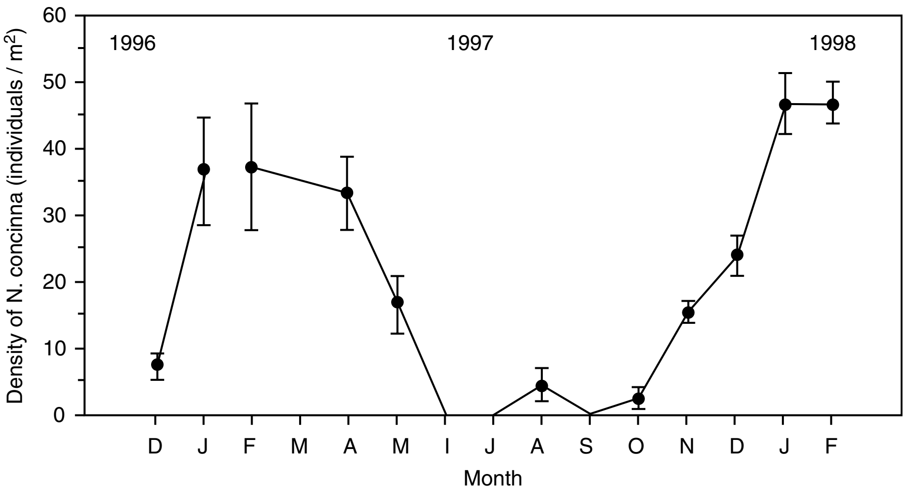


FIGURE 11.3 Seasonal changes of mean densities with standard error of *Nacella concinna* in the middle intertidal of King George Island from December 1996 to February 1998. (From Kim, D., *Ber. Polarforsch.*, 397, 23. With permission.)

considerably from locality to locality and during the season (Figure 11.3). In general the dominant populations are found in the sublittoral. In many localities, especially on the Antarctic Peninsula area and the Scotia Arc Islands, the small byssate bivalve *Kidderia subquantrulatum* forms dense populations at the bases of the algae in the lower half of the eulittoral zone (Castellanos and Perez 1963; Stout and Shabica 1970; Castilla and Rozbaczylo 1985). Associated species reported by Castellanos at Melchor Island include the bivalves *Lassarca miliaris, Philobrya olstadi*, and *Lasaea consanguinea*, the chiton *Tonicina zschaui*, the gastropods *Eatoniella caliginosa*, *E. kerguelensis, Laevlittorina coriacea, L. elongata, L. umbilicata, Laevilacunaria bransfieldensis*, the amphipods *Pontogenia antarctica* (dominant), *P. magellanica*, *Eurymera monticulosa, Bovallia gigantia* and *Pariphimedia integricaudata*, the isopod *Cymodocella tubicauda*, the nemertine *Amphiphoxus michaelseni* and the turbellarians *Procerade gerlachi* and *P. wondeli*.

Away from the impact of ice, the littoral flora and fauna becomes more varied. Smith and Simpson (1985) have

TABLE 11.1
Zonation Patterns on Antarctic Coasts

	Basic Pattern	Iles Des Pétrels[a]	South Shetland Islands[b]
Upper littoral fringe	Lichens *Verrucaria*	Lichens	
Lower littoral fringe	Lichens *Verrucaria*	Lichens	
Eulittoral	? Lichens	↑*Ulothrix*	Tide pools with crustose corallines
	Seasonal growths of diatoms and filamentous green algae	1 m australis	*Phyllophora appendiculata*
		↓	
		↑	
		1.5 m Diatoms	*Plocamium secundatum*
		↓	
Sublittoral fringe	Red algae esp.	↑*Monostroma hariotii*	*Leptosomia*
	Leptosomia spp.	2–3 m	*Patinigera*
	Patinigera	↓ *Leptosomia simplex*	*Odonaster*
Upper sub-littoral zone	*Desmarestia spp.*	*Desmarestia menziesii*	*Desmarestia spp.*
	Phyllogigas grandifolius		*Phyllogigas grandifolius*
	Ascosiera mirabilis		*Ascosiera mirabilis*
	Cystosphaera jacquinotii	*Phyllogigas grandifolius*	*Cystosphaera jacquinotii*
	Patinigera		*Adenocystis utricularis*
	Odonaster		
	Red algae		

[a] Based on Delepine and Hureau (1968).
[b] Based on Neushul (1968).

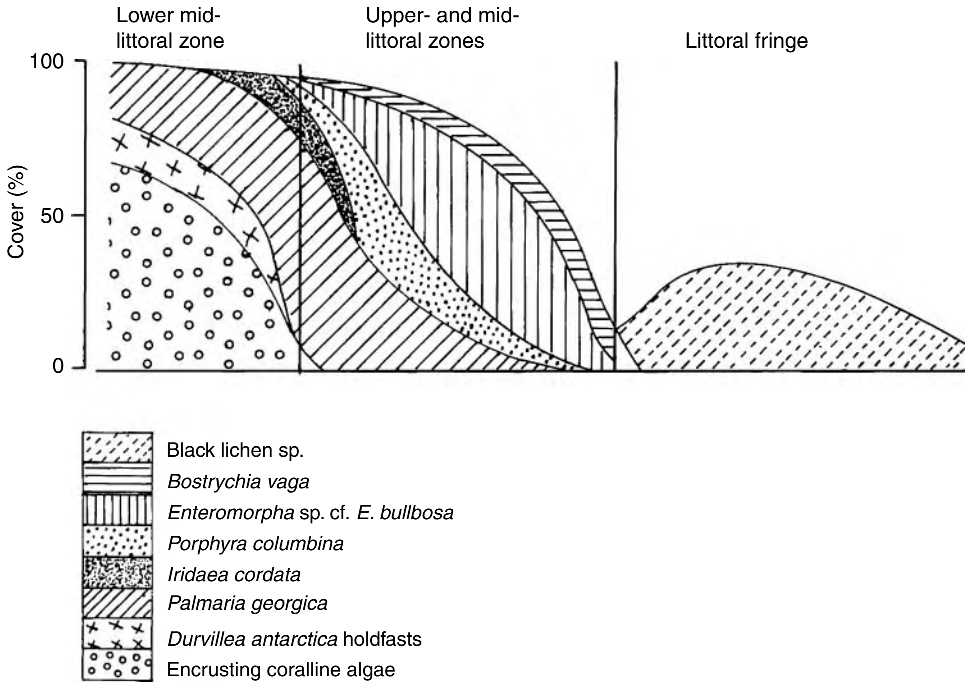


FIGURE 11.4 Proportional cover by plant species in the littoral zone of Heard Island rocky shores. (From Smith, J. M. B. and Simpson, R. D., *Polar Biol.,* 89, 1985. With permission.)

recently described zonation patterns on the rocky shores of Heard Island (73°30″E, 53°05″S) which lies to the south of the Antarctic Convergence. The littoral fringe is characterized by a covering of black lichen colonized by arthropods, especially the beetle *Mesembriorhinus brevis*. The upper and mid littoral zones are covered by filmy and filamentous algae (Figure 11.4), predominantly reds (especially *Porphyra columbina* and *Iridaea cordata*) lower down and green algae (especially *Enteromorpha* spp.) higher up. The littorinid *Laevilitorina heardensis* and the small bivalve *Kidderia bicolor* occur in crevices and in sheltered situations. Where the algae forms a spongy ma, abundant oligochaetes occur. The lower eulittoral is dominated by the bull kelp *Durvillaea antarctica*, between the holdfasts of which encrusting pink coralline algae form an almost complete cover. Other small red algae also grow there, including *Ballia callitricha, Iridaea cordata*, and *Palmaria georgica*. The limpet *Nacella kerguelensis* is abundant and the chiton *Hemiarthrum setulosum* common. Encrusting corallines dominate the fringe of the upper sublittoral.

11.4 SHALLOW SUBLITTORAL COMMUNITIES

Sampling through tide cracks, seal breathing holes and holes dug through the fast ice by members of the early expeditions to Antarctica revealed a rich and abundant fauna, especially of epibenthic invertebrates. With the establishment of permanent stations, the pace of work on benthic ecology increased. The quality of this work was enhanced and the output considerably increased from the mid 1960s by the introduction of SCUBA diving at a number of stations, notably Grytvikin on South Georgia, McMurdo in the Ross Sea, Mirny, Moldezhnaya, Palmer on Anvers Island, Signy on the South Orkneys, and Syowa. More recently remotely controlled vehicles with TV cameras and still cameras enabling stereophotographs to be taken have extended the possibilities of estimating the distribution of the benthos, especially in deeper water (Hamada et al. 1986).

11.4.1 BENTHIC MICROALGAE

Two groups of microscopic algae are included within the benthic microalgae: the sediment microalgae in the top few millimetres of the sediments and the epiphytic algae growing on rock surfaces or attached to macroalgae and the epibenthos. In addition to diatoms and blue green algae, bacteria and protozoa are abundant in the microalgal films. These microbial films are the main food resource for microphagous herbivores such as gastropods. There have been only a limited numbers of studies of the benthic microalgae in Antarctic coastal waters. Palmisano et al. (1985c) and Dayton et al. (1986) have studied the ecology of benthic diatoms in McMurdo Sound; Krebs et al. (1987) investigated the microalgae in Arthur Harbour; Ahn and Kang (1994) and Kloser (1998) gave accounts of the microalgal communities on King George Island; Gilbert

(1991a, 1991b) investigated benthic microalgal biomass and production in shallow waters at Signy Island; Everitt and Thomas (1986) and Thomas and Jiang (1986) have studied the seasonal changes of epiphytic diatoms near Davis Station.

Table 11.2 presents data from Dayton et al. (1986) for the standing stock of chlorophyll *a* and phaeopigments for the east McMurdo Sound (from north to south, Cape Royds to Cape Armitage) and west McMurdo Sound (New Harbour). From this table it can be seen that there are seasonal (summer–winter), substrate and depth differences, as well as differences due to the amount of light that penetrates through the fast ice and snow cover. Off Cape Armitage, where the snow cover was removed from the ice above a sponge spicule mat at a depth of 6 m, the chlorophyll *a* concentration in a little over two weeks increased from 756 to 960 mg chl *a* m^{-2} and the chlorophyll *a* phaeopigment ratio doubled from 7.4 to 15.9. The effect of season on chlorophyll *a* and phaeopigment can be seen in Table 11.1. At the Cape Armitage 6-m site, the chlorophyll *a* concentration fell from 457 to 96 mg chl *a* m^{-2} between December and June. The mg chl *a* m^{-2} at the 18 m site fell from 310 to 95 between 22 November and 25 March. By 18 August the chlorophyll *a* was as low as 47 mg m^{-2}. Similar differences between winter and summer values can be seen at other sites.

Standing stock estimates for the West Sound New Harbour site were much lower than in the East Sound sites (Table 11.2). Two comparable sites on the east and west sides of the Sound are Cinder Cones and New Harbour with chlorophyll *a* concentrations of 241 and 326 mg chl *a* m^{-2} at Cinder Cones compared to 145 and 45 mg chl *a* m^{-2} at New Harbour at 19 and 25 m, respectively. Values of 18 to 60 mg chl *a* m^{-2} are typical of the deeper New Harbour areas; for similar substrates, depths and seasons, the comparable values in the East Sound are 300–900 mg chl *a* m^{-2}.

Some of the standing stock data recorded by Dayton et al. (1986) are extremely high. Most of the high readings occur in sponge spicule mats and there are a number of reasons for this. Firstly, the sponge spicules form a complex lattice. Each spicule provides a substratum for diatoms, thus providing a tremendous increase in surface area which is covered with diatoms. In addition, this structure affords benthic microalgae protection from grazers. It also allows ice algae and phytoplankton settling out from the water column to accumulate in the interstices between the spicules. The shift in the ratio of chlorophyll *a* phaeopigments, which decreases markedly in the winter, give a preliminary estimate of the degradation of the microalgae.

Palmisano et al. (1985c) have studied the photosynthesis–irradiance relationship of a dense community of shade–adapted benthic microalgae dominated by the diatom *Trachyneis aspersa* in the sponge spicule mat in depths of 20–30 m off Cape Armitage. Ambient irradiance was less than 0.6 μE m^{-2} sec^{-1} due to light attenuation by surface snow, sea ice, ice microalgae and the phytoplankton in the water column. Photosynthesis-irradiance relationships determined by the ^{14}C method revealed that the benthic diatoms were lightsaturated at only 11 μE m^{-2} sec^{-1}, putting them among the most shade–adapted microalgae reported. Unlike most shadeadapted microalgae, however, they were not photoinhibited by irradiances even as high as 300 μE m^{-2} sec^{-1}. This contrasts with sea ice algae at the same site, which may be photoinhibited by irradiances above 25 μE m^{-2} sec^{-1} (Palmisano et al. 1985b).

The seasonal pattern of benthic microalgal biomass (as measured by chlorophyll concentrations) at a near shore site (12 m depth) on the east coast of Signy Island, South Orkney Islands is shown in Figure 11.5 (Gilbert 1991a). Seasonal chlorophyll levels showed distinct seasonal variation related to the photon flux density reaching the benthos. The benthic microalgae responded rapidly to higher light intensities following the breakout of the sea ice. Low rates of sedimentation of material from the water column during the benthic bloom indicated that the benthic microalgae were mostly responsible for increase in sediment chlorophyll concentrations. In December at the peak of the benthic microalgal bloom, a primary productivity rate of 700.9 mg C m^{-2} day^{-1} was measured (Gilbert 1991b). However, in January at the peak of the phytoplankton bloom when light intensities reaching the benthos was greatly reduced, a rate of 313.4 mg C m^{-2} day^{-1}, about half of that in January, was measured. In March, when the phytoplankton bloom died off, benthic light intensities had increased and production was 391.4 mg C m^{-2} day^{-1}.

Kloser (1998) working in Potter Cove, King George Island, sampled a variety of habitats including rock surfaces, various types of algae, ascidian tests and muddy substrates. The different substrates were characterized by specific microalgal assemblages. On the muddy substrates he found large clumps ("sausages") of *Odontella litigiosa*. Species found in tidepools included *Fragillaria striatula, Pseudogomphonema camtchatica, Melisira numuloides* and the tube-dwelling species *Parlibellus delognei* and *P. rhombica.*

Riaux-Gobin and Bourgoin (2001) investigate the standing stocks of benthic microalgae at the Kerguelen Islands. High productivity periods were in most cases linked to austral spring and summer (up to 30–50 μg chl *a* g^{-1} dry wt in intertidal sheltered sands; > 170 μg chl *a* g^{-1} dry wt in sheltered subtidal muds). On subtidal muddy sites, the high phaeopigment concentrations (up to 195 μg phaeo *a* g^{-1} dry wt) were attributed to kelp and epiphyte degradation and sedimentation.

In inshore areas measurements of the productivity of the benthic microalgae prior to the development of the dense growth of the ice algae in October are required before estimates of their production can be made. It is probable that the benthic microalgae play an important role in providing carbon and energy to the abundant benthic macrofauna in McMurdo Sound, especially prior to the release of algae from the sea ice in January and the onset of the water column phytoplankton bloom. It is clear that benthic microalgal production plays an important role in the seasonal primary production cycle in inshore waters.

TABLE 11.2

Station Location, Depth, Annual Ice Thickness, Snow Cover, Percentage Surface Downwelling Irradiance, Benthic Substrate; Mean (±95% Confidence Interval) Chlorophyll a and Phaeopigments for Benthic Microalgae in McMurdo Sound During the Austral Summer 1975–1976 and Winter 1977

Location	Season	Annual Ice Thickness (m)	Snow Cover (m)	Depth (m)	Substrate	Chl a (mg m^{-2})	Phaeopigments (mg m^{-2})	Chl *al* phaeo.	%Surface Down-Dwelling Irradiance
Cape Royds	Summer	—	—	25	Mud and gravel	273 ± 109	253 ± 38.0	1.06 ± 0.33	2.78
Cape Evans	Summer	0.1–0.2	0	19	Sand	293 ± 93.2	110 ± 71.1	2.86 ± 1.13	—
					Mud and sand	913 ± 185	499 ± 119	1.87 ± 0.14	—
Turtle Rock	Summer	—	—	25	Mud and gravel	139 ± 24.2	127 ± 30.1	1.11 ± 0.22	—
				40	Mud and gravel	60.8 ± 28.1	146 ± 42.0	0.43	—
Cinder Cones	Summer	—	—	19	Mud and gravel	241 ± 157	308 ± 131	0.81 ± 0.46	
				25	Mud and gravel	325 ± 73.3	283 ± 147	1.21 ± 0.38	
				40	Sponge spicule	360 ± 146	86.4 ± 51.7	4.33 ± 1.19	
Hutt Point	Summer	2.6	0.02	25	Mud and gravel	156 ± 106	310 ± 98.3	0.50 ± 0.26	0.31
				40	Sponge spicule	515 ± 399	99.7 ± 43.8	5.38 ± 4.30	
				40	Sponge spicule	610 ± 255	192 ± 43.4	3.43 ± 2.28	
				31	Sponge spicule	611 ± 230	175 ± 52.2	3.56 ± 1.18	
				43	Sponge spicule	561 ± 468	99.4 ± 9.8	5.66 ± 0.69	
Cape Armitage	Summer	2.0–2.5	0.05–0.3	6	Mud and gravel	269 ± 84 to 457 ± 128	50.5 ± 14.3 to 349 ± 262	1.08 ± 0.67 to 7.12 ± 0.92	ND-0.05
	Winter			6	Mud and gravel	96 ± 55	110 ± 89.6	0.89 ± 0.19	
	Summer			18	Mud	265 ± 80.2 to 533 ± 206	78.2 ± 36.5 to 316 ± 30.5	0.97 ± 0.30 to 6.90 ± 0.64	
	Winter			18	Mud	47.3 ± 14.4 to 76.2 ± 24.7	90.1 ± 27.8 to 179 ± 36.8	0.43 ± 0.14 to 0.54 ± 0.14	
	Summer			24	Sponge spicule	736 ± 253 to 960 ± 220	94.5 ± 63.2 to 186 ± 225	5.58 ± 4.38 to 15.90 ± 4.3	
	Winter			24	Sponge spicule	227 ± 76 to 374 ± 177	62.2 ± 15.1 to 118 ± 62.8	3.18 ± 0.67 to 3.63 ± 0.69	
	Summer			42	Sponge spicule	317 ± 91 to 518 ± 261	30.8 ± 11.2 to 128 ± 44	4.14 ± 1.41 to 10.50 ± 2.99	

See Figure 12.1 for locations.

Source: Data from Dayton, P. K., et al., *Polar Biol.*, 6, 105, 1986. With permission.

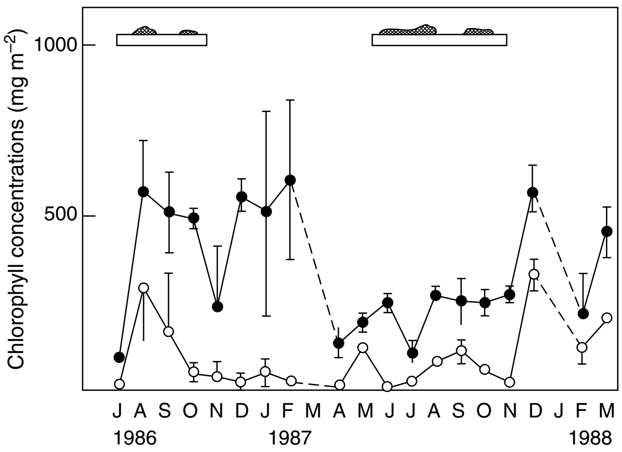


FIGURE 11.5 Seasonal variation of benthic total chlorophyll concentration (●) and chlorophyll *a* (○) in the top 5 cm of the sediment at a nearshore site (12 m) on the east coast of Signy Island, South Orkney Islands. The blocks at the top of the graph represent sea ice and snow cover (stipled) up to a maximum depth of 10 cm. (From Gilbert, N. S., *Est. Coastal Shelf. Sci.,* 33, 89, 1991. With permission.)

11.4.2 BENTHIC MACROALGAE

About 700 species of benthic macroalgae belonging to 300 genera have been recorded from the Southern Ocean. In addition to the classical overviews of Southern Ocean marine algae by Gain (1912) and Skottsberg (1941, 1964), more recent accounts include those of Zinova (1958), Papenfuss (1964), Delepine (1966), Delepine et al. (1965), Zaneveld (1966a, 1966b, 1968), South (1979), Heyward and Whitaker (1984), Miller and Pearse (1991), Cormaci et al. (1992), Kloser et al. (1994), and Wiencke (1996). Neuschul (1968) estimated that about 35% of the algae were endemic. However, many records are fragmentary, often identifications are suspect and there is an urgent need for critical reviews of many of the genera (South 1979; Heywood and Whitaker 1984). Most of the species appear to have a circumpolar distribution and many also occur in the warmer Subantarctic waters. Skottsberg (1964) distinguishes a Subantarctic flora using the 0°C surface isotherm as a rough guide. Many algal genera in the Subantarctic zone are not found in the Antarctic zone and vice versa; South Georgia appears to be situated on the boundary having representatives from both zones (Skottsberg 1964; Neuschul 1968).

11.4.2.1 Distribution Patterns

The distribution of the littoral algae has been described above. Here the shallow sublittoral communities will be dealt with. Below extreme low water, there is a zone (0–5 m) where algae are sparse due to the abrasive action of ice. Where this is severe, the only species on exposed rock surfaces are encrusting calcareous red algae *Lithophyllum aequable* and *Lithothannion granuliferum*. The obligate submerged marine lichen *Verrucaria serpuloides* grows here down to a depth of 9 m. Sheltered crevices support small clumps of mostly annual species such as the brown alga *Adenocystic utricularis* and green algae of the genera *Enteromorpha, Ulothrix*, and *Cladophora*. Further north on the islands of the Scotia Arc where ice action is less severe, more luxuriant algal growths occur. On Signy Island parts of the upper sublittoral have dense algal growths (Picken 1985a). Red seaweeds, *Leptosarca simplex* and *Gigartina apoda*, and the brown *Adenocystis utricularis* are common in the 2–5 m range. Below 5 m large browns dominate: *Ascoseira mirabilis*, dense thickets of *Desmarestia menziesii* and *D. anceps* up to 1 m high, and *Himantothallus grandifolius*. Of these perennial brown alga, *Himanothallus* becomes dominant below 9 m. Beneath the canopy formed by these four large species, there is often a rich “understory” of reds: *Iridaea obvata, Myriogramme magini, Plocamium secundatum, Porphyra umbilicalis*, and species of *Gigartina*. However, the algal biomass at these depths on Antarctic shores is significantly lower than that at comparable sites on temperate shores because of the effects of ice abrasion, unstable hard substrates in the shallow sublittoral zone, and short periods of available light for primary production (Richardson 1972).

Miller and Pearse (1991) studied the distribution of the dominant species of macroalgae at several sites in McMurdo Sound. The depth-related distribution pattern of the three dominants off Cape Evans is shown in Figure 11.6, with *Iridea cordata* in shallow water, *Phyllophora antarctica* abundant and fertile at intermediate depths and *Leptophytum coulmanicum* dominant below 20 m. The vertical distribution of the species is correlated with irradiance levels. At sites with thinner annual ice and less snow accumulation, vertical distributions are shifted downwards relative to sites that remain covered most of the year with thick or snow-covered fast ice.

In Potter Cove, King George Island, Quartino et al. (2001) recorded 22 species of macroalgae. In many areas they found that the brown algae *Desmarestia anceps* and *D. menziesii* were able to exclude other agal species by competition for light. Macroalgal biomass in Potter Cove (mean biomass 1.390 g dry wt m^{-2}) was relatively high compared to other localities on the Antarctic Peninsula and in the Ross Sea (Miller and Pearse 1991; Amsler et al. 1995).

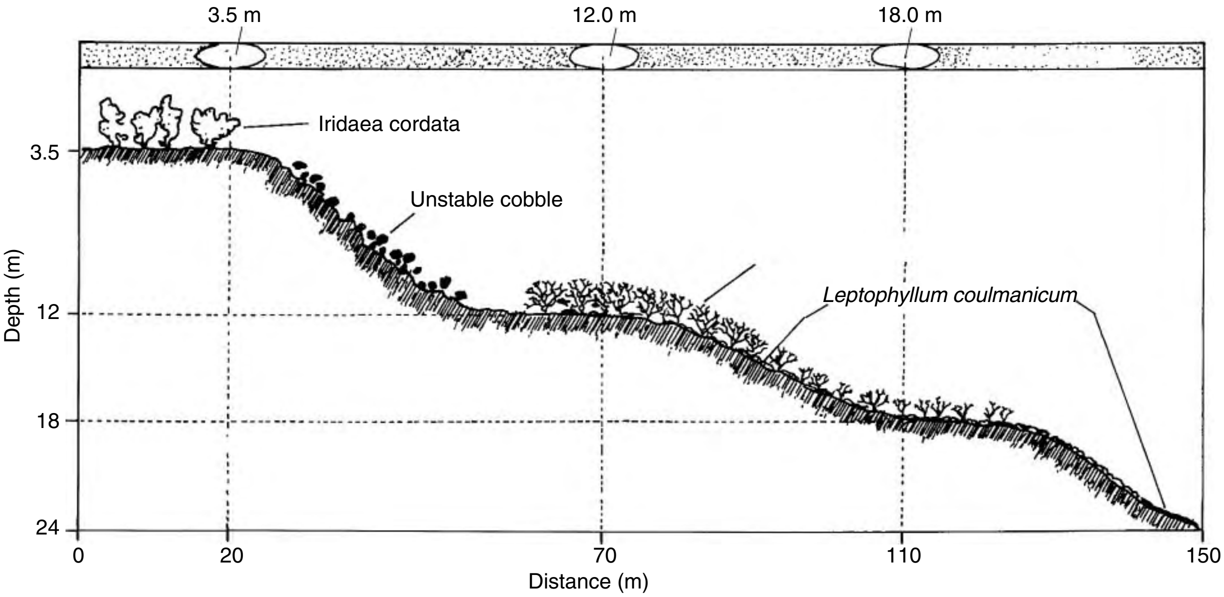


FIGURE 11.6 Macroalgal zonation at Cape Evans, Ross Island, McMurdo Sound. (From Miller, K. A. and Pearse, J. S., *Amer. Zool.,* 31, 35, 1991. With permission.)

A characteristic feature of the macroalgal flora of the Antarctic Peninsula region is the dominance of brown algae. This contrasts with the macroalgal flora of the Ross Sea, which is dominated by red algae (Cormaci et al. 1992, 1998). Overall there was a tendency for macroalgae to grow on fine substrates with increasing depth. Species richness decreased at 20 m depth, probably due to limiting light conditions.

Throughout those regions of the Antarctic in which algal zonations have been explored, the vegetation becomes richer with depth. Shallow water species such as *Curdiea, Leptosomia, Iridaea, Ascoseira mirabilis*, and *Gigartina papillosa* appear increasingly in the more exposed situations. *Desmarestia ligulata, D. anceps*, and *D. menziesii* often dominate down to a depth of 10–25 m, often extending to greater depths. Below about 25 m, the largest Antarctic brown alga *Himanothallus grandifolius* tends to be dominant, and it has been reported well below 50 m.

11.4.2.2 Environmental Factors

The available data concerning growth conditions for sublittoral algae in the Antarctic have recently been discussed by Drew and Hastings (1992), Kloser et al. (1993), and Wiencke (1996). In winter, algae are exposed to darkness or dim light due to ice cover and the seasonal light regime. This is followed by a period of high light conditions after sea ice break-up from October to November until the end of December. Later in summer and autumn, low light conditions again prevail due to the discharge of turbid meltwater and the development of phytoplankton blooms. Day length, which varies with latitude, is an important trigger for the development of macroalgae. Concentrations of nutrients are high and nonlimiting for algal growth (Drew and Hastings 1993; Kloser et al. 1993).

Macroalgae in the eulittoral and supralittoral are subjected to considerable changes in water content, salinity, temperature and light conditions dependent on seasons, tides and weather conditions. In spring the suralittoral is flushed by meltwater. This is followed by a period of desiccation during the summer, which is interrupted by temporary rehydration after precipitation or extremely high tides (Kappen and Redon 1984). Salinity varies greatly in this habitat due to the combined effects of tides, salt spray and desiccation on the one hand and precipitation on the other. Temperatures are generally similar to coastal water temperatures but may increase in tide pools at low tide up to almost 14°C in the summer (Kloser 1994). In both habitats light conditions vary greatly with the seasons due to snow and ice cover in the winter and high light conditions in the summer.

Seasonal Development. The seasonal development of macroalgae is generally triggered by light, temperature and/or nutrient conditions (Lüning and Dieckman 1989). The life history strategy of the endemic Antarctic macroalgae are an adaptation to the strong seasonal variation of light conditions at high latitudes (Weincke 1996). Weykam and Wiencke (1996) investigated the seasonal photosynthetic performance of the most common Antarctic red alga, *Palmaria decipeins*, under fluctuating Antarctic daylengths. It showed strong annual optima of light-saturated net photosynthesis, *x*, and chl *a* and phycobilin concentrations in October (spring).

Light Demands and Depth Zonation. Antarctic macroalgae show a pronounced ability to tolerate dark periods of up to 1 year without suffering damage (Wiencke 1980). Light demands for the completion of the life cycle of

Antarctic macroalgae are very low (Wiencke 1990). Microthalli and juvenile macrothalli of Antarctic brown algae are able to grow at very low photon flouescence rates and growth is light saturated already at 4–12 μmol photons m^{-2} sec^{-1} (Weincke 1990a). In contrast to algae from other regions, Antarctic macroalgae show almost no decrease in growth-high light conditions. As a result, light compensation (l_c) and light saturation (l_k) points are very low in Antarctic species and range between 1.6 and 14.7 and between 14.3 and 48.6 μmol photons m^{-2} sec^{-1}, respectively, (Wiencke et al. 1993).

Antarctic algae are not only adapted to low light conditions but can also cope with very high photon fluence rates in summer due to their ability for dynamic photoinhibition, a protective mechanism by which excessive energy is rendered harmless by thermal dissipation (Krause and Weis 1991; Hanelt et al. 1997). The intertidal brown alga *Adencyctis utricularis*, and the red alga *Palmaria decipiens* from the lower intertidal and upper sublittoral, show photoinhibition of photosynthesis starting before midday and with the lowest photosynthetic rate in the early afternoon.

Gomez et al. (1997) and Hanlet et al. (1997) have investigated the photosynthetic requirements and the effects of high light stress on the depth zonation of Antarctic macroalgae. Despite light limitation due to ice cover and the attenuation of light penetration due to phytoplankton blooms or melt-water during the summer, the occurrence of Antarctic macroalgae in deep water (+40 m) has frequently been reported. The very low light requirements of these species for growth and photosynthesis are a prerequisite for survival in deep water (Wiencke et al. 1993; Gomez et al. 1997). Weincke (1996) considers that the capacity for dynamic photoinhibition during exposure to high light conditions, as well as the general degree of adaptation of photosynthesis to different light regimes, most probably determines the depth distribution of the macroalgae.

Temperature Demands and Geographical Distribution. Endemic Antarctic macroalgae exhibit very strong adaptation to low temperatures (Wiencke et al. 1994). They grow at temperatures upto 5 or 10°C and show upper survival temperatures of between 11 and 13–17°C. The optimum temperatures for photosynthesis vary from 1 to 10°C for *Ascoseira mirabilis* (lowest), 10–15°C for *Himantothallus grandifolous,* to 15°C for *Palmaria decepiens* and *Gigartina skottsbergii*. The northern distribution limit of endemic Antarctic species are mainly determined by the algal temperature growth patterns.

Effect of Desiccation and Salinity on Supra- and Eulittoral Algae. Photosynthetic rates in many species is controlled by the water content. Desiccation, which lowers the water content, results in decreased photosynthesis. While some species, such as the green algae *Enteromorpha bulbosa* and *Ulothriz subflaccida,* can grow in salinities of 68, others such as *Acrosiphonia arata* grow at high rates only between salinities between 17 and 35 (Jacob et al. 1991; Karsten et al. 1991).

11.4.2.3 Macroalgae as a Food Resource for Other Organisms

Macroalgae contribute to the food resources of the shallow water ecosystem, either as living algae or as degraded organic material. Iken (1999) investigated the trophic relations between living macroalgae and herbivores in Potter Cove, King George Island. Hervivorous (or omnivorous) animals feeding on fresh macroalgae in Potter Cove include gastropods, amphipods, polychaetes, isopods and fish (Iken 1999). Among the herbivores, specialists and generalists can be distinguished. Specialists, which feed only on a small number of macroalgal species, are the limpet *Nacella concinna* and the isopod *Plakarhrium punctatissum. N. concinna* feeds mainly on crustose red algae and the brown alga *Ascosiera mirabilis,* while *P. punctatissum* feeds on the red alga *Curdea racovitzae* and the brown alga *Ascoseira mirabilis*. Other herbivores, such as the gastropod *Laevilacunaria antarctica,* the amphipod *Gondogeneia antarctica*, and the fish *Notothenia coriiceps* are generalists grazing on a large variety of algal species (Figure 11.7). Eighteen algal species contribute 40% by weight to the diet of *Notothenia coriiceps*. These algae include 2 green algae, 10 red algae and 6 brown algae, with *Monostroma hariotii, Palmaria decipiens*, and *Desmarestia menziesii* comprising the bulk of the algal biomass.

Iken et al. (1999) quantified the consumption of the herbivorous gastropod *Laevilacunaria antarctica*. With a mean abundance of 292 ind. m^{-2}, the mean consumption was estimated to be 37.6 mg dry wt algae m^{-2} day^{-1}. The annual consumption of this species in Potter Cove was estimated to be 9 g dry wt algae m^{-2} yr^{-1}. Among the algal species consumed, *Palmaria decipiens, Monostroma hariotii, Desmarestia menziesii*, and *Iridaea cordata* were significantly preferred, whereas *Himantothallus grandifolius* and *Desmarestia anceps* were significantly avoided compared to their availability. It is well known that algae have developed metabolites that deter grazers (Hay and Fenical 1992). However, feeding assays with extracts of three brown algal species did not show any deterrent effect.

Large amounts of drift algae are often deposited on the beaches of the Antarctic and Subantarctic Islands. The degradation of these deposits has been extensively studied at various Southern hemisphere localities (e.g., South Africa: Stenton-Dozey and Griffiths 1983; New Zealand: Inglis 1989; New Zealand Subantarctic Islands: Knox 1963). The beds of drift algae are colonized and consumed by a variety of invertebrates including amphipods, isopods, molluscs, beetles, kelp fly larvae (Diptera), mites, nematodes and oligochaetes. Chown (1996) has studied the degradation of kelp on South Georgia beaches by the larvae of the Kelp fly *Paractora trichosterna* and compared his results with those from a study at Husvik Harbour, South Georgia (Pugh and MacAlister 1994) and Marion Island (Crafford 1984; Crafford and Scholtz 1987) and Possession Island (Trehen and Vernon 1982). Crafford and Scholtz (1987) showed that the larvae of *Paractora dreuxi* were responsible for a 35% loss of kelp dry mass

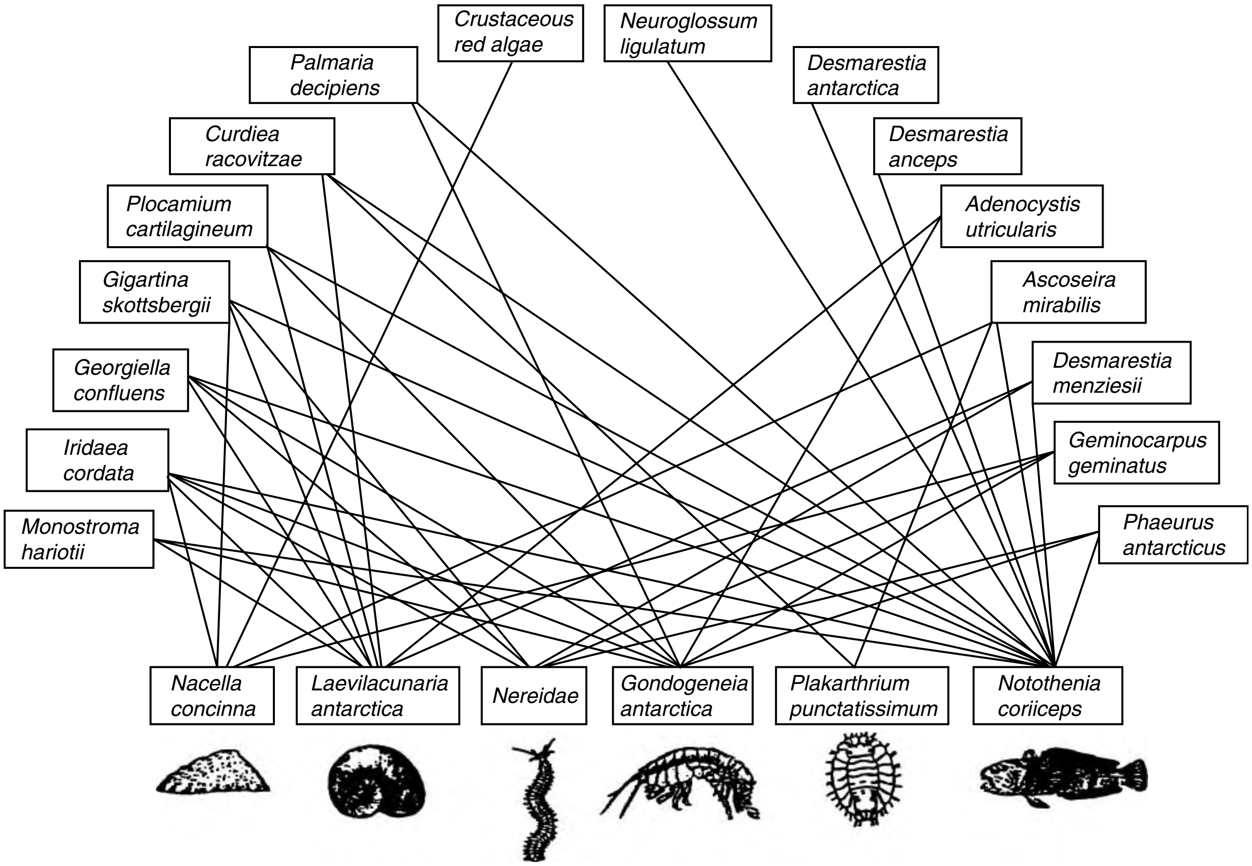


FIGURE 11.7 Trophic relationships between herbivores (below) and macroalgae (above) in Potter Cove, King George Island. Each connecting line characterizes that the herbivore is feeding on the algae. (From Iken, K., *J. Exp. Mar. Biol. Ecol.,* 236, 1999. With permission.)

during decomposition. In his study, Chown (1996) found that *P. trichosterna* larvae had a consumption rate of 0.734 mg dry mass kelp mg dry mass larva^{-1} day^{-1}. By day six at Husvik, kelp biomass in the exposed and protected beds had declined to 60 and 75% of the original dry mass, respectively; whereas by day six at Marion Island, the kelp biomass had declined to 40% of its original value in an exposed bed and 60% in a protected one. By day thirty, kelp biomass in the protected beds at both localities had declined to about 30% of its original value. Differences in the decay rates can be attributed to the differing composition of the kelp community. Organic matter washed out from the decaying beds will provide food for a range of detritivoures.

In general only ~10% of the macroalgal production is consumed directly by grazers and, as detailed above, the bulk enters the detrital food chain as particulate and dissolved organic matter (Mann 1982). Norhko et al. (2004) investigated the ecological role of drift algae in coastal soft bottom communities at Cape Evans, Ross Island. The dominant benthic primary producer in terms of biomass from 10 to more than 30 m depth was the red alga *Phyllophora antarctica*. The vast majority of the biomass occurred in drift accumulations. Figure 11.8 depicts the depth distribution of the attached and drift algae. Attached *Phyllophora* was only found at depths less than 15 m, with a biomass of 66 ± 15 g dry wt m^{-2}. In contrast, drift *Phyllophora* accumulations occurred throughout the depth range sampled with peak biomasses of 140 ± 30 g dry wt^{-2} in the 15–25 m depth strata.

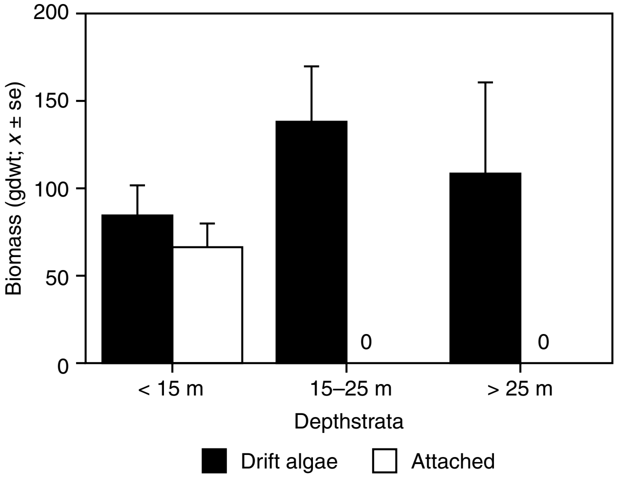


FIGURE 11.8 The depth distribution and biomass of drifting and attached *Phyllophora* at Cape Evans in 2001. *0*, No attached algae recorded. (From Noroko, A., et al., *Polar Biol.,* 27, 486, 2004. With permission.)

The impact of the algal drifts on the soft-sediment macrofaunal communities was investigated. In total, 62 benthic invertebrate taxa were recorded in the infaunal samples. Only one taxon, isopods in the family Stenetriidae, was persistently found in higher numbers under the algal drifts. Apart from the polychaete *Polygordius* sp., which was the dominant taxon, six of the most frequently occurring taxa were crustaceans (the tanaid *Nototanias* sp, the isopods *Austrosigneum grande* and Sterietiidae, the amphipod *Heterophacus videns,* ostracods), two were gastropods (*Onoba* spp.), and one a polychaete (*Syllidia inerma).* There were clear differences in total numbers of individuals between bare sediment and those under the drifts, with lower abundances under the algae compared to the bare patches ($F_{128}=5.19$, $p=0.22$).

Carbon and nitrogen stable-isotope investigations of the polychaetes and amphipods associated with the drifts suggested that macroalgal detritus entered the food web, and although the process was slow, *Phyllophora* accumulations might serve to dampen the seasonality of food supply providing higher trophic levels with a more constant food source.

11.5 EPIFAUNAL COMMUNITIES

Because of the availability of hard substrates, rock, boulders, pebbles and coarse sediments, extensive growths of macroalgae and sessile particle feeding invertebrates are a feature of the benthos below the region of ice scour. The composition of these communities varies with latitude. The most profuse algal growths are found in the northern part of the Antarctic region, particularly on the islands of the Scotia Arc, while dense multistoried growths of suspension-feeding invertebrates are to be found under the fast ice around the margins of the continent.

11.5.1 Sublittoral Epifaunal Communities in the Weddell Sea

Studies on benthic zonation at Signey Island (Barnes 1995a, 1995b) are among the most comprehensive and detailed that have been carried out in Antarctic waters. Barnes found dense and taxonomically rich communities which, however, varied significantly with substratum type, substratum profile and depth. Algae were generally the largest occupiers of space, but the area of substratum colonized by animal taxa increased with depth, particularly whenever the profile approached vertical. Shallower than 15 m, disturbance effects, largely from ice, restricted the development of the fauna. Bryozoans and, to a lesser extent, sponges were the most abundant animal phyla. From 2 to about 3.5 m, the biota was dominated by various forms of coralline algae (*Hildenbrandia, Lithothamnion*) and macroalgae; animal taxa inclued serpulid polychaetes, cnidarians, ascidians and characteristically early colonizing bryozoans *Celleporella bougainvillei, Inversiula nutrix*, and *Escharoides tridens.* The deeper zone from 4 to about 5.3 m was characterized by bryozoans (especially *Baenia erecta* and *Arachnopusia inchoata*) and sponges. Representative profiles of the faunal distribution are shown in Figure 11.9. Amongst the bryozoans, species with an encrusting growth form occurred at the shallowest depths followed by encrusting massive/-foiaceous species, and at 40 m, the erect flexible forms. Encrusting massive forms were abundant in the shallowest water, followed by erect flexible and than erect rigid forms with increasing depth.

Barnes and Brockingham (2003) investigated benthic faunal abundance, diversity and biomass at Adelaide Island, Antarctic Peninsula. Representative of 16 phyla, 25 classes, 34 orders, and at least 75 species were found. The fauna was rich, especially for a polar location. Faunal abundance increased logarithmically from less than 100 to greater than 10,000 individuals m^{-2} from the intertidal to 35 m. Annelids and bryozoans were the most numerous, and cryptofauna exerted a major influence on both patterns and absolute values of diversity. Subtidal biomass increased from 500 to 10,000 g m^{-2} at 5 to 35 m, respectively, and was, overall, the highest from any polar locality within the 5–40 m depth range. The echinoid *Sterechinus meumayeri* was responsible for these high values, as it dominated the biomass at all subtidal depths, although the limpet *Nacella concinna* were particularly important in the shallows.

11.5.2 Epifaunal Communities in Mcmurdo Sound

The best documented shallow sublittoral benthic epifaunal communities are those found in McMurdo Sound (Dayton et al. 1970, 1974). Here three vertical zones have been described (Figure 11.10): zone I (upper), or the "bare zone" from 0 to 15 m; zone II (intermediate), the "coelenteratehydroid zone" from 15 33 m; and zone III (lower), the "sponge zone" from 33 to 100+m. The upper zone is essentially devoid of sessile animals because of the annual certainty of ice scour by drifting ice and disturbance through anchor ice formation. The intermediate zone is below the limit of ice scour but is still influenced by anchor ice formation. Below 33 m anchor ice does not form, and scouring and other physical disturbances rarely occur. Littlepage (1965) found that at 75 m in McMurdo Sound the mean annual temperature was 1.87°C (SD=0.11), the mean annual salinity 34.7 (SD=0.19), and the dissolved mean annual oxygen concentration 6.79 ml l^{-1} (SD=0.38). Thus the physical environment is a very uniform one.

The substratum in zone I consists of rock, pebbles, and volcanic debris. Zone II has a cobble rocky bottom with coarse sediment between. The substratum below 33 m is a mat of siliceous sponge spicules, which varies in thickness from a few cm to more than 2 m thick. Below the sponge spicule mat, there is usually a layer of bivalve shells (mostly *Limatula hodgstoni*).

The bare zone is briefly colonized during icefree periods by the detritusfeeding echinoid *Sterechinus neumayeri* and

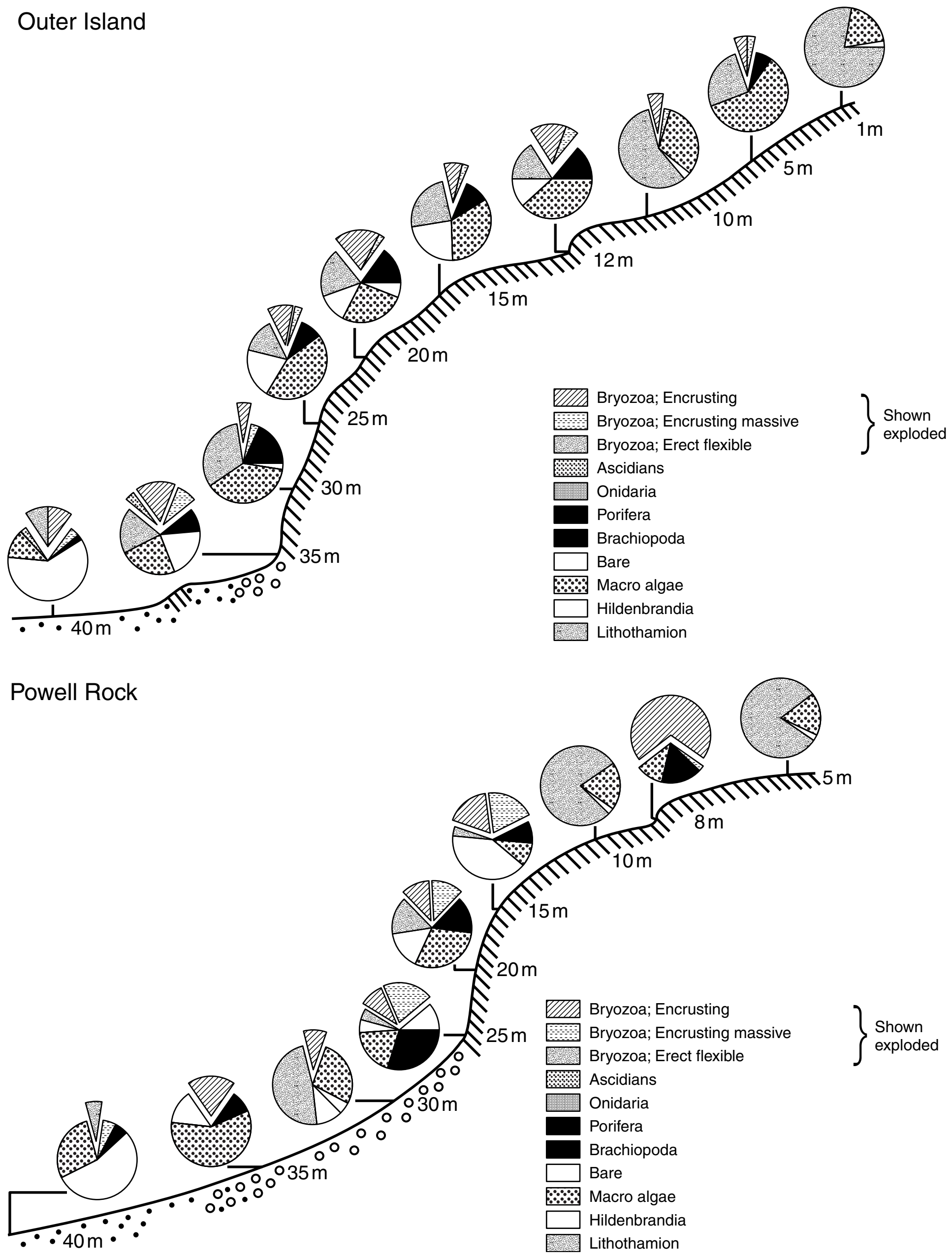


FIGURE 11.9 Substratum profile of transect sites below the ice foot zone on Signy Island, with percent substratum cover by colonizing benthos, represented as pie charts. (Substratum types: *hatching* rock face; *circles* rock/pebble rubble; *dots* sediment. Pie chart data presented as mean of five samples of percentage area of substratum occupied. Sections of each pie representing the Bryozoa is shown exploded.) (From Barnes, D. K. A., *Mar. Biol.,* 121, 457, 1995b. With permission.)

starfish *Odonaster validus*, as well as the nemertine *Lineus corrugatus*, the large isopod *Glyptonotus antarcticus*, a few pycnogonids and fish. In contrast, Zone II is colonized by an abundant fauna of soft corals, anemones, hydroids and ascidians. The alyconarian, *Alcyonium prassleri*, and the anemones, *Artemidactis vitrix, Isotelia antarctica, Urticinopsis antarctica*, and *Hormathia lacunifera* are the largest and most conspicuous sessile components of this zone. The stoloniferan, *Clavularia frankliniana*, and the hydroids, *Tubularia hodgsoni* and *Lampra parvula* grow in discrete patches. There are a few scattered individuals of the hydroid *Halecium arboreum*, and a few clumps of sponges in the lower part of the zone. In most areas the large ascidian, *Cnenidocarpa verrucosa*, is also present. The most conspicuous motile animals in this zone again are *Odonaster, Sterechinus, Lineus*, and the fish *Trematomus bernachii* and *T. centronotus*. The pycogonids, *Thavmastopygnon striata, Colossendeis robusta*, and *C. megalonyx* are also common.

Zone III begins abruptly at 33 m and continues down to at least 180 m. Sponges are the most conspicuous sessile

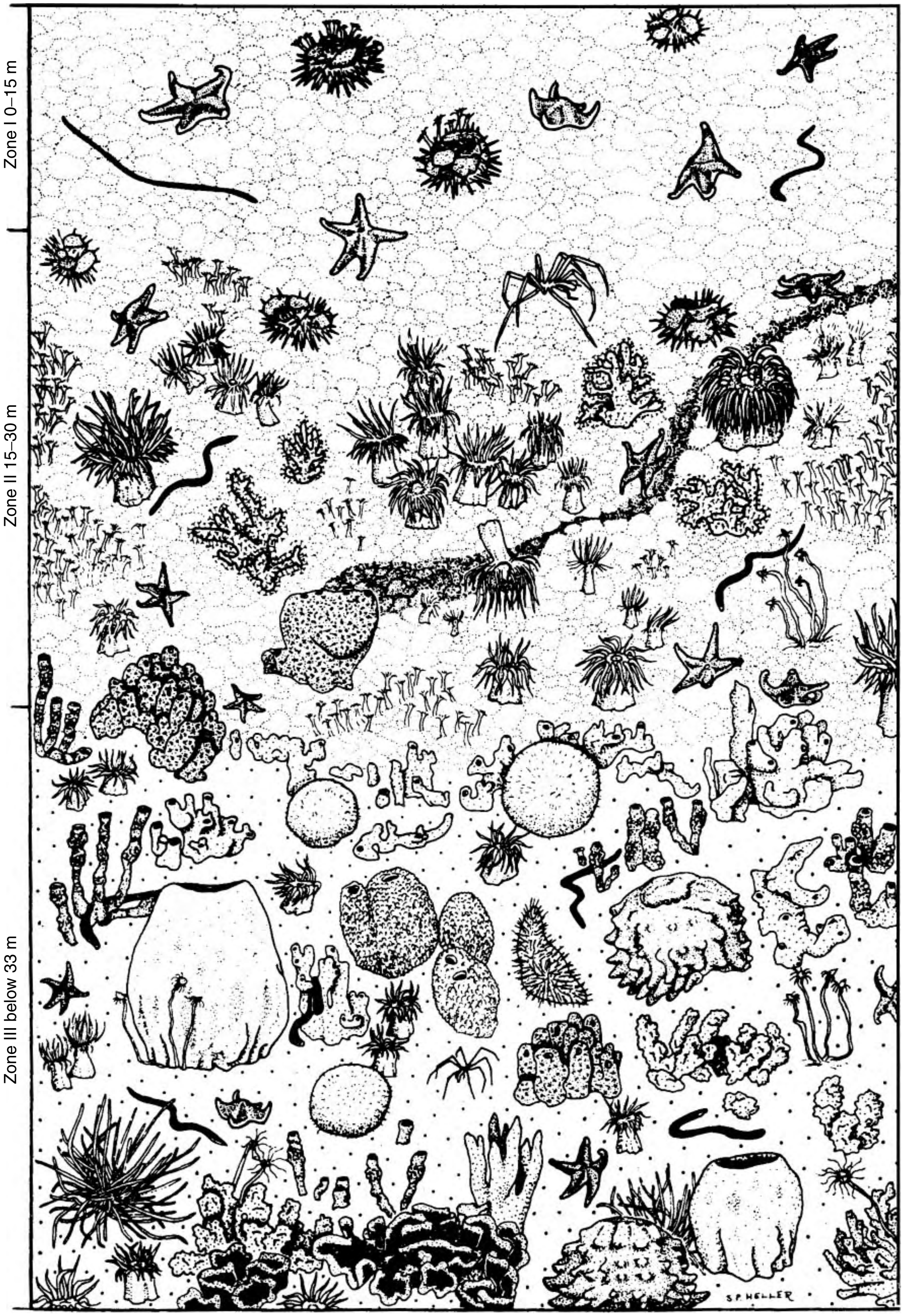


FIGURE 11.10 Vertical zonation of the benthos off the east coast of Ross Island, McMurdo Sound. A few motile animals forage into Zone I, which is otherwise bare of sessile animals. The sessile animals of Zone II are almost exclusively coelenterates, while those of Zone III are predominantly sponges. (From Dayton, P. K., Robilliard, G. A., Paine, R. T., *Antarctic Ecology,* Vol. 2, 244, 1970. With permission.)

TABLE 11.3
Abundance of Sponges at 30–60 m Depth, Cape Armitage, McMurdo Sound, in Terms of Percentage Cover of Benthic Surface and Percentage of Total Biomass

Sponge Species	Percentage Cover	Percentage of Sponge Biomass
Rosella racovitzae	41.8	70.9
Volcano sponge	3.8	18.3
Tetilla leptoderma	3.2	6.7
Cinachyra antarctica	1.2	0.6
Haticlona dancoi	1.1	0.2
Myacale acerata	1.1	2.4
Polymastia invaginata	1.0	0.5
Dendrilla membranosa	0.8	0.08
Gellius tenella	0.6	—
Sphaerotylus antarcticus	0.5	0.3
Leacetta leptorhapsis	0.2	0.04
Gellius benedeni	0.08	—
Calyx arcuarius	0.03	<0.01
Isodictya setifera	0.02	<0.01
Kirkpatrickia variolosa	0.02	<0.01
Kirkpatrickia coulmani	0.01	<0.01
Isodictya erinacea	0.01	<0.01
Pachychalina pedunculata	0.01	<0.01

Total percentage cover of sponges = 55%; byozoans, actinarians, hydroids etc. = 5.4%; free space = 29.1%. Total area surveyed = 410 m^2.

Source: From Dayton, P. K., Robilliard, G. A., Paine, R. T., and Dayton, I. B., *Ecol. Monogr.*, 44, 105, 1974. With permission.

species covering almost 55% of the surface area. These sponges, some of which resemble staghorn corals, large fans, bushes, volcanoes, sheaves, etc., contribute most of the remarkable vertical structure of the community and provide refuges for motile species and attachment sites for a range of sessile animals. Prominent among the 18 species of sponges identified by Dayton et al. (1974) are *Rosella nuda* and *Scolymastra joubini* (white volcano sponges up to 2 m tall and 1.5 m wide), *Rosella racovitzae* (light grey), *Myacale acerata* (slimy, white), *Polymastia invaginata* (grey cone sponge), *Cinachyra antarctica* (grey spiky sponge), *Tetilla leptoderma* (white basketball sponge) and *Haliclona dancoi* (white finger sponge). Table 11.3 lists the abundance of the sponges in terms of percent cover of the benthic surface and percent biomass.

In addition to the sponges, the most conspicuous epibenthic sessile species are the anemones *Stompia selaginella, Artemidactis vitrix, Isotelia antarctica, Hormantha lacunifera*, and a few individuals of *Urticinopsis antarcticus*, the alcyonarium *Alcyonium paessleri*, the hydroids *Lampra paevula, L. microrhiza, Halecium arboreum, Tubularia hogsoni* and many other unidentified hydroids, a few sabellid polychaetes, some bryozoans, especially *Hippadenella carsonae, Terepora frigida*, and *Caberea darwinii*, some ascidians, especially *Cnemidocarpa verrucosa*, the pterobranch *Cephalodiscus antarcticus*, and many molluscs. The most abundant mollusc is the bivalve *Limatula hodgsoni*. Within the sponge spicule mat, there is a rich infauna for which Dearborn (1967) recorded more than 12,500 individuals representing an unspecified number of species per cubic decimetre.

The asteriods *Perknaster fuscus antarcticus, Acondonaster conspicuus, A. hodgsoni, Odonaster meridiionalis*, and *O. validus* and the dorid nudibranch *Austrodoris mcmurdensis* are the most conspicuous predators on sponges. Several other nudibranchs prey on stoloniferans and hydroids. Hydroids and actinians are also eaten by pycogonids. The bivalve *Limatula hodgsoni* is consumed by the asteroids *Diplasteras brucei* and *O. valadus*, and the gastropod *Trophon langstaffi*. The sea urchin *Sterechinus neumayeri*, and especially *O. validus*, are conspicuous detritus feeders, while *O. valadus* and the nemertine *Lineus corrugatus* are efficient scavengers. The actinian *Urticinopsis antarcticus* is an efficient predator of echinoderms and medusae.

Faunal distributions similar to those outlined above have been described from many localities round the Antarcic Continent; e.g., by Watanabe et al. (1982) and Hamada et al. (1986) from the coast off Syowa Station. Propp (1970) has described the shallow water benthos at the Halswell Islands in East Antarctica. He identified an upper zone (2–10 m) with a community of diatoms, the dominant species belonging to the genera *Pleurosigma, Fragilariopsis, Amphiprora, Achantes* and *Nitzchia*, the asteroid *Odonaster validus* and the hydroid *Tubularia ralphy*. A second zone (6–25 m) was dominated by the red alga *Phyllopora antarctica*, calcareous algae, and the sea urchin *Sterechinus neumayeri*. Both of the above zones were subject to anchor ice formation. From 25 to 30 m a third zone dominated by the alcyonarian *Eurephthya* sp. had a varied fauna of some 70–80 species. Below 30 m, sponges *Rosella racovitzae* and *Stolymastra joubini*, the hydroid *Oswaldella antarctica* and ascidians dominated the community. It would appear that with some regional variation the shallow water benthic communities are similar right round the Antarctic Continent.

Starmans et al. (1999) have described what they call mega-epibenthic communities on the shelf areas of the Amudsen and Bellinghausen Seas and the Weddell Sea (Figure 11.10). It can be seen that there are substantial differences in the overall proportions of the dominant higher taxa. Sponges dominated in the Weddell Sea; whereas, in the Amunsden and Bellingshausen Seas they were a minor component in a community dominated by Anthozoa, Bryozoa, and Echinodermata. Assemblages of suspension-feeders dominated by sponges and bryozoans were prevalent on the shelf of the eastern Weddell Sea, but were almost absent in the Bellingshausen and Amundsen Seas. Numbers of taxa and abundances were highest in the Weddell Sea. Some were strongly dominated by a single taxa (e.g., the sponges *Rosella racovtzae, R. antarctica* and *Stylocordyla borealis*). Similar Arctic communities are dominated by echinoderms and lack the bryozoans found

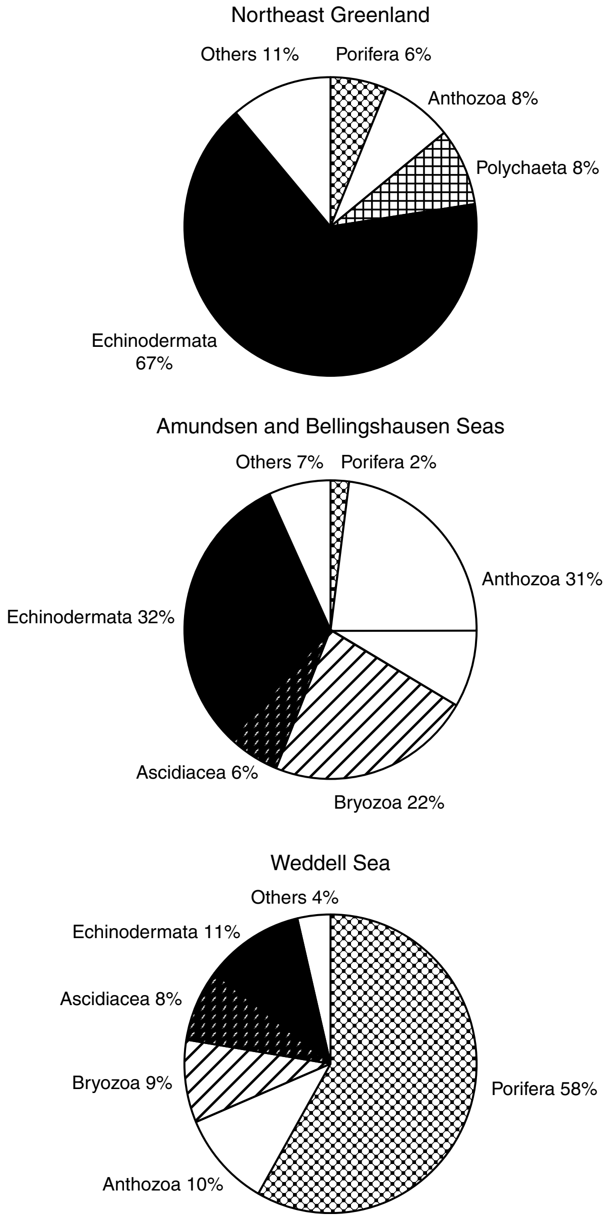


FIGURE 11.11 Overall proportions of the dominant higher taxa for the three areas investigated. (From Starmans, A., Gutt, J., Arntz, W. E., *Polar Biol.,* 135, 276. With permission.)

in Antarctic communities, while Anthozoans and sponges are poorly represented (Figure 11.11).

11.5.3 Epifaunal Community Dynamics

There are only a limited number of studies of the dynamics of the shallow water epifaunal communities. The most comprehensive and detailed study is that of Dayton and his coworkers (Dayton et al. 1970, 1974; Dayton and Oliver 1977; Dayton 1979; Oliver et al. 1982; Oliver and Slattery 1985) on the biological interactions in the complex epifaunal community along the coast of Ross Island, McMurdo Sound. In their investigations, they concentrated on the role played by competition and predation in this community living in a physically constant environment. The composition of the community has been described above.

Dayton et al. (1974) studied the relative growth rates of the dominant sponges and the feeding rates of their predators, using cages to exclude predators and observing the predator's feeding rates by SCUBA diving. Field experiments demonstrated that, with the exception of *Myacale acerata*, the growth rates of the sponges were too low to measure in one year. *Myacale*, however, was observed to increase its mass by as much as 67%. Because of its rapid growth rates, *Myacale* appears to be the potential dominant in competition for substratum space, the resource potentially limiting to sessile species. This conclusion was supported by observations of *Myacale* growing over and, in some cases, apparently having smothered other sessile species representing at least three phyla (other sponges, such as "Volcano" sponge, *Rosella racovitzae*, *Haliclona dancoi*, *Polymastia invaginata*, *Kirkpatrickia variolosa*, and *Calyx acurarius*; the anemones *Hormathia lucinifera* and *Artmidactis vivtrix*; and the solitary ascidian *Cnemidocarpa verrucosa).*

The densities, percent feeding, dietary composition, and energy consumption was determined for the sponge predators. The predator populations tended to be characterized by low densities and broad diets. Table 11.4 lists the annual effects of the predators on their sponge prey. Of the predators listed, *Odonaster validus* spent less than 30% of its feeding time consuming sponges, and the balance of its diet consisted of molluscs, hydroids, bryozoans and detritus. The data from the field survey and the energetics studies suggested that *Myacale* is prevented from dominating the space resource by the predation of two asteroid species, *Perknaster fuscus* and *Acandaster inconspicuous*. Adult *Perknaster* is the dominant predator or on *Myacale*, and the sponges provides a small proportion of the diet of *A. inconspicuous*. The latter species and the dorid nudibranch *Austrodoris mcmurdensis* were the most important predators on three species of rosellid sponges (*Rosella racovitzae*, *R. nuda*, and *Scolymastra joubeni*). Despite the relatively high consumption of sponges by their predators, and despite the fact that none of the sponges has a refuge during growth from potential mortality from *A. inconspicuous,* very large standing crops of the rosellid sponges accumulate.

Dayton et al. (1974) consider that the McMurdo Sound epibenthic community, similar to other marine epibenthic communities, is structured by biological interactions, especially predatorprey interactions. Selective predation tends to counter the more effective growth and greater competitive abilities of *Myacale acerata*. Thus this community of organisms in a physically stable environment can be considered to be "biologically accommodated" in a similar manner to deep sea communities where the physical environment is stable, and in which there is an increasingly significant role for interspecific competition along a gradient of decreasing physical stress (Sanders 1969, 1979).

TABLE 11.4

Estimated Annual Effects of Predators on their Sponge Prey in the McMurdo Sound Epibenthic Community Standing Crop (Biomass) of Sponges in Terms of kcal 100 m^{-2} and Year's Supply of the Sponge Species to Predators

Predator Species	**Density (no. 100 m^{-2})**	***Rosella racavitzae***	**Volcano spange**	***Tetilla lepto-derma***	***Haliclona dancai***	***Myacale aceria***	***Polymastia invagiuata***	***Gellius tenella***	***Calyx acurarius***	***Isodictya setifera***	***Kirkpa-trickia variolosa***	***Pachychalina pedunculata***
Odonaster meridionalls	12.8	4.39	2.55		0.23	2.07	5.55	0.46	0.93	1.16		0.23
Odonaster validus	267	75.14	42.25	134.91								
Acodonaster conspicuous	5.6	96.51	344.53	358.06	75.76	20.74					7.22	
Acodonaster hodgsoni	0.3	0.88			1.74			0.83	1.74			
Perknaster fuscus antarcticus (adult)	1.0		1.21	1.21		48.01						
Perknaster fuscus antarcticus (juvenile)	±10			1.24	1.24	3.72	1.24			1.24		
Austrodoris mcmurdensis	3.3	23.22	19.81	1.03	2.44		0.70	2.11	4.49	0.32		
Total		200.14	410.35	496.45	81.41	74.54	7.49	3.4	7.16	1.48	8.46	0.23
kcal 100 m^{-2}		277398	128629	80698	1667	6141[a]	5532	Not known	15	12	66	12
No. of year's supply to predators		1286	311	163	20	82[b]	739	Not known	2	8	9	30

[a] kcal useful to predators; this figure is 51.8% of the kcal m^{-2} as determined by bomb calorimetry since 48.2% of the dry weight of *Mycale acerata* is sponging, which is not consumed by the predators but which contributes to the calorific value as determined by bomb calorimetry.

[b] Also corrected for the presence of sponging.

Source: From Dayton, P. K., Robilliard, G. A., Paine, R. T., and Dayton, I. B., *Ecol. Monogr.*, 44, 105, 1974. With permission.

11.6 INFAUNAL COMMUNITIES

Only recently has the community structure of Antarctic soft bottom communities received attention. There are now a number of quantitative studies of the soft bottom macrobenthos at a range of localities around the continent, including Arthur Harbour, Anvers Island (Lowry 1969, 1975, 1976; Richardson 1972; Richardson and Hedgpeth 1977); Admiralty Bay, King George Island (Arnaud et al., 1986; Jazdzewski et al., 1986); Potter Cove, King George Island (Kowalke and Abele 1998); Maxwell Bay, King George Island (Ahn and Kang 1991); Chile Bay and Foster Bay, South Shetland Islands (Gallardo and Castilla 1970, 1970; Gallardo et al. 1977; Larrian 1981; Retamal et al. 1982; Gallardo 1988); Signey Island, South Orkney Islands (Hardy 1972; White and Robins 1972); King Edward Cove, South Georgia (Platt 1980); McMurdo Sound (Dayton and Oliver 1977) and Mowbry Bay, Cape Hallett and Cape Bird, Ross Island (Lowry 1976); Terra Nova Bay (Gambi et al. 1994; Cattaneo-Vietti et al. 1998); and the Ross Sea (Gambi and Bussotti 1999). These studies have shown that the soft substrates are generally characterized by a high density, diversity and biomass of polychaetes, molluscs, and crustaceans.

11.6.1 Distribution Patterns

Table 11.5 compares the data on species diversity, density and faunal composition from three studies in Arthur Harbour, Cape Hallett, and Cape Bird. At depths of 26–40 m in Arthur Harbour (68° 48″S, 64° 06″W), Lowry (1969, 1976) recorded 64 species with a mean density of 3001 individuals m^{-2}. The dominant species were the tube-building peracarid crustaceans *Ampelisca baureri* and *Gammaropsis* (*Megamohorus*) sp., and the burrowing polychaete *Aspitobranchus*. Other important species were the pericarids *Eudorella* sp. and *Harpina* sp., the oligochaete *Torodrilus lowryi* (11% of the individuals in the yearly population), and the polychaetes *Haploscoloplos kerguelensis*, *Paraonis gracilis*, and *Capitella peramata*. The dominant groups were the peracarids and the polychaetes, which together made up 88% of the population (Table 11.5). Although bivalves made up 10% of the species, they constitute only 2% of the individuals, most of which represented the conspicuous protobranch *Yoldia eightsi*.

In a more wide-ranging survey in Arthur Harbour, sampling in depths from 5 to 700 m, Richardson and Hedgpeth (1977) recorded 282 taxa with densities (retained on a 0.5-mm screen) ranging from 2891 to 86,514 individuals m^{-2}, with an overall mean of 35,668 m^{-2}. The numbers retained on a 1.0-mm screen ranged from 1,317 to 43,267 individuals m^{-2}, with an overall mean of 16,426 m^{-2}. The latter values are four times greater than those reported by Wigley and McIntyre (1964) for the inner continental shelf off New England, and five times greater than those reported by Gallardo et al. (1977) for Discovery Bay, Greenwich Island. Richardson and Hedgpeth attributed the high macrofaunal densities to high productivity, physical stability, and increasing organic input with depth.

In Mowbry Bay, Cape Hallett (72°18″ S, 170°12″E) in depths of 104–250 m, Lowry (1976) recorded 147 species with a mean density of 3102 individuals m^{-2} (similar to that in Arthur Harbour). The most important species were the sedentary polychaetes *Spiophanes tcherniai* and *Perkinsiana antarctica*. Other important species were the eulamellibranch *Thyasira bongraini*, the sedentary polychaetes *Leonice cirrata, Neosabellides elongatus*, and *Maldane sarsi*, the tubificid oligochaete *Torodrillus lowryi*, and the foraminiferan *Pelosina* sp. In the shallower samples (104 and 134 m)

TABLE 11.5
Species Diversity, Density and the Percentage Composition of the Crustacean, Polycheate, and Bivalve Components of the Benthic Infaunal Communities from Various Antarctic Localities Compared with Selected Sub-Antarctic and Temperate Localities

Locality	Latitude (°S)	Number of Species	Mean Density (no. m^{-2})	Composition of Population (% of total)		
				Crustacean	Polychaeta	Mollusca
Stewart Island (Lowry, 1976)	43°	107	2965	9.0	41.0	45.0
Auckland Islands (Lowry, 1976)	50°	83	47122	20.0	51.0	27.0
Port Foster (Larrain, 1981)	62°	43	9074	83.7	13.4	1.4
Chile Bay (Larrian, 1981)	62°	65	996	10.0	66.0	8.0
Arthur Harbour (Lowry, 1976)	64°	64	7502	53.0	35.0	2.0
Cape Hallett (Lowry, 1976)	72°18′	147	7755	25.0	50.0	5.0
Cape Bird (Lowry, 1976)	77°13′	72	34024	39.0	39.0	0.5
McMurdo sound, west (Dayton and Oliver, 1977)	77°45′	—	4087	17.2	68.8	4.4
McMurdo sound, east (Dayton and Oliver, 1977)	77°45′	—	140021	17.7	16.5	1.9

the most common species, along with *S. tcherniai* and *P. antarctica*, were the polychaetes *N. elongatus* and *Myxicola* sp., and the peracarids *Leaun antarctica*, *Orchomene franklini*, *Metaphoxus* sp., *Leptognathia antarctica*, and *Neoxenodice cryophile*. In the deeper samples (208 and 250 m), the eulamellibranch *T. brongraini* and the oligochaete *T. lowryi* became more conspicuous. Polychaetes and peracarids dominated the community, with peracarids making up 42% of the total number of species and one quarter of the individuals. Polychaetes made up another third of the species and half the population. Bivalves were relatively insignificant.

Although there were less than half the number of species (72) in the Cape Bird (77°13″ S, 166°26″ E) samples (35–54 m depth), as in the samples from Cape Hallett, the sampled population was over ten times larger (34,024 individuals m^{-2}). The dominant species were the myodocopid ostracod *Philomedes heptathrix*, the burrowing anemone *Edwardsia* sp., and the tube-building polychaete *Spiophanes tcherniai*. These three species together made up 70% of the population sampled. The peracarid *Nototanais dimorphus* and an Archinaellid sp. were also well distributed and abundant. Other relatively abundant species occurring in all samples included the isopods *Austrosignum glaciale* and *A. grande*, the cumacean *Eudorella splendida*, and the amphipods *Heterophoxux videns* and *Orchomene franklini*. Aside from *S. tcherniai* and the Archianellid sp., other annelids well represented in the samples included the sedentary polychaetes *Tharyx* sp. and *Haploscoloplos kerguelensis* and the oligochaete *Torodrilus lowryi*. At Cape Bird the structure of the major component groups differed from that of the other areas studied by Lowry (1976). Peracarids and myodocopids formed a crustacean component that together accounted for 39% of the population. Together with the polychaete component they comprised 78% of the individuals. If the burrowing anemone is included, then the total is 97% of the individuals. Bivalves were an insignificant component, and together with the nematodes, sipunculids, gastropods and asteroid and ophiuroid echinoderms, they made up the remaining 3% of the population. In Table 11.5 the data from the three studies discussed above is compared with that from other selected Antarctic, Subantarctic, and temperate localities.

Dayton and Oliver (1977) have shown that the soft bottom benthos of the east and west sides of McMurdo Sound are characterized by diagrammatically different assemblages (see Chapter 12 for a discussion of the

TABLE 11.6
Number of Organisms per Square Metre of Different Taxa from Various Localities in the Ross Sea and Urdo Sound (Depths of the Various Studies are Given in Brackets). Bers, with Percentages in Brackets

		McMurdo Sound						
		West Sound				East Sound		
	Ross Sea (74°58′S, 170°48′E) (500 m)	Garwood Valley (30 m)	Ferrar Galcier (30 m)	New Harbour (30–40 m)	Marble Point (30 m)	McMurdo Station Jetty (20 m)	Cape Armitage Soft Bottom (20 m)	Cape Armitage Sponge Spicule Mat (30 m)
Ostracods	70	18	110	132	6586	948	55	4354
Cumacea	40	55	367	885	2150	31548	12950	937
Tanidacea	25	73	239	282	579	19932	53512	69596
Isopoda	43	18	110	132	1185	23392	19339	33285
Amphipoda	56	184	294	207	3059	11728	9975	8432
Other Arthropoda	214 (10.9)	348 (15.9)	1120 (18.5)	1638 (16.3)	13559 (29.9)	87548 (73.7)	95891 (61.6)	116604 (79.9)
Total Arthropoda	16	55	37	55	55	0	496	6282
Total Mollusca	230 (11.7)	403 (18.4)	1057 (19.2)	1693 (16.8)	13614 (30.0)	87548 (73.7)	96387 (61.9)	122886 (84.3)
Polychaeta	560 (28.5)	128 (5.8)	184 (3.0)	1102 (10.9)	184 (0.4)	136 (0.1)	770 (0.5)	7660 (5.2)
Other Vermes	1070 (54.6)	1598 (73.1)	3896 (64.6)	4718 (47.0)	27142 (59.9)	11276 (9.5)	52143 (33.5)	9500 (6.5)
Total Vermes	70	55	147	2060	3913	19752	6281	5735
Echinodermata	1140 (58.1)	1653 (75.6)	4043 (67.0)	6778 (67.5)	31055 (68.5)	31028 (26.1)	58415 (37.5)	15235
Miscellaneous	8 (0.4)	0	0	0	0	0	0	0
Total	2	0	643	463	441	0	0	0
Number of samples	1960	2184	6027	10036	45294	118712	155572	145781

E Category “other vermes” refers to all other soft-bodies worms such as Memerteu. Edwardsia, Phoronidae and Oligochaeta.

Source: From Dayton, P. K. and Oliver, J. S., *Science* 197:55–58, 1997. With permission.

reasons for these differences). Data from this study is given in Table 11.6. A deepwater station in the Ross Sea is included for comparison. The most obvious trend in the Table 11.6 is the difference of an order of magnitude in the faunal densities between the east and west sides of the Sound, a difference that is particularly evident in the crustacean densities. Molluscs are poorly represented in the samples and almost all of the bivalves recorded were recently settled and metamorphosed pectens, *Adamusium colbecki*. Another trend is the southtonorth gradient along the coast of the West Sound. The standing crops of the benthic organism at the southerly sites in the West Sound are similar to those of the deep shelf and bathyal habitats. Due to the small size of the sample used, species living on the surface of the sediments, such as adult pectens and ophiuroids (*Ophionereis victoriae*) were not sampled. Dayton and Oliver (1977) note that at New Harbour the latter species occurs at a relatively constant density of 1.7 m^{-2}. In the East Sound the recorded densities are among the highest recorded in the world's oceans.

Kowalke and Abele (1998) found that the soft bottom Potter Cove was dominated by pericarid crustaceans (41%), small bivalves (22%), polychaetes (27%), priapulids (4%), and coelenterates (5%) (Figure 11.12). The mean density was 4,202 ind. m^{-2}, showing a decrease from 7,233 ind. m^{-2} in 10 m depth to 1,779 ind. m^{-2} in 50 m depth. Below 20 m, individual numbers of all taxa decreased sharply with the exception of polychaetes. A replacement of bivalves by polychaetes with increasing water depth is a general trend that has previously been observed by Hardy (1972) at Signy Island and by Gallardo et al. (1977) at Greenwich Island and Jazdzewski et al. (1986) at King George Island. The species in the upper zone were usually mobile, such as the amphipods and some polychaetes, fast growing species like the pennatularians, or small bivalves such as *Yoldia eightsii*. This zone experiences strong ice impact during the summer months. On the other hand, some ice growlers can disturb epi- and infaunal communities down to 15 m resulting in a rich food source of dead and decaying organisms for scavengers such as amphipods. The largely undisturbed zone below 20 m was dominated by solitary ascidians. However, pericarid crustaceans, mainly amphipods and cumaceans, occurred in reduced numbers below 20 m.

The mean annual density of 4202 ind. m^{-2} was much higher than that found by Ahn and Kang in the adjacent Marion Cove. These authors found a mean density of 190 ind. m^{-2} using the same mesh size of 1 mm^2. Jazdzewski et al. (1986), using a 0.5 mm^2 mesh, found approximately 12,000 ind. m^{-2} in 15 m and ca. 5,000 ind. m^{-2} in Ezcurra Inlet, Admiralty Bay.

Gambi and Bussott (1999) investigated the soft bottom macrobenthos at 3 localities in the Ross Sea located at 810 m (74°41″ S, site A), 500 m (74°00″ S, site B) and 450 m (72°30″ S, site C). Sites A and B were characterized by biogenic mud and clay sediments, while Site C featured sandy sediments mixed with a conspicuous biogenic component characterized by shells and tests of calcareous invertebrates (mainly barnacles). The macrofauna of sites A and B was mainly composed of infaunal polychaetes and bivalves. The assemblages comprised both surface and subsurface deposit feeders, including some conveyer-belt polychaetes (Maldanidae and Capitellidae) that were responsible for high sediment mixing and bioturbation. The macrobenthos of site C was dominated by crustaceans, polychaetes, and echinoderms (ophiuroids), and mainly by filter feeders and epifaunal or interstitial forms. Abundances were higher (up to 1,400 ind. m^{-2}) at site B than at sites A and C (430 and 516 ind. m^{-2}, respectively). At sites A and B the benthos was mainly concentrated in the upper 5 cm of the sediment, and abundances declined sharply in the deeper sediment layers. Sites A and B represented areas where the organic input to the sea floor by sedimentation from the upper water column is high. The community at site C probably is physically controlled by frequent disturbance events (e.g., bottom turbid currents, sediment reworking, and displacement).

Sponge Spicule Mats. Sponge spicule mats are a conspicuous feature of the sea bed between 80 and 120 m in McMurdo Sound (Dayton et al. 1970; Battershill 1989) and Terra Nova Bay (Cattaneo-Vietti et al. 1998) and elsewhere in coastal Antarctica where epifaunal assemblages of filter feeders dominated by sponges occur. Sponge siliceous spicules, especially those of hexactinellids, take a long time to dissolve and can form mats up to 1.5 m thick. At Cape Armitage, Ross Island, these are composed mainly of *Cinachyra antarctica* spicules (Battershill 1989), while the thick spicule mats described from deeper waters by Dayton (1974) are built up by an accumulation of spicules coming from many sponge species. At Terra Nova Bay, spicule mats are formed by hexactinellid spicules, particularly from *Rosella* sp. Chl *a* and invertebrate biomass and species richness values are higher in areas rich in spicules (Dayton 1974). The sponge spicules create a three-dimensional substratum on which a larger diatom population can develop. This supports a rich associated fauna as observed by Dearborn (1967) in McMurdo Sound. This is enhanced by the opal spicule capacity of conveying light as natural optical fibres (Cattaneo-Vietti et al. 1996).

11.6.2 INFAUNAL COMMUNITY DYNAMICS

From the data given in Table 11.5 and discussed in the previous section, a number of trends can be detected. Infaunal densities appear to be related to latitude, generally increasing with higher latitudes. Such increases appear to be related to the input of microalgal production to the benthos. Dayton et al. (1986) have shown that in the shallow waters of McMurdo Sound, the benthic microalgal production is important in such inputs, and may be important in explaining the differences in infaunal biomasses between the east and west sides of the Sound. There are also significant differences in the community composition of Antarctic, shallow water

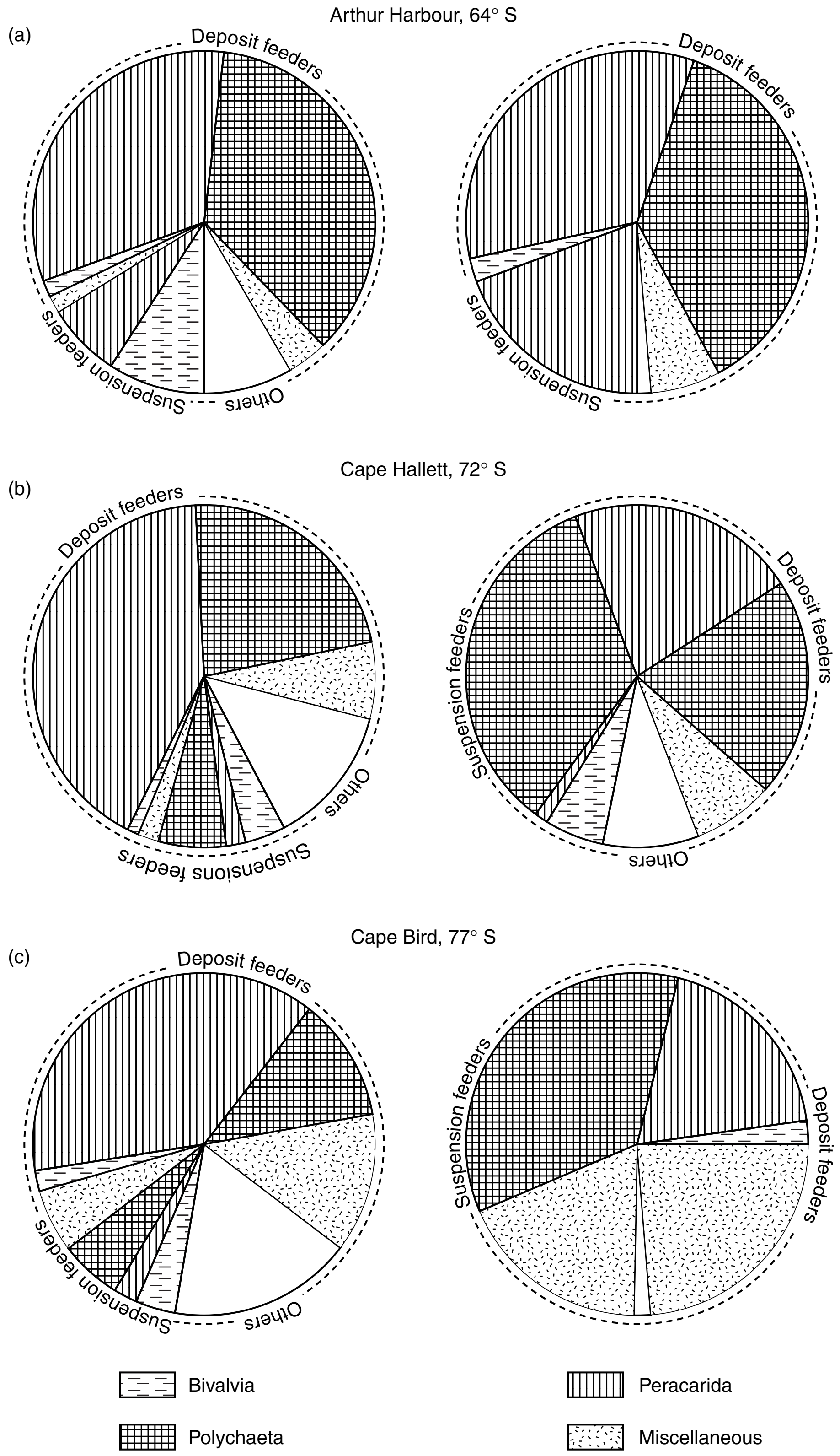


FIGURE 11.12 Trophic structure of: (a) the deposit-feeding community in Arthur Harbour, Anvers Island; (b) the mixed suspension-deposit-feeding community in Moubray Bay, Cape Hallett, Ross Sea; and (c) the suspension-feeding community at Cape Bird, Ross Island. (From Lowry, J. K., Ph.D. diss., University of Canterbury, 1976. With permission.)

soft bottom communities when compared with those of temperate and tropical waters.

Lowry (1976) has compared species diversity, trophic structure and species composition of the soft bottom benthos in a latitudinal transect between 47 and 77°S. A comparison of the species diversity of the macrobenthic communities along the latitudinal gradient showed no correlation between diversity of the macrobenthos and latitude. Macrobenthic communities with the highest species diversity occurred at Cape Hallett (72°S), Port Pegasus, and Stewart Island (47°S). These communities have very similar mixed suspension, deposit-feeding structure. They occur on silty-sand to sandy-silt bottoms. The macrobenthic communities with intermediate density are found in Arthur Harbour (64°S) and Perserverence Harbour, Campbell Islands (52°S), and both occur on sandymud bottoms and have a deposit-feeding structure. The macrobenthic communities with the lowest diversity occur at the Auckland Islands (50°S), and at Cape Bird (77°S), and both are found on predominantly sandy bottoms.

The proportion of suspension-feeding and deposit-feeding animals at Cape Hallett was 41 and 50%, respectively, (Figure 11.12). These mixed suspension, deposit-feeding communities have high species diversity due in part to the fact that communities with mixed trophic structure provide more niches, and thereby support more different kinds of benthic animals than other macrobenthic communities. In contrast to similar communities in temperate waters, e.g., Port Pegasus, Stewart Island, where bivalves constitute some 45% of the individuals, bivalves make up only 5% of the population. Polychaetes made up 32% of the species and 50% of the individuals. Sabellid and spionid polychaetes were the dominant suspension-feeders. Peracarids were a significant proportion of the deposit-feeding component.

In Arthur Harbour the proportion of suspension and deposit-feeders in the population was 22 and 74%, respectively, (Figure 11.12). Bivalves were an insignificant component comprising 11% of the species and only 2% of the individuals. The suspension-feeding component is dominated by the ampeliscid amphipod (*Gammaropsis (Megamphopsis*) sp.). Among the peracarid, amphipods were the most diverse group.

The community with the lowest diversity was that at Cape Bird in which suspension-feeders comprised 54% of the individuals. Bivalves represented 22% of the species but only 1% of the population. Polychaetes comprised 33% of the suspension-feeding species and 64% of the individuals. The dominant species was the spionid *Spiophanes tcherniai*. The densely packed tubes of *Spiophanes* trap and stabilize the sediment, providing a sustrate for surface deposit-feeders. The most abundant suspension-feeder was the actinarian *Edwardsia* that makes up 35% of the suspension-feeding individuals. Amongst the polychaetes the only actively burrowing polychaete was *Haploscoloplos kerguelensis*, while the most abundant species were the surface deposit-feeding maldanids and cirratulids. Peracarids made up a significant proportion of the deposit-feeders, while ostracods, particularly *Philomedes heptathrix*, are the most abundant deposit-feeders making up over 50% of the deposit-feeding population. Deposit-feeding pericarids included the tanaidacean *Nototanais dimorphus*, and the cumaceans *Diastylis helleri* and *Eudorella splendida*, the isopod *Austrosignum glaciale* and the amphipods *Heterophoxus videns*, *Orchomene frankini* and *Gammaropsis longicornis*.

Figure 11.12 shows that in the shallow coastal waters between southern New Zealand and McMurdo Sound, the major components were the Bivalvia, Peracarida, and Polychaeta. The percentage composition of the bivalve molluscan species on the Campbell Plateau remained fairly constant between 11 and 14% from southern Stewart Island to Campbell Island. South of the Antarctic Convergence, the percentage composition decreased from 10% of the infaunal benthos at Anvers Island to about 5% along the Victoria Land coast. Peracarid crustaceans formed a mirror image of the bivalve distribution, and always made up a larger proportion of the shallow water benthos than the bivalves. The percentage composition of the peracarid species was fairly constant from 14% of the benthos at Stewart Island to 31% at Campbell Island. There was an increase in the percentage composition of peracarids south of the Antarctic Convergence. At Anvers Island the peracarid component comprised 41% of the benthos and along the Victoria Land coast the range was 35–41%. The polychaetes showed a slightly decreasing percentage composition from 41% of the benthos at Port Pegasus, Stewart Island to 31% in McMurdo Sound, Ross Sea. There was no significant change across the Antarctic Convergence.

Oliver et al. (1982) and Oliver and Slattery (1985) have drawn attention to the effects of small crustacean predators on the species composition and population structure of softbodied infauna in the shallow waters of McMurdo Sound. The macrofaunal density at their study site (20 m) varied from 90,000 to 150,000 individuals m^{-2}. The assemblage was dominated by eleven species that maintained populations of over 2,000 individuals m^{-2} (Table 11.7). Most of the larger species were tube dwellers with 30–50% of the sediment volume and weight made up of their tubes. The dense assemblage was divided into three faunal guilds with similar ecological characteristics: canopy species (the suspension-feeders *Edwardsia* and *Spiophanes*); understory species; motile species living in the top 0–1 cm of the sediment (deposit-feeders and predators, including the crustaceans *Heterophoxus, Monoculodes, Nototanais, Austrosignum* and *Eudorella*, and the protozoan *Gromia*); and subsurface species (mainly polychaetes, *Tharyx, Haploscoloplos, Axiothella*, and *Maldane*).

Oliver and Slattery (1985) postulated that the tanaid (*Nototanias*) and especially the phoxocephalid amphipod (*Heterophoxus*) regulated the species composition and population size of the softbodied infauna (primarily the polychaetes) by preying on small species and small individuals of large species. Small individuals of these larger species were rare in the community. Evidence for their regulatory role came from: the gut contents; from laboratory experiments where the crustaceans consumed spionid larvae

TABLE 11.7
Abundant Members of the Benthis Infaunal Assemblage Near McMurdo Station Jetty, Cape Armitage, McMurdo Sound. Means and Standard Deviations in 12 Cores

Organism	Functional Group	Number 0.018 m^{-2}	Number m^{-2}
Polychaetes			
Myriochele cf. *herri*	t	379±208	21224
Spiophanes tcherniai	t	64±48	3584
Tharyx sp.	m	40±19	2240
Axiothella sp.	t	14±9	784
Maldane sp.	t	15±14	840
Haploscoloplos kerguelensis	m	8±4	448
Crustaceans			
Austrosignum grandis I	m	519±191	29064
Nototanais dimorphus T	t	310±114	17360
Heterophoxus videns A	m	114±32	6367
Eudorella splendida C	m	95±49	5342
Monoculodes scabriculosus A	m	65±41	3627
Others			
Edwardsia meridionalis	sb	268±84	15012
Gromia sp.	m	87±30	4877
Oligochaeta	m	86±89	4826
Total individuals		2064±978	115595

I, isopod; A, amphipod; T, tanaid; C, cumacean; t, tube; sb, sedentary burrow; m, mobile.

Source: From Oliver, J. S. and Slattery, P. N., *Ophelia*, 24, 155, 1985. With permission.

or juveniles, and small polychaete species; from field experiments where the abundances of crustaceans and small polychaetes were negatively correlated after the colonization of defaunated sediments; from experiments demonstrating that depth in the sediment provided a refuge from predation; and from community patterns along a gradient in water depth where the abundance of the crustaceans was negatively correlated with the abundance of small species and individuals of the larger polychaete species. Because most of the softbodied species have a size refuge from the crustaceans, the dense assemblage was dominated by large and longlived forms.

Interspecific competition is thought to be the major biological process that structures benthic communities in physically constant environments (Sanders 1969, 1979; Grassle and Sanders 1973). Even when predators are ascribed an important community role, it is by virtue of preying on competitive dominants and, thus, mediating the effects of interspecific competition (Dayton and Hessler 1972; Dayton et al. 1974). However, the results of the study by Oliver and Slattery (1985) strongly support the primary role of predators that prey on the young of many species. The dense infaunal communities in the shallow water of Antarctica have evolved in the absence of bottomfeeding mammals comparable to the walrus and grey whale (Ridgeway and Harrison 1981; Gaskin 1982; Oliver et al. 1983), and essentially no flatfish, skates, rays, or other disruptive demersal fish (DeWitt 1971). Their persistence is due to the absence of such disruptive species.

The population densities of the three dominant groups (molluscs, polychaetes, and crustaceans) show trends similar to the species composition, but even more pronounced. Bivalves drop from the most abundant group in the benthos of southern New Zealand with 39% of the population to an insignificant group, making up only 4% of the population at Campbell Island. Below the Antarctic Convergence, they never make up more than 6% of the benthos, and in McMurdo Sound they make up only one percent of the population.

The peracarid population shows the largest fluctuations among the three groups. From only 16% in Port Pegasus, they increase to make up 21% of the Auckland Islands population, and 43% of that at Campbell Island. Even though the peracarids maintain the highest proportion of the macrobenthic species on the Antarctic shelf, their proportion of the population decreases sharply from a high of 50% in Arthur Harbour to a low of 16% at Cape Bird. At Cape Bird the peracarids appear to be in direct competition with the equally successful, though less diverse, ostracods. If the ostracods are included along with the peracarids, then the crustacean and polychaetes are equally abundant at Cape Bird, each with 40% of the macrobenthos. Polychaetes generally are the most abundant animals over the entire latitudinal range.

Bivalve molluscs do not appear to be a very important or successful part of the Antarctic shelf benthos. In the Antarctic, benthic fauna families, genera, and species of bivalves are all depauperate (Table 11.8), and compare favourably only with the Arctic cold water fauna. On the other hand, peracarid crustaceans increase in the number of species, and have higher population densities, with increasing latitude, while polychaetes remain basically unchanged with regard to numbers of species and population densities along the latitudinal transect. The obvious differences in these groups along the latitudinal gradient are due to the different responses to

TABLE 11.8
Families, Genera, and Species of Bivalves from Various Regions

Geographic Area	Families	Genera	Species
Antarctic (Nicol, 1967)	19	32	68
Arctic (Nicol, 1967)	23	37	66
New Zealand (Dell, 1964)	44	142	400
Panamic Province (Kenn, 1958)	46	147	555

Source: From Nicol, D., *J. Paleont.*, 41, 1330–1340, 1967. With permission.

selective pressures operating along the gradient. The cold-water Antarctic environment selects slow-growing, longlived animals that brood their young. They may be large or small, but if they require large amounts of calcium, they are usually small. The depauperate nature of the Antarctic bivalve molluscan fauna appears to be due to an inability to adapt to these requirements.

Kennett (1968) has discussed the question of the calcium carbonate compensation depth (CCD) in the Ross Sea. Using the depth distribution of calcareous and arenaceous benthic foraminifera, he determined the CCD to be at 550 m, which is very shallow compared with other areas of the world's oceans. He attributed this shallow solution boundary to the very low temperatures and high salinities of the Ross Sea. The low calcium saturation of the water means that extracting calcium carbonate for shell building and maintenance requires relatively more energy than in warmer waters. Nicol (1967) and Kennett (1968) have remarked on the thin and chalky appearance of Antarctic bivalve shells, and Arnaud (1974) has commented on the exceedingly fragile nature of the Mollusca, Echinodermata, and Bryozoa living on the Antarctic shelf. Nicol (1964a, 1964b) has demonstrated that the Antarctic bivalve fauna is the smallest such fauna known.

In contrast the Peracarida are a very successful group in the Antarctic macrobenthos. Peracarids are brooders, a strong requirement for success in cold waters. They are mainly generalized deposit-feeders, which means that they have a continuous food supply and do not have to adapt their reproductive behaviour to a short summer plankton cycle. In addition, peracarids are not reliant on large amounts of calcium carbonate for exoskeleton production. Large reptant decapod crustaceans with heavily calcified shells and pelagic larvae are absent from the Antarctic shelf fauna. In adjusting to a cold water environment, the polychaetes were at an advantage because of their generalized feeding habits. Their major change has been the suppression of the pelagic trochophore larvae into a form which develops demersally, either in the tubes of sedentary forms or on the body of errant forms (Hartman 1967; Arnaud 1974).

11.7 SHELF AND UPPER SLOPE COMMUNITIES

The benthic communities of the Weddell Sea continental shelf and upper slope have been described by Voβ (1988), Galeron et al. (1992), Gerdes et al. (1992), Antz and Gutt (1997, 1999), Antz and Brey (2001), and Knust et al. (2003). Vo (1988), on the basis of about 450 taxonomic groups, separated the fauna of the eastern Weddell Sea shelf into three different communities: an Eastern Shelf Community, a Southern Shelf Community and a Southern Trench Community. Subsequently, Gerdes et al. (1992) sampled 233 multibox core samples along the southeastern Weddell Sea shelf and continental slope and identified by means of cluster analysis three different macrobenthic communities. Cluster B closely resembled Voβ 's (1988) eastern shelf community. It was dominated by sponges and bryozoans and was rich in species and diversity. Echinoderms and polychaetes were secondary dominants. Cluster C in the Filchner depression area (Voβ's southern trench community) was characterized by the virtual absence of sponges and bryozoans (less than 2% of the biomass), with other taxa such as polchaetes (46.3%), hemichordates (10.2%) and crustaceans (7.8%) dominating. Cluster A resembled Voβ's southern shelf community. It was dominated by polychaetes (70.9%), with molluscs (12.6%) and crustaceans (7.4%) as subdominants.

11.8 DEEP SEA COMMUNITIES

Until recently, compartively little sampling of the deep sea benthos had been carried out in Antarctic waters. The prevailing view was that it was species poor and that the density and biomass was low. Brandt (2004) stated: "The deeper waters of the Scotia and Weddell Seas are one of the least explored parts of the world's oceans and we know about nothing of the bottom-dwelling (benthic) animals that inhabit them." This gap in our information on the deep sea benthos has been filled by the ANDEEP (Antarctic benthos DEEP-sea Biodiversity Programme of the RV Polarstern). More than 300 species have been recorded during ANDEEP 1 and 2 in 2002. In comparison, after more than 100 years of research, 371 species of isopods were known from the Antarctic continental shelf. Benthic species richness was as high in the Southern Ocean deep sea in all size classes, comparable or higher than on the shelf for most taxa. Depth gradients were clear for most macro- and meiobenthic taxa and assemblages, species richness was highest at about 3,000 m depth. Abundance and biomasses generally decreased with depth, whereas species richness mostly increased.

Gutzmann et al. (2004) investigated the meiofaunal communities along an abyssal depth gradient (2,774–5,194 m depth) in the Drake Passage. The major groups of metazoan meiofauna belonged to the typical soft bottom meiofauna of bathyal and abyssal sediments. All samples were rich in higher level taxa, since nematodes, copepods, kinorhynchs, loriciferans, tantulocarids, ostracods, and tardigrades were found at each station. A total of 13 higher taxa were identified; the number of taxa per core ranged from 3 to 13, with a significant decrease ($p < .005$) of the density of taxa with increasing depth. The meiofaunal assemblage was dominated by nematodes with up to 94%, followed by copepods with respectively lower percentages. Values of the same order have been found for the meiobenthos of the Weddell Sea and an Antarctic shallow water habitat at Signy Island. Total metazoan meiofauna densities ranged between 2,731 ind. cm^{-2} at 2,290 m depth and 75 ind. cm^{-2} at 3,597 m depth. Additionally, the densities of nematodes at the shallower stations were higher than the average found at similar depths in other oceans. At the deepest station (5,200 m), there were higher stocks of nematodes in comparison with mid-depth stations. It is therefore clear that the deep sea benthos is not impoverished and that the diversity and biomass of the meiofauna is relatively high.

Recent investigations of the deep sea in the Atlantic sector by the RV Polarstern have confirmed the conclusion that the deep Antarctic sea is not impoverished (Brandt 2004). Brandt analysed the isopods from these expeditions. Some 317 species were sampled. Of these, 177 were new to the area and the degree of endemism at 84.7% was very high.

11.9 MICROBIAL COMMUNITIES

White et al. (1993) have reviewed the information on Antarctic microbial communities. One of the first desciptions of a sedimentary microbial community in Antarctic waters was that of Walls (1967), who determined that bacteria from deep sea sediments at the Antarctic Convergence conformed to the general pattern of sediment microorganisms of other oceans. Investigations of sediment microbial communities from nearshore Antarctic marine sediments from two distinct regions revealed similar communities (Smith et al. 1989). In the top 2 cm of both McMurdo Sound and Arthur Harbour, microalgae amounted to about 37% of the total microbial community, and eubacteria to about 24%, including 3% obligate anaerobes (predominately sulphate-reducing bacteria). The remainder (approximately 16%) of the microbiota was composed of other microeucaryotes. The marine microeucaryotes of the aerobic and euphotic nearshore Antarctic environments are microalgae (primarily diatoms), foraminiferans, dinoflagellates, some protozoana, and fungi. *Pseudomonas*, cyanobacteria, *Bacillus,* and *Vibrio* are the dominants in nearshore environments. Anaerobic, eubacterial, sulfate-reducing bacteria are present when suitable environmental conditions exist.

Foraminifera are prominent in Antarctic sediments (Lipps et al. 1972, 1979). Lipps et al. (1979) reported 11 species of Foraminifera from sediment samples collected at 68/5 m depth in George VI Sound. In Port Foster and Deception Island on the Antarctic Peninsula, the five dominant species were *Fursenkoina fusiformis, Nonionella bradyii, Miliammina arenacea, Trochammina malovensis*, and *Globocrassidulina crassa.* From the Bransfield Strait area, about 12 foraminiferan species dominated the community profile of 85 species identified.

Comparatively large bacterial communities of about 21.0×10^8 cells g dry wt sediment^{-1} (McMurdo Sound; Smith et al. 1986) and about 1.2×10^8 cells g dry wt sediment (Arthur Harbour; Smith et al. 1989) have been recorded. The value for McMurdo Sound is comparable to that recorded in a Florida estuary.

11.10 MEIOFAUNA

In comparison with other regions, there have been a limited number of investigations of the meiofauna of the Antarctic region. Investigation in shallow waters include those of Vanhove et al. (2000) at Signy Island, Vanhove et al. (1998) and Veit-Köhler (1998) in Potter Cove, King George Island, and Danovaro et al. (1999) in Terra Nova Bay. Studies in deeper waters include those of Fabiano and Danovaro (1999) in the Ross Sea, Vanhove et al. (1995) off Kapp Norvegia, Weddell Sea, and Herman and Dahms (1992) off Halley Bay, Weddell Sea.

Vanhove et al. (2000) studied the sediments and meiofauna fortnightly for 18 months in a shallow bay at Signy Island. They identified 28 nematode genera which dominated the meiofaunal community. Its structure resembled that of communities in other shallow, subtidal sediments. An extremely high meiofaunal standing stock was found throughout the sampling period (average density was 6.2×10^6 ind. m^{-2} and average biomass was 1.4 g dry wt m^{-2}). The peak density in May 1991 (18.8×10^6 ind. m^{-2} and 13.3 g dry wt m^{-2}) was higher than that reported for any other sediment (Vanhove et al. 1998). Based on annual P:B values for temperate nematodes, annual production was estimated to be between 2.2 and 38.4 g C m^{-2} for P:B ratios between 4 and 69 (Vranken and Heip 1986), and 5.0 g C m^{-2} for a P:B of 9. These values greatly exceed those calculated for nematodes in north seas (average 1.2 g C m^{-2} yr^{-1}, Heip et al. 1985; max. 2.6 g C m^{-2} yr^{-1}, Vincx 1989). Productivity was related to water column primary production. For example, harpacticoid copepod numbers followed the patterns of water-column productivity, with higher densities during productive periods and low numbers in late winter. Meiobenthic variables were correlated with temperature. The reproductive and development rates of nematodes are positively correlated with temperature. For example, at Kerguelen Islands, Bouvy and Soyer (1989) found that nematode development time varied between 30 and 75 days at 10 and 2°C, respectively.

Danovaro et al. (1999) investigated the meiofaunal assemblages associated with scallop beds (*Adamussium colbecki*) in the coastal sediments of Terra Nova Bay. Three sites were sampled, one without scallops and the other two with 18 and 85 ind. m^{-2}, respectively. The sediments were generally characterized by large amounts of chloropigments and labile compounds (dominated by proteins), indicating high inputs of primary organic matter. Meiofaunal densities for the site with no scallops and the one with 18 ind. m^{-2} (5.6 ± 2.1 and 4.6 ± 2.0 ind.$\times10^6$ m^{-2}, respectively) were comparable with those reported from the most productive areas worldwide (Vanhove et al. 1998), and about 15–20-fold higher than those in the site with 85 scallops m^{-2} (0.3 ± 0.18 ind.$\times10^6$ m^{-2}). There was clear evidence of the effect of resuspension and macrofaunal disturbance on the meiofauna. The scallop assemblages apparently played an important role in structuring the meiofaunal communities. Nematodes were largely dominant at the site without scallops (91% of the total meiofaunal density). The sites with scallops were characterized by large densities of gastrotrichs, which were found in the highest densities reported in the literature. Harpacticoid copepod densities were low. It is clear from the two investigations in coastal Antarctic waters that meiofaunal densities in Antarctica are very high.

Vanhove et al. (1995) investigated the meiofauna in the region off Kapp Norvegia (Weddell Sea) in depths from between 211 and 2,080 m. Total meiofaunal abundances ranged from 815 to 5,122 individuals 10 cm^{-2} and total biomass from 126 to 966 μg 10 cm^{-2}. Nematodes dominated the samples (range 83–97%), followed by harpacticoid copepods, polychaetes and kinorhynchs. The meiofaunal communities were primarily influenced by bathymetric depth and food availability (e.g., organic matter and macrobiota) which in turn are directly related to phytoplankton blooms and associated sediment pulses.

Herman and Dahms (1992) analysed the meiofaunal communities from 10 stations along a depth transect from approximately 500 to 2,000 m off Halley Bay Station (Weddell Sea). Representatives of about 30 small-sized taxa were found. At one of the stations a maximum of 22 taxa occurred, with the mean number of taxa ranging from 7 to 16. Nematoda, Harpacticoida, Ostracoda, Polychaeta, and Bivalvia were present at all sites. Nematodes were always dominant representing more than 90% of the individuals per sample, followed by harpacticoids (3%) and kinorhynchs (1.3%). Maximal density was 3,000 individuals 10 cm^{-2}, with the mean number per station ranging from 790 to 3,720 individuals 10 cm^{-2}, with an overall mean of 1,700 individuals 10 cm^{-2}.

In terms of standing stock, the Southern Ocean showed generally has higher values than other world oceans. The dominant taxa are nematodes (77–98%), as is generally the case in marine sediments. The nematode communities are characterised by very high genus diversity, ranging from 15 to 78 genera per station along the continental margin. Both abundance (up to about 20×10^6 individuals m^{-2}) and biomass (almost 15 g dry wt m^{-2}) of nematodes are significantly higher compared to similar water depths from elsewhere.

11.11 BIOGEOGRAPHY AND ORIGIN OF THE BENTHIC BIOTA

The Antarctic Continent is the most isolated of all the continents. Its shores are 960 km from South America, 4,020 km from South Africa, and 3,380 km from New Zealand, the nearest land masses. While the shelf and slope connect with the deep ocean basins in the Atlantic, Indian, and Pacific Oceans, there are three comparatively shallow-water connections to the north. These are the Scotia Arc, the island chain from South America through the Falkland Islands, South Georgia, South Sandwich and South Orkney Islands to the Antarctic Peninsula, and the MacquarieBalleney and the KerguelenGausberg Ridges, which rise within 1,800 and 200 m of the surface, respectively.

A number of authors have discussed the origin and relationships of the Antarctic fauna. Pertinent general reviews include those of Ekman (1953), Hedgpeth (1969, 1970), Dell (1972), Knox and Lowry (1977), White (1984), Picken (1985a), Dayton (1990), Antz et al. (1994, 1997), Clarke (1996), and Clarke and Johnston (2002). Aspects of the biogeography of the Southern Ocean with special reference to the Pacific sector have been dealt with by Knox (1960, 1963, 1970, 1975, 1979, 1980) in a series of papers. Others have presented accounts based on the distribution and affinities of particular groups: for example, fish (Andriashev 1965), polychaetes (Knox 1979), polychaetes and amphipods (Knox and Lowry 1977), isopods (Kussakin 1967), amphipods (Thurston 1972; Broyer and Jazdzewski 1993), molluscs (Powell 1965), echinoderms (Fell and Dawsey 1969; Fell et al. 1969), ascidians (Kott 1969, 1971a, 1971b) sponges (Koltun 1969) and benthic macroalgae (Delepine 1966; South 1979).

When one examines the distribution patterns detailed in the papers listed at the beginning of this section, a number of major distribution patterns are seen to occur in all groups. These can be summarized as follows (modified from Knox and Lowry 1977):

1. Circum-polar, throughout the Antarctic and including the Magellanic area and the Subantarctic islands.
2. Circum-Antarctic, throughout the Antarctic and the Scotia Arc.
3. Circum-Subantarctic, throughout the Subantarctic islands and the Magellanic area, and sometimes extending into the Scotia Arc.

The affinities of these faunal components suggest that they originated from (Figure 11.13):

1. A relict autochthonous fauna
2. Eurybathic species derived from the adjacent deep-water basins of the south Atlantic, the south Pacific, and the south Indian Ocean
3. Abyssal species often endemic at the generic level
4. Species of Magellanic origin which have migrated to Antarctica via the Scotia Arc, and subsequently spread to a greater or lesser extent round the continent
5. Species of Antarctic origin which have migrated in the opposite direction northwards along the Scotia Arc
6. Subantarctic species of predominantly northern origin.

The current view is that the Antarctic marine fauna evolved in situ since the Cretaceous or even earlier when the continents were still connected (Clarke and Crame 1997a). Many recent publications support this view including those on gastropods (Clarke and Crame 1977a) and the isopod families Serolidae and Arcturidae (Brandt 1990). Many workers have commented on the distinctiveness of the Antarctic fauna, especially notable for the high degree of endemism at the specific level. For the groups listed in Table 11.9, this varies from 57 to as high as 95%. There is, however, much greater variation in endemism at the generic level, varying from as low as 5 to as high as 70%. This presumably is related to the evolutionary history of the groups concerned. The high degree of endemism is indicative of the long isolation of Antarctica from other land areas and their associated shelf and slope regions, and the active speciation that has occurred during this isolation.

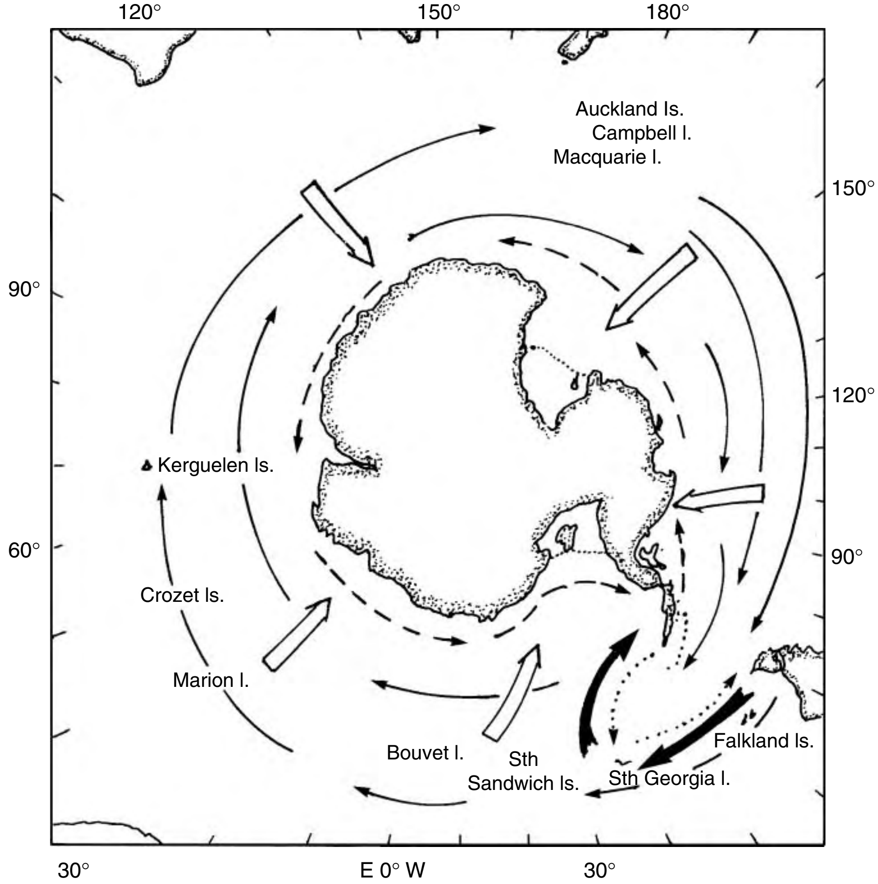


FIGURE 11.13 Origins and dispersal of the Antarctic marine benthic fauna (1) dispersal by the Antarctic Coastal Current (dashed arrow); (2) dispersal by the Antarctic Circumpolar Current (thin solid arrow); (3) migration of abyssal forms onto the Antarctic shelf (open arrow); (4) northward migration along the Scotia Arc (thick solid arrow); and, (5) southward migration along the Scotia Arc (dotted arrow). (From Knox, G. A. Lowry, J. K., *Polar Oceans*, Dunbar, E. J., Ed., Arctic Institute of North America, Calgary, 423, 1977. With permission.)

Some groups are absent from the Antarctic fauna nowadays, although they were common in former times, like reptantia, which were found to be rich in fossils in the Cretaceous and the Eocene. Today there are almost no reptants in the high Antarctic but the few specie that have established themselves are often very abundant (Antz et al. 1991). Shallow-water balanomorph barnacles became extinct in recent times probably due to ice scour (Dayton 1990). Other groups show a pronounced radiation into closely related species. Clarke and Crame (1997a) give examples among pycnogonids, gastropods, echinoderms, and ascidians).

11.12 FACTORS RESPONSIBLE FOR SHAPING THE ANTARCTIC BENTHOS

Antz et al. (1994) have reviewed the factors responsible for shaping the Antarctic benthic fauna. These are:

1. The similarity of conditions found in the sea around the continent and the circumantarctic current system results in a large proportion of the species being circumpolar in their distribution.
2. The Antarctic Convergence, which acts as a barrier to exchanges with ocean north of the convergence.
3. Long-term stability of the environmental conditions. While the polar environment has been in existance for a considerable period, there have nevertheless been considerable fluctuations over geological time.
4. Disturbance has been (and is) frequent in the benthic environment.
5. Low temperatures per se do not seem to have been a problem in the development of rich and diverse faunas.
6. The advance and retreat of the ice caps may explain the high eurybathy of the Antarctic benthic fauna.
7. The extremely seasonal input of food from the sea ice and the water column has been a major factor in the evolution of the fauna (Clarke 1988, 1990a). This has led to the evolution of species which are adapted to exploit such seasonal and fluctuating food resources (Wagele and Buto 1990).
8. The comparative lack of terrestrial input. In contrast to temperate and tropical systems, organic and nutrient input from river systems is lacking.

TABLE 11.9
Degree of Endemism in Selected Antarctic Benthic Groups

Group	Endemic Genera (% of Total)	Endemic Species (% of Total)	Source
Fishes	70	95	Andriashev (1965)
Isopoda and Tanaidacea	10	66	Kussakin (1967)
Pycnogonida	14	>90	Fry (1964)
Echinodermata	27	73	Ekman (1953)
Echinoidea	25	77	Pawson (1969b)
Holothuroidea	5	58	Pawson (1969a)
Bryozoa	—	58	Bullivant (1969)
Polychaeta	5	57	Knox and Lowry (1977)
Amphipoda	39	90	Knox and Lowry (1977)
Chlorophyta			
Sub-Antarctic	—	16	Heywood and Whitaker (1984)
Low Antarctic	—	33	Heywood and Whitaker (1984)
High Antarctic	—	67	Heywood and Whitaker (1984)
Phaeophyta			
Sub-Antarctic	—	41	Heywood and Whitaker (1984)
Low Antarctic	—	73	Heywood and Whitaker (1984)
High Antarctic	—	83	Heywood and Whitaker (1984)
Rhodophyta			
Sub-Antarctic	—	70	Heywood and Whitaker (1984)
Low Antarctic	—	92	Heywood and Whitaker (1984)
High Antarctic	—	100	Heywood and Whitaker (1984)

Source: From Knox, G. A. and Lowry, J. K., in *Polar Oceans*, Dunbar, M. J., Ed., Arctic Institute of North America, Calgary, 1977, 423; Heywood, R. B. and Whitaker, T. M., in *Antarctic Ecology*, Vol. 2, Laws, R. M., Ed., Academic Press, London, 1984, 373–419; Dayton, P. K., in *Polar Oceanography, Part B: Chemistry Biology and Geology*, Smith, W. O. Jr., Ed., Academic Press, San Diego, CA, 1990, 631–685. With permission.

9. The central position that krill play in Antarctic food webs.

Clarke (1996) has also reviewed the environmental factors influencing ecological processes in the Southern Ocean marine benthos. Major factors identified were temperature and iceberg scour.

The seasonal variation in temperature is small and hence is unlikely to drive seasonal changes in biology. Since this seasonal variation is very low, physiological processes would have to be unduly thermally sensitive for temperature variation to be a forcing variable.

11.12.1 IMPACT OF ICEBERG SCOUR

According to a recent assessment, iceberg scouring is one of the 5 most significant impacts on any ecosystem on Earth (Gutt and Starmans 2001). Along the Antarctic coast, tabular icebergs calve from the ice shelves, which make up 46% of the coastal length mainly in the Ross and Weddell Seas. Smaller icebergs originate from an additional 45% of the coastline where there are glaciers, ice streams, and grounded ice walls. A total "population" of more than 300,000 icebergs (>10 m wide) were calculated for the entire Antarctic in 1981–1984 (Orheim 1985). They have an average half-life expectancy of 4 years. The grounding of these icebergs are one of the main sources of disturbance with significant physical impact on the sea floor and on the benthos (Lien et al. 1989; Clarke 1996; Gutt et al. 1996). (For an overview see Barnes 1999; Gutt 2001; Knust et al. 2003.) Although the impact on the benthic communities can be "catastrophic" (Peck et al. 1999) there are hints that the disturbance regime is one important driving force for a higher between-habitat diversity (beta-diversity) and/or overall gamma-diversity of benthic shelf systems. Iceberg impacts can occur from the intertidal to depths of around 500 m.

The extent of iceberg impact depends on the nature of the seabed (rock, cobble, or soft sediment). Icebergs affect soft substrata in three ways: they plough the seabed, which forces the surface layers away from the point of contact; they trample it, whereby icebergs rock backwards and forwards crushing underlying organisms and seabed; and water flowing around the bergs either caused by movements of the berg, natural oceanic currents, or salinity-induced water movements can resuspend and transport sediment. If the seafloor is relatively even, icebergs make contact with the bottom and continue to drift, leaving relatively long scour marks behind them which are randomly distributed. When icebergs run aground on relatively steep slopes, they buildup concentrations called "small iceberg banks." Another category is called "large iceberg banks," in which the effects of the two other categories is combined. It has been estimated that approximately 5% of the Antarctic shelf is affected by grounding icebergs (Gutt 2000). However, locally it may be much higher. Statistically, once in every 340 years, each square meter of sea floor on the Antarctic shelf that is less than 500 m is devastated by grounding icebergs (Gutt 2001).

The impact of iceberg scour and the timing and extent of recovery depends on its frequency. Barnes et al. (2003) estimated iceberg scour at two shallow depths (9–17 m) at Adélie Island, Antarctic Peninsula, by checking the time grids of markers that were struck. At the least disturbed site, 24% of the markers were destroyed per year, whereas at the most disturbed site, 60% of the markers were destroyed. Compared with nearshore environments elsewhere, faunas of both sites were characteristic of high disturbance regimes, exhibiting low percent cover, diversity, ages, and a high proportion of pioneers. At the most disturbed site, bryozoan communities have half the number of species, two-thirds the space occupation and twice the mortality level of those in the least disturbed site. Maximum age in the most disturbed site was half that in the least disturbed site.

Impact on the Benthos. One of the most detailed investigations of the impact of iceberg scour is that of Gerdes et al. (2003) on the Weddell Sea shelf. They sampled 84 stations in depths ranging from 225 to 305 m. The stations were classified into three categories: young scours, old scours, and undisturbed areas. The three categories of stations were significantly different in all tested parameters. The average biomass of major taxa in the cores of undisturbed areas was significantly higher (14,716 g wet wt m^{-2}) than in old (405.3 g wet wt m^{-2}) or in young scour marks (9.2 g wet wt m^{-2}). The habitat taxon richness, too, was highest in undisturbed areas; on average 11.8 taxonomic units occurred per core, decreased in old scour marks (9.0) and was lowest in young scours (6.8). There were striking differences in the composition of the communities in the three categories (Figure 11.14).

In undisturbed areas (Cluster B) there was a highly developed community structure dominated by sponges (with a biomass share of up to 95%). Young scours differed from all other areas by the absence of large-sized sessile epifauna; instead, motile organisms such as polychaetes, crustaceans and ophiuroids predominated (Cluster A). In contrast to the undisturbed areas, the biomass in the young scours was much more evenly distributed among the taxa. Sponges contributed less than 20%, whereas motile forms such as echinoderms, crustaceans and polychaetes were important. Bryozoans, which were said to be pioneers (Gutt et al. 1996), also occurred quite frequently.

In total, 167 polychaete species were recorded from the samples. They revealed significant differences between disturbed and unaffected areas. The mean abundances offered significantly 784 in the undisturbed stations, 389 in the old scours and 242 ind. m^{-2} in the young scours. Habitat species richness (11.6, 5.5, and 3.1, respectively) showed a similar trend. The rich and three-dimensional undisturbed sites had a wide variety of feeding types and life-styles. In contrast, the impoverished fauna in the young scours consisted mainly of discretely motile or sessile deposit-feeders.

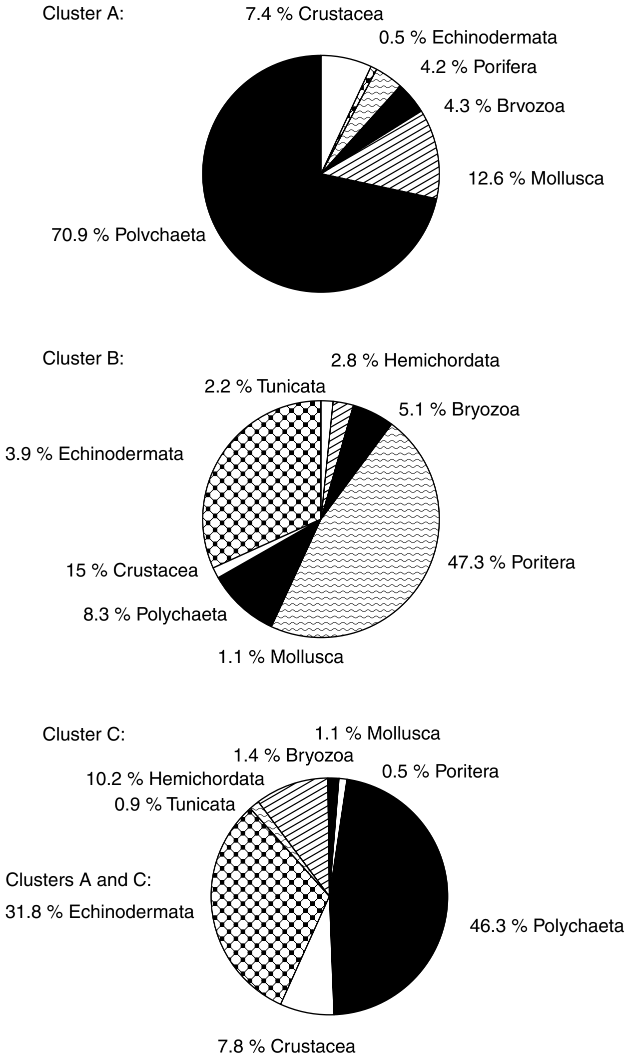


FIGURE 11.14 Taxonomic composition of benthic communities (wet biomass proportions) in disturbed (Cluster A and C) (by iceberg scouring) and undisturbed locations (Cluster B) in the south eastern Weddell Sea Shelf. (From Gerdes, D., Hilbig, B., Montiel, A., *Polar Biol.,* 26, 298, 2003. With permission.)

Studies on the Weddell Sea shelf (Gutt and Piepenburg 2003) have provided evidence that the effects of iceberg scouring on the megabenthic assemblages differ, depending on spatial scale. At a local scale (1–100 m), undisturbed glass sponge-associated habitats were significantly more diverse than disturbed ones. At a regional scale (1–100 km), increased habitat heterogeneity caused by iceberg scouring enhanced species diversity. This result emphasizes the relevance of scale in the evaluation and interpretation of diversity.

On the continental shelf off Kapp Norvegia, Lee et al. (2001a, 2001b) found that meiofaunal abundance and taxonomic diversity were significantly reduced in fresh scours. The highest abundance and diversity was found in the older scours as compared with undisturbed sites. Meiofaunal abundance in the fresh scours was only 10% of that in old scours and undisturbed sites. Scouring also changed the nematode community structure resulting in a decrease in selective deposit-feeders.

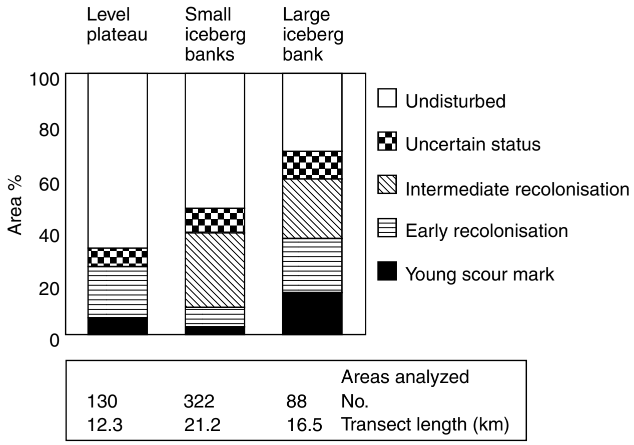
Brenner et al. (2001) investigated the trophic niches of fish of the genus *Trematomus* in the eastern Weddell Sea. They found that *Trematomus eulepidotus*, *T. lepidorhinus* and *T. scotii* dominated undisturbed areas, whereas *T. nicolai* and especially *T. pennelli* dominated disturbed areas.

Recolonization and Recovery. Recovery of iceberg scours have been investigated by Peck et al. (1999), Gutt and Starmans (2001), Lee et al. (2001), Gerdes et al. (2003), Knust et al. (2003). The return of species to an impacted site is controlled by several factors. The earliest to return to the disturbed sites are those that are motile, such as amphipods and isopods. Other groups depend on external forces, or new recruitment via larvae to recolonise the sites. Intense storms may transport small bivalves such as *Mysella charcoti* to disturbed sites. Larger bivalves must recolonise impacted sites via larval dispersal.

Texido et al. (2004) investigated the response of the SE Weddell Sea shelf benthic community to iceberg disturbance. Changes in the space occupation of benthic organisms along the recolonisation stage was observed. Uncovered sediment characterised the early stages ranging from 98 to 91% of the coverage. The later stages showed high (70.5%) and intermediate (52.5%) values, whereas demosponges, bryozoans and ascidians exhibited a high number of patches and taxa. Overall, maximum areas of patches increased as recovery proceeded. Early stages were characterised by the presence of pioneer taxa, which only partially covered the bottom sediment but were locally abundant (e.g., the bryozoan *Cellarinella* spp. and the gorgonian *Primnoasis antarctica* with a maximum coverage of 13 and 3% and 51 and 30 patches m^{-2}, respectively). Soft bush-like bryozoans, sheet-like sabellid polychaetes, and tree-like sponges, gorgonians, bryozoans, and asacidians were the first colonisers. Mound-like sponges and ascidians, as well as tree-like organisms with a long lifespan, defined the later stages.

Gutt and Starmans (2001) defined five different stages of recolonization of disturbed areas. Knust et al. (2003) in investigations in the Weddell Sea adopted their classification. The relative proportions of these stages in the Kapp Norvegia are are shown in Figure 11.15. The classification relies on the abundance and degree of coverage of the seafloor by sessile epibenthic organisms. Mobile epibenthic organisms such as ophiuroids, crinoids, amphipods or sessile pioneer species such as the sponge *Stylocordyla borealis*, ascidians and bryozoans are some of the first agents in the recolonization process. The time schedule in which recovery takes place is as yet unknown. Picken (1985a) has stated that community recovery from iceberg disturbance may require many years. Colonization of settlement plates in Antarctic waters is at least an order of magnitude slower than in temperate or tropical waters (Stanwell-Smith and Barnes 1991; Barnes 1996). However, recovery following iceberg scouring at Signy Island varied between faunal groups, both in the method and timing, with some groups returnimg in a matter of days (Peck et al. 1999).

Lee et al. (2001b) has investigated meiofaunal recolonization in a shallow coastal area at Signy Island. They found that the recovery of the meiofaunal community was considerably faster than that of the larger benthos. The return of the major meiofaunal groups to control levels was accomplished in 30 days. The pioneering meiofaunal colonisers were copepods and ostracods, followed by nematodes. *Microlaimus* sp. was the dominant nematode throughout the colonization period. Epistratum feeders and nonselective deposit-feeders were highly dominant over selective deposit-feeders and predators/omnivores. In spite of the disturbance, the nematode community structure was not affected by the iceberg impact and there was no evidence of succession during recovery. Lee et al. suggested that the shallow subtidal coastal meiofaunal community is well adapted to ice disturbance. However, the recovery of the



Redrawn from Gutt & Starmans 2001

FIGURE 11.15 Proportion of the different recolonization stages of ice scour on different morphological substrates in the Weddell Sea. (From Gutt, J., Starmans, A., *Polar Biol.,* 24, 615, 2001. With permission.)

shelf communities is a slower process which may take years (Lee et al. 2001b).

A number of authors (Gammie 1995; Gutt et al. 1996; Gerdes et al. 2003) consider that the significance of iceberg disturbance is likely to increase in the future due to global warming and accelerated melting of Antarctic ice shelves.

11.13 BIOGEOGRAPHICAL SCHEMES FOR THE ANTARCTIC REGION

Ideally, biogeographic syntheses should be based on the analysis of distribution patterns of whole communities of organisms. So far this has not been attempted for the benthic flora and fauna of the Antarctic and Subantarctic, apart from the analysis of the zonation patterns of the littoral zone by Knox (1960). The early work on Antarctic biogeography was carried out by ichthyologists (Regan 1914; Nybelin 1947). Andriashev (1965) revised their work and proposed a scheme, based on coastal fish, that integrated their work with more recent findings.

The results of the polychaete study by Knox and Lowry (1977) indicated an old homogeneous fauna with a slow evolutionary rate. Many of the species are widespread, vertically (eurybathic), and laterally (circumpolar). This type of distribution supports the theory of a fauna able to advance and recede from deep to shallow water, as glaciation receded and advanced. At the same time its age, cosmopolitan nature, and slow rate of evolution would allow it to advance laterally around the continent, forming the type of fauna which occurs there today. This fauna is characterized by a moderately high endemism at the species level (approximately 60%), a very low endemism at the specific level (approximately 5%), and many widespread eurybathic species.

Of the various biogeographical schemes that have been advanced, that of Hedgpeth (1969), with various minor modifications, has been most generally accepted (Figure 11.16). In this scheme the Antarctic Region covering the whole of the area south of the Antarctic Convergence, is divided into two subregions: the western Antarctic (composed of the Antarctic Peninsula, and the Scotia Arc) and the Continental Antarctic. The Subantarctic region includes the area between the Antarctic Convergence and the Subtropical Convergence. New Zealand is not included in the Subantarctic region, but southern South America is included. Heard Island is included as an extension of Continental Antarctic, and a Scotia subregion and a South Georgia District are recognized.

11.14 DIVERSITY, ABUNDANCE, AND BIOMASS

The traditional view is that the Antarctic benthos is characterized by a high biomass and large number of individuals (White 1984; Clarke and Crame 1997a; Clarke 1996). Early investigations in the Antarctic Peninsula region found relatively high abundance values (6,000–8,000 ind. m^{-2}) at Arthur Harbour (Lowry 1975), similar values in Chile Bay (3,000–6,000 ind. m^{-2}), but much lower ones in Discovery Bay, Grenwich Island (Gallardo and Castilla 1969). Mean biomass in Chile Bay was 160–180 g wet wt m^{-2}. Abundance on the southwestern shelf of the Antarctic Peninsula (median 2,505 ind. m^{-2}) was significantly lower than that around the Scotia Arc islands (median 8,642 ind. m^{-2}). The corresponding median biomass was 9.05 g wet wt m^{-2}. Abundance values for the southeastern Weddell Sea ranged from 131 to 12,846 m^{-2}, and biomass values from 0.12 to 1,644.2 g wet wt m^{-2} (Gerdes et al. 1992).

In Section 11.7, the high densities of some Antarctic benthic infaunal communities were highlighted. These high densities in general occur in shallow shelf areas in depths not exceeding 100 m. The studies in Arthur Harbour by Richardson and Hedgpeth (1977) demonstrated a reduction of about one order of magnitude for sites below 300 m when compared to shallow sites under 75 m. Although their maximum recorded density was 86,514 individuals m^{-2}, Dayton and Oliver (1977) recorded higher densities in eastern McMurdo Sound of up to 155,572 m^{-2} (these are among the highest densities recorded anywhere).

It is probable that these high densities are attributable to the high (but seasonal) primary production and to the diverse substrate characteristics (e.g., the sponge spicule mat provides a wide range of microhabitats thus enhancing both density and diversity). As noted in Chapter 3, a high proportion of the summer pulse of phytoplankton production sediments to the bottom to provide energy input to the benthos. In addition, as Dayton et al. (1986) have documented, for the shallow areas of McMurdo Sound, benthic microalgal standing stocks reach very high levels in the summer months. The stability of the physical environment, along with the slow growth rates and life cycles attuned to the summer pulse of primary production, tends to lead to the evolution of an efficient stable community structure with low annual turnover rates.

While general observations of the shallow water benthos of the Antarctic gave rise to the view that the Antarctic shelf supported a high biomass of benthic macroinvertebrates, especially sessile epifaunal suspension-feeders, there have been only a few quantitative studies to support this view. However, a number of generalizations can be made on the basis of the reported data. Values for epifaunal biomass are very much greater than those for infaunal biomass, up to 4,200 g m^{-2} for the former and up to 700 g m^{-2} for the latter. On hard substrates the epifaunal biomass in shallow depths (1–5 m) is low (20–25 g m^{-2}), but high (450–4,200 g m^{-2}) in intermediate depths (8–50 m). Below 200 m there is a rapid decrease in biomass; e.g., off the Sabrina Coast the biomasses at 200, 300, 2,000, and 3,500 m^{-2} were 1,363, 183–483, 28 and 1.4 g m^{-2}, respectively.

Biomass values have been summarized by White (1984), Dayton (1990), and Brey and Clarke (1993), who compared them with data from boreal and subtropical regions. Biomass generally decreases from shallow to deeper water (Clarke and Crame 1997a; Brey and Clarke 1993). Compared to boreal and subtropical regions, the fauna of shallow waters is lower, due to heavy ice impact. While there is considerable

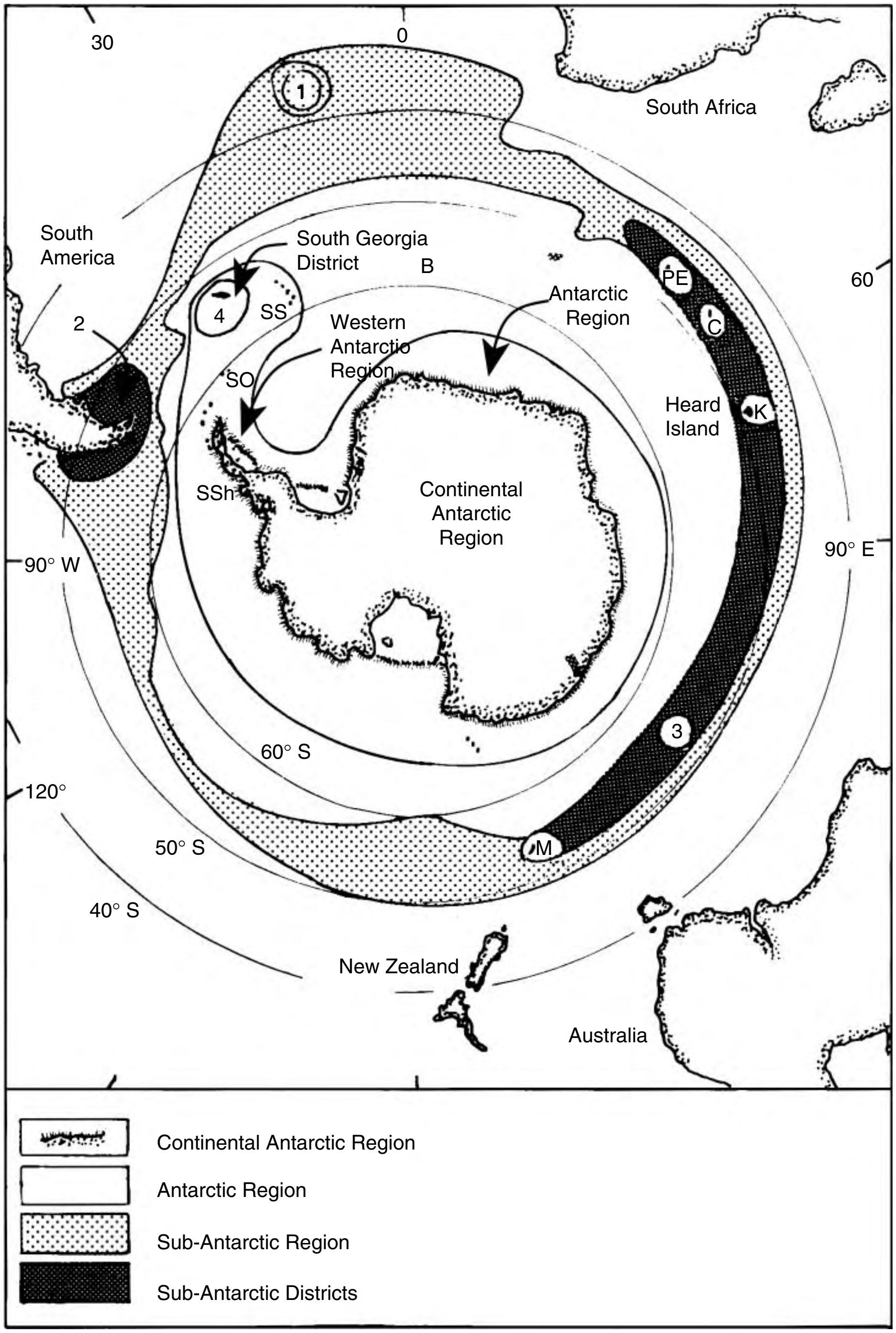


FIGURE 11.16 Biogeographical regions for the benthos of the Southern Ocean. Numbered Subantarctic districts or subregions are: (1) Tristan da Cuhna District; (2) Magellanic Subregion or Province; (3) Kerguelen Subregion or Province. Numbered Antarctic district is: (4) South Georgia District. Islands identified by letters are: (B) Bouvetoya; (C) Crozet; (F) Flaklands; (H) Heard; (K) Kerguelen; (M) Macquarie; (PE) Prince Edward and Marion; (SO) South Orkney; (SSa) South Sandwich; (SSh) South Shetland.

variation, the macrobenthos biomass on the Antarctic shelf and slope in general is distinctly higher than in boreal and subtropical areas of equal depths. At greater depths (below 1000 m), Antarctic and nonAntarctic biomass levels do not differ very much. Meifaunal values in general are similar to those found elsewhere in the world's oceans.

Brey and Gerdes (1997) estimated the production and productivity (*P*/*B* ratio) of the high Antarctic Weddell Sea and Lazarev Sea. Average community production decreases with depth from 4.8 g C m^{-2} yr^{-1} (100–300 m) to 1 g C m^{-2} yr^{-1} (1500–4300). Taking into account the effects of water depth on production and of temperature on

P/B ratio, Antarctic communities show no evidence of unique characteristics with respect to overall energy flow.

11.14.1 DIVERSITY

Recent reviews of Antarctic benthic diversity include those of Antz et al. (1994, 1997), Clarke (1996), Gray (2001), Clarke and Johnston (2002), and De Broyer et al. (2003). Early epifaunal studies in Antarctica revealed high species richness and diversity and this was also the case for studies of benthic infauna such as those of Lowry (1975), Dayton and Oliver (1977), and Richardson and Hedgpeth (1977). However, while several groups, among them sessile suspension-feeders (sponges, bryozoans), motile benthos (e.g., amphipods) and taxa with a wide range of trophic niches (polychaeta), are species rich; other are less diverse (bivalves, gastropods, isopods) and others, as mentioned above, are absent (stomatopods) or restricted to a few species, such as cirripedes and natant decapods. Many authors have commented on the high degree of endeniam of the Antarctic marine fauna (see Dell 1972; White 1984; Picken 1985a 1985b; Dayton 1990; Clarke 1996) (Table 11.9). The percentage of endemic species range from greater than 50% (polychaetes, Holothurians, bryozoans) to 90% or more (amphipods, pycnogonids).

Clarke and Johnston pose the question: “How many species are there in Antarctica?” (2002) Clarke and Johnston (2003) have compiled species richness data for the Southern Ocean (Table 11.10). The total number of species for the Southern Ocean was estimated to exceed 4,100 (Table 11.10). Antz et al. (1997) estimated that the number of species could exceed 5200. This is much larger than most people expected. It had been assumed that the extremely cold waters, covered by ice for a large part of the year and primary production restricted to a short period in the spring and summer would be detrimental to the development of a varied fauna. However, early epifaunal studies (Dearborn 1968; Dell 1972; Dayton and Oliver 1977) revealed high species richness and diversity. Antarctic infauna has been shown to be rich and diverse, with some areas such as Arthur Harbour coming close to maximum diversity. Several groups, among them sessile suspension-feeders (sponges, bryozoans), motile epibenthos (amphipods) and taxa, which cover a wide range in terms of mobility or trophic function (polychaetes), are rich in species; others seem to occupy an intermediate level (bivalves, gastropods, isopods) and a few groups are missing altogether (stomatopods) or restricted to a few representative (e.g., cirripedes and natant decapods). Within taxon, diversity is quite variable; some families or genera have radiated enormously, while others have not. Among isopods, three families account for at least half of the Antarctic species (White 1984), which now total over 300 species (Brandt 1990). A study on the eastern Weddell Sea shelled gastropods and bivalves (Hain 1990) revealed a remarkably high taxonomic diversity; the 145 gastropod species belong to at least 26 families and 69 genera, while 43 bivalve species belong to 17 families and 35 genera.

Lowry (1976) compared the diversity of the macrobenthic communities at the localities that he studied in the Antarctic with that of a latitudinal range of studies from tropical, temperate and Arctic habitats, including both shelf and deep-sea communities. Heterogeneity, species richness and species equatability showed no correlation between macrobenthic diversity and latitude in the shallow shelf communities. However, heterogeneity and species richness correlated well with trophic structure, with suspension-feeding communities having the lowest equatability. Mixed suspension- and deposit-feeding communities, such as those in Mowbry Bay and Port Pegasus, Stewart Island, are more diverse than deposit-feeding communities such as those at Arthur Harbour and Perserverence Harbour, Campbell Island, which in turn are more diverse than the suspension-feeding communities, such as those at Cape Bird and the Auckland Islands. Arctic communities are characterized by a low heterogeneity, due probably to insufficient food input.

The deep sea (except for the Arctic) and the Antarctic shelf have similar heterogeneity, which tends to support the conclusion of Sanders (1969) that species diversity is enhanced in physically stable environments. They also have a similar percentage composition in the major groups (polychaetes, peracarids, bivalves), but the Antarctic benthos is up to at least 23 times more densely populated.

11.14.2 LATITUDINAL GRADIENT IN SPECIES DIVERSITY

In the Northern Hemisphere, it is generally agreed that there is a lattudinal gradient in benthic species richness with the number of species increasing from the Arctic to the tropics. In the south it was believed that benthic species richness would be greatest around the Subantarctic Islands such as South Georgia and would decline southward through the maritime Antarctic to the high Antarctic regions of the Ross and Weddell Seas. An early study (Moe and DeLaca 1976) on macroalgal distribution revealed a statistically significant decline in species richness from Elephant Island (61°S) to Marguerite Bay (68°S). A broader-scale analysis of Southern Hemisphere marine algal distribution has confirmed this general pattern (John et al. 1994). However, recent work has increased the number of macroalgal species at various sites. In general, data on Antarctic benthic diversity supports Clarke’s (1992, 2003) contention that the latitudinal gradient of decreasing species richness towards Antarctic does not hold for the Southern Hemisphere. The benthic fauna of the Southern Ocean is far more diverse than the Arctic primarily as a result of a long evolutionary history in situ (Clarke and Crame 1997a, 1997b).

11.15 FOOD AND FEEDING

As Arnaud (1974) points out, trophic processes in the Antarctic are determined principally by: (1) the seasonal discontinuity of phytoproduction (phytoplankton, ice algae, and benthic microalgae); and, (2) the relatively small

TABLE 11.10
Estimated Number of Benthic Species in the Antarctica

			Estimated species richness		Reliability
Phylum	**Subphylum or Class**	**Order**	**Arntz**	**Clarke and Johnston**	**This study**
Porifera			∼300	250	B
Symplasma			–	29	A
Cnidaria					
	Medusozoa		∼200	186	C
	Anthozoa		85	86	C
Ctenophora			nd	nd	C
Platyhelminthes	*Turbellaria*		nd	nd	C
Gastrotricha					
Priapula			3	3	A
Kinorhyncha			nd	*nd	C
Nematoda			nd	nd	C
Tardigrada			nd	nd	C
Arthropoda	Crustacea				
	Malacostraca	Amphipoda	520	496	B
		Isopoda	346	257	A
		Tanaidacea	50	80	B
		Decapoda	(19)	13	A
	Cirripedia		37	50	C
	Ostracoda		nd	nd	C
Chelicerata					
	Arachnida	Acarina	nd	45	C
	Pycnogonida		>150	175	A
Nemertea			nd	31	B
Mollusca					
	Polyplacophora			<10	C
	Gastropoda		nd	530	A
	Bivalvia		nd	110	
	Scaphopoda			6	C
	Cephalopoda			∼34	B
Sipuncula			∼15	15	A
Echiura			nd	9	A
Annelida					
	Polychaeta		>650	645	C
	Clitellata		nd	nd	C
Pogonophora			nd	3	C
Entoprocta			nd	nd	C
Brachiopoda			16	19	B
Bryozoa			310	322	A
Hemichordata			nd	nd	C
Echinodermata					
	Crinoidea		22	28	B
	Asteroidea		nd	108	B
	Ophiuroidea		nd	119	B
	Echinoidea		44	49	B
	Holothuroidea		88	106	B
Chordata					
	Urochordata		>130	118	B
	Vertebrata	Agnatha	nd	2	A
		Chondrichthyes	nd	8	A
		Osteichthyes	nd	198	A

Reliability of estimates are graded from A (good) to C (poor).

Source: From Clarke, A. and Johnston, N. M., *Oceanogr. Mar. Biol. Annu. Rev.*, 41, 78, 2003. With permission.

amounts of terrigenous sedimentation. Five types of diet are considered to be adaptive to these conditions: suspension-feeding, necrophagy, deposit-feeding, omnivory, or opportunistic diet, herbivores and predators. The study of the food and feeding habits of the Antarctic benthos has received considerable attention.

Suspension-Feeding. The extraordinary development of assemblages of suspension-feeders on the Antarctic shelf, as first described by Beylev and Usachov (1957), has been described above. Such assemblages are dominated by hexactinellid sponges, demosponges, hydroids, gorgonians and bryozoans, and contain a high proportion of polychaetes, ascidians, actinarians, scleractinian corals, stylasterine corals, brachiopods, and many motile animals, especially holothurians, crinoids, asteroids, crustaceans, and pycnogonids. The dendrochirotid holothurians, living mainly on the shelf, are sessile suspension-feeders. Bottom currents transport an abundance of organic detritus (diatoms, protozoans, faecal pellets, exuvia and the remains of planktonic metazoans), as well as living plankton, larvae and eggs to the waiting filtration mechanisms of the sessile suspension-feeders. Tatian et al. (2005), in an investigation of suspension-feeding in Potter Cove, King George Island, found that the gut contents of the species examined contained very small amounts of microalgae, while particles of macroalgal detritus and fecal pellets comprised the bulk of the contents.

Necrophagy. Arnaud (1970) was the first to draw attention to the fact that numerous Antarctic invertebrates are potential carrion eaters, or scavengers, and that others adopt this method of feeding seasonally in winter. Arnaud used the term necrophagy for this type of nutrition. In subsequent papers Arnaud (1974, 1977, 1992) explored the concept further and more recently, Presler (1986) has examined the species composition and seasonal changes in the assemblage of necrophagous invertebrates in Admiralty Bay. As Arnaud (1977) points out, scavengers are present in every marine ecosystem, but the numbers are higher in Antarctic benthic communities than elsewhere. Presler (1986) identified 23 species as necrophagous in Admiralty Bay with a further 10 being suspected of necrophagy. It is widespread among amphipods, gastropods, ophiuroids, echinoids, and nemertines.

Deposit-Feeders. There is a wide range of deposit-feeders in the Antarctic benthos, with the holothurians and the polychaetes the most prominent. Many holothurians and polychaetes are surface deposit-feeders, either moving over the surface ingesting the sediments or in the case of the polychaetes, using a variety of palps and tentacles to collect organic matter or sediment microalgae from the surface. Many polychaetes are burrowing species ingesting the sediment below the sediment surface.

Herbivores. These are mainly shallow water species that either graze on macroalgal films or consume macroalgae. They have already been discussed in Chapter 14 of Section 4.2.3.

Omnivorous and Opportunistic Diet. Many Antarctic benthic invertebrates are omnivorous and feed on a wide variety of prey. For example, Dearborn (1967) found that the diet of the giant isopod *Glyptonotus antarctica* was surprisingly varied: ophiuroids (52.3%), gastropods (19.3%), isopods (17.4%), echinoids (14.7%), ectoprocts (6.4%), but also pycnogonids, sponges, crinoids, brachiopods, algae, amphipods (especially *Orchomene*), and carrion.

Amphipod feeding has been extensively studied. Herbivorous species, mainly gammarideans, are common only in areas where there are macroalgae (Knox and Lowry 1977). Most amphipods in the Weddell Sea are either scavengers, predators or omnivores utilizing food resources year round (Klages 1993). Slattery and Oliver (1986) investigated the feeding habits of the two *Orchomene* species in McMurdo Sound. *O. plebs* is a scavenger, whereas *O. pinguides* preys on invertebrates, particularly on planktonic copepods, which approach the bottom in winter. While some isopods, such as the Acturidae, are filter feeders, the majority are omnivores or predators. Most Antarctic shrimps are omnivorous (Gorney 1992).

Gastropods are either herbivores or omnivores. Among the nudibranchs, the Austrodoridae and Aegiretidae are exclusively sponge eaters; *Aegires albus* feed on calcareous, *Austrodoris kerguelensis* on siliceous sponges, *Tritoniella belli* on ascidians, and *Tritonia* spp. on *Cephalodiscus* (Tentaculata). Bathydoridae (3 spp.) are omnivorous, whereas *Notaeolidia subgigas* consume hydrozoans exclusively (Wagle and Buto 1990).

The different ecological niches of the holothurians have been described by Gutt (1988, 1991). Most ophiuroids are benthos or zooplankton predators (Dearborn et al. 1986). For example, *Astrotoma agassizii* feeds on copepods, mysids, chaetognaths and euphausiids (Dearborn et al. 1986). *Ophionotus victoriae* ingests benthic microfloea (Kellogg et al. 1983), but also consumes a variety of phyla including krill *Euphausia crystallorophias.* The starfish *Labidiaster annulatus* is a predator and scavenger that consumes macroinvertebrates and even small fish. *Odonaster validu,* the most abundant starfish, has opportunistic feeding habits, whereas other asteroids (*Acodonaster hodgsoni, Perknaster fuscus antarcticus*) which feed on sponges, are very restricted in their diets.

11.16 BENTHO–PELAGIC COUPLING

An account of particle flux and sedimentation in Antarctic waters is to be found in Chapter 14. Annual vertical flux of particulate organic matter varies from 0.133 to 130 g C m^{-2} yr^{-1}, although the majority of the flux rates generally range between 5 and 40 g C m^{-2} yr^{-1} (Schalk et al. 1993). Flux rates are dependent on the extremely seasonal nature and short duration of the blooms of primary production and the production of fecal pellets by the pelagic consumers. Figure 11.17 shows the changes which occurred in the sedimentation of organic detritus (seston) in shallow waters off Zukov Island, Halswell Islands (66°32″ S, 93°00″ E). The seston peaked in mid-January, with a secondary peak in March, declined to a low level in May and remained low until it began to increase again in November. In addition to the

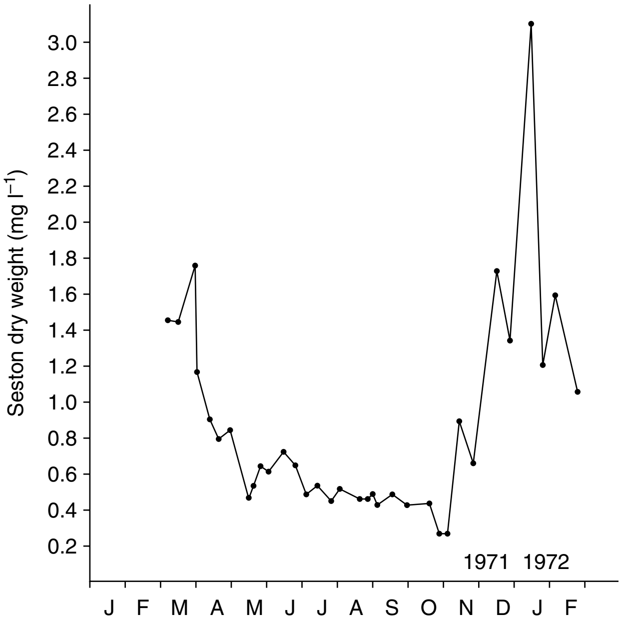


FIGURE 11.17 Changes in the quantity dry weight of seston throughout the year at a shallow water station off Zykov Island, Halswell Islands. (From Gruzov, E. N., *Adaptations Within Antarctic Ecosystems,* Llano, G., Ed., Smithsonian Institution, Antarctica, 263, 1977.)

input of primary production, detrital fallout occurs from the sea ice during the pack ice retreat and melting. This may be important to benthic communities at certain times (Dayton 1990).

Minks et al. (2005) conducted a seasonal study of the flux and fate of phytodetritus, and its impact on benthic community dynamics in a transect crossing the West Antarctic Peninsula shelf. They hypothesized that much of the particulate organic matter produced during the summer bloom period is deposited rapidly on the seafloor, where it is subducted into the sediments by the activities of the benthos. If microbial activity is limited by consistently low temperatures, this phytodetritus may degrade slowly, and could represent a persistent "food bank" for detritovores. Flourometric determination of chloropigments in the sediments indicated occurrence of a highly seasonal depositional event. However, inventories of chloropigments and enzymatically hydroysable amino acids (EHAA) in the top 10 cm of sediment remained relatively constant year-round. At the innermost shelf station, where organic matter deposition was considerably higher, microbial biomass inventories were high year-round. Sediment community oxygen consumption rates ($\sim$1.2 mol C m^{-2} yr^{-1}) were comparable to rates measured in warmer temperate sediments and did not fluctuate significantly throughout the year. Despite relatively high values of microbial biomass (2–12 mg g^{-1} in surface sediments), the supply of labile organic material in the sediments was not depleted, even during low-flux winter months. The data indicated the presence of a persistent "food bank" which could support detritovores year-round. It was concluded that labile organic pools in West Antarctic Peninsula shelf sediments are not drawn down to the low levels seen in other deep-sea sediments. Warming of Antarctic sediments could lead to enhanced respiration of organic material by bacteria, resulting in decreased food reservoirs for benthic detritovores in winter months.

11.17 ECOLOGICAL STRATEGIES

"Antarctic poikilotherms exhibit a number of features such as slow seasonal growth, delayed maturation, longevity, large size, low fecundity, large egg size, nonpelagic larval development, seasonal reproduction and low metabolic rate, that appears to be associated with a suite of mechanisms by which the organisms respond to cold, highly seasonal environments where primary production is confined to a brief period during the summer" (White 1984).

11.17.1 REPRODUCTION AND DEVELOPMENT

In early studies of the life histories of Antarctic poikilotherms, a number of features were postulated as being typical, many of which were either deduced from studies in the Arctic, or were hypothesized agianst the background of specific environmental conditions in polar seas such as the extreme cold, and the highly seasonal environment where primary production was confined to a brief period during summer (White 1994). These features comprise:

- Prolonged gametogensis
- Delayed maturation
- Seasonal reproduction
- Low fecundity
- Large yolky eggs
- Nonpelagic development "Thorsons rule"

- Brooding, brood protection (Thorson 1950; Pearse et al. 1986)
- Slow embryonic development
- Advanced newly-hatched juvenile stages
- Slow growth rate
- Seasonal growth
- Large adult size
- Prolonged longevity
- Low mortality
- Low metabolic rate, low activity

These topics have been discussed in reviews by Picken (1980) and White (1984), and papers by Arnaud (1978) and Picken, (1985a, 1985b).

In marine invertebrates, four reproductive patterns are generally recognized (Mileikovsky 1971), two of which can be called "free development" and two "protected development." Species with free development characteristically discharge large numbers of small eggs into the sea where they develop through intermediate pelagic or nonpelagic stages. There is no free larval stage in species with protected development. A small number of large yolky eggs are produced, and to ensure a high level of survival, they are generally protected during development. Maximum protection is obtained when the developing eggs are brooded by the adult, either inside, or outside the parent's body, and by either sex (Arnaud 1974). The majority of Antarctic species whose reproduction is known have no pelagic larval stage, and there is a strong tendency towards protected development.

The duration of embryonic development of gammaridean amphipod species increases exponentially with decreasing habitat temperature. The duration of the embryonic development of the giant predatory amphipod *Eusirus perdentatus* lasts a minimum of 14 months (Antz et al. 1992; Klages 1993). Much longer development times, as compared to related species living in temperate regions, have been reported for Antarctic molluscs, the extreme case being prosobranch gastropods with a development time of about two years until hatching (Hain 1990). Long-lasting metamorphosis in echinoderms has been reported by Boesch et al. (1987) from McMurdo Sound and by Gutt (1991a, 1991b) for holothurians. In most cases, long development times have been found to be connected with large egg size and, consequently, low fecundity. Examples include the polychaete *Scoloplos marginatus* (Hardy 1967), mysids, with a low number of offspring, the amphipods *A. richardsoni, P. gibber, and E. perdentatus,* the egg diameters of which (1.1–2 mm) are about 2.5 times greater than those of gammarids in temperate or tropical areas (Klages 1993) octopod cephalopods (Kuhl 1986) and other molluscs.

The timing and pattern of reproduction varies. White (1977) suggested that the timing of reproduction is largely controlled by the degree to which adults or juveniles are dependent on the summer production. The onset of summer production is predictable in offshore waters, but in shallow inshore waters, the presence of sea ice can drastically affect the timing (White 1977). Reproductive activities, such as gametogenesis, spawning and liberation of ova may either be synchronized with the annual production cycle or may be independent of it. White (1977) proposed a model that includes the various breeding cycles found in Antarctic invertebrates (Figure 11.18).

The various species can be grouped as follows:
Group 1. Species with a nonseasonal breeding cycle where the young stages are released throughout the year, and both adults and young are independent of the elevated summer

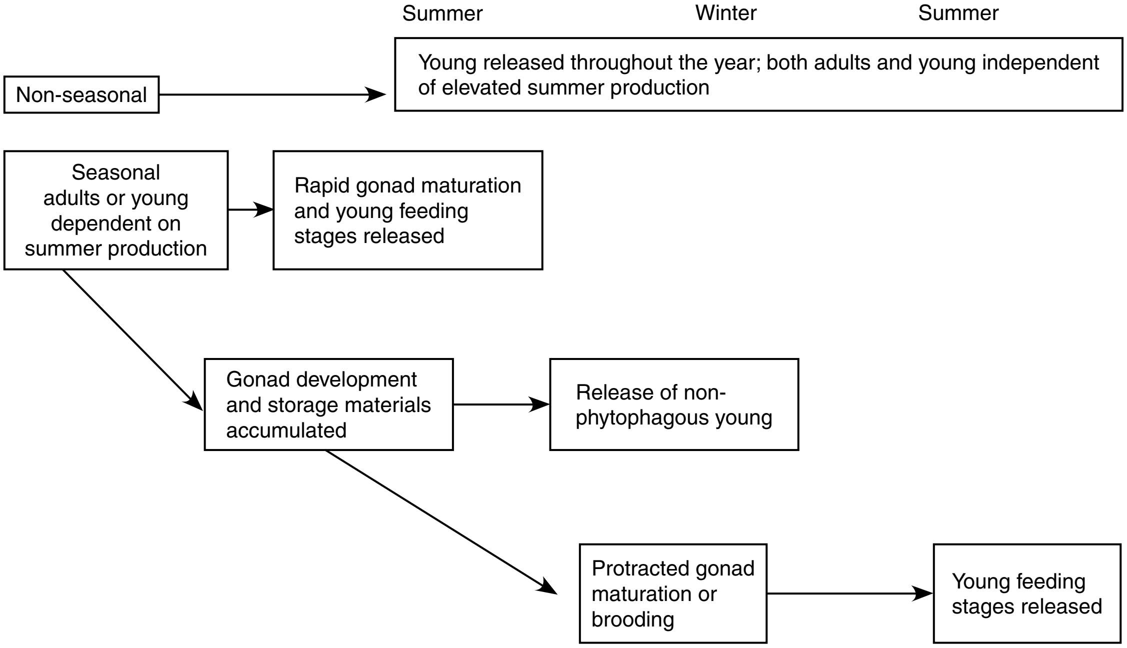


FIGURE 11.18 Model of Antarctic benthic invertebrate breeding cycles. (From White, M. G., *Adaptations Within Antarctic Ecosystems*, Llano, G., Ed., Smithsonian Institution, Washington, DC, 197, 1977. With pemission.)

production level. Most species are predator-scavengers with highly adaptable diets such as the giant isopod *Glyptonotus antarcticus,* which has prolonged development rates and breeds continuously (Dearborn 1967; White 1975).

Group 2. These are species that have seasonal breeding cycles in which the adults, or young, or both are dependent on the summer pulse of primary production. Cyclic growth rates are typical. Subgroup 2a, such as many planktonic herbivores, have life histories that are completed in one year. A group of species (Subgroup 2b) which included the echinoderms *Odonaster validus* and *Sterechinus neumayeri*, and the polychaete *Scoloplos marginatus mcleani* have prolonged breeding cycles and protracted gonad development. They accumulate energy reserves during the summer, in some cases over more than a year, with the release of young nonphytophagous stages during the winter. Subgroup 2c species have similar prolonged life cycles and protracted gonad development, and the young may be brooded, with young feeding stages being released during the subsequent summer season. Typical species are amphipods such as *Cherimedon femoratus*, *Bovallia gigantea*, and *Paramoera walkeri*.

11.17.2 BROODING AND LACK OF PELAGIC LARVAE

The predominance of brooding species in the Antarctic benthos and the “relative absence” of pelagic larvae, have been discussed extensively (e.g., Picken 1978a, 1978b, 1980, 1985a, 1985b; White 1985). This dates back to “Thorson’s rule” (Thorson 1950). Thorson hypothesized—mainly from evidence collected in the Arctic—that there is a strong tendency towards nonpelagic development and brood protection in polar waters due to the insecurity of prolonged larval life in these waters where production is restricted to a short period each year. However, the general validity of this rule has been challenged by Pearse et al. (1986) and Berkman et al. (1991) because of the increasing number of species that have been found to have pelagic larvae. Antz et al. (1997) lists 21 of such species. Some groups do exhibit unusually high incidences of brooding.

In sponges, more than 80% of the species exhibit brood protection (Arnaud 1974). Brood protection is the principal adaptation of the lamellibranchs (Soot-Ryen 1951; Dell 1965, 1972), and brood protection and viviparity are common among the echinoderms and widespread in the isopods and amphipods (Arnaud 1974). More than 59% of the Antarctic ophiuroids whose type of reproduction is known exhibit brood protection, and this is a much higher proportion than is found in other parts of the oceans, including the Arctic (Mortensen 1936). In the echinoids, two of the three Antarctic families are dominated by species that brood (Arnaud 1974), while the third family is represented by a single species which produces demersal larvae (Pearse and Giese 1966). Seventeen species of Antarctic holothurians exhibit brood protection (Arnaud 1974), while eleven species of crinoids are known to brood in the Antarctic (John 1938, 1939) compared to only three species known to brood elsewhere.

Several theories have been advanced to explain the tendency towards nonpelagic and protected development among high latitude marine invertebrates. The most satisfactory explanation is that of Thorson (1950), who proposed that in the polar oceans a combination of a short period of phytoplankton production, and low water temperatures, which would slow the rate of development, increase the difficulty of completing pelagic development before food becomes scarce in surface waters. Under such conditions, nonpelagic development, either by large yolky eggs, brood protection, or viviparity are adaptations that ensure the survival of the offspring to the juvenile state. Nonpelagic development by demersal larvae is a similar development, since food will be present on the sea floor long after the phytoplankton bloom is over.

11.17.3 GROWTH AND LONGEVITY

Slow growth, large final size and prolonged longevity have often been considered characteristics of polar benthic species (White 1984). However, Antarctic invertebrates show a wide range of growth rates (Everson 1977a; White 1977; Clarke 1980b). When species with a similar maximum size and ecology are compared (Ralph and Maxwell 1977a, 1977b, 1977c), the polar species have been found to grow more slowly than their temperate counterparts. Similar relationships have been demonstrated for fish (Everson 1977a, 1977b; Arnaud 1977), echinoderms (Pearse 1965), and crustaceans (Luxmore 1982). Associated with this slow growth rate is a slowing of embryonic development as discussed above, with a prolonged period of larval development; e.g., the brooding incubation period for Antarctic crustacea is 5–8 months, compared to temperate species which have incubation periods of 8 days to 2 months, generally (Bregazzi 1972; White 1984).

However, there are some exceptions to the generalization that the growth rates of Antarctic invertebrates are low. The three species of bivalves with comparatively fast growth have been mentioned above. The sponges *Mycale acerata* and *Homaxinella balfourensis* in McMurdo Sound (Dayton et al. 1974; Dayton 1990) and the ascidians *Ascidia challengeri, Cnemidocarpa verrucosa* and *Molgula pedunculata* at King George Island (Rauchet 1991) revealed remarkably fast growth in comparison with other species in the same environment. Everson (1977) showed that three species of Antarctic bivalves (*Kidderia bicolor, Lissarca miliaris*, and *Yoldia eightsii*) grew slower than the temperate *Venus striatula*, but another three species (*Adamussium colbecki, Gaimardia trapesina*, and *Laternula elliptica*) grew faster. A relatively fast growth rate has also been determined for the Antarctic limpet, *Nacella coincinna,* (Clarke 1996).

Clarke (1987) was the first to explore how the relation between temperature and basic metabolism may affect reproduction. He analysed two measures of reproductive metabolism: gonad productivity (GP), i.e., annual mass-specific gonad production, and reproductive effort (RE), i.e., the share of assimilated energy used for reproductive purposes. From model compilations, Clarke (1987) concluded that GP and RE are affected in different ways by temperature. In animals of similar size and ecology, either GP will decrease with decreasing temperture if RE remains constant, or RE will increase with decreasing temperature if GP remains constant. Brey (1995) analysed the available data on population dynamics of marine benthic invertebrate populations to establish whether or not there are general trends in GP and RE related to temperature. He concluded that the evolutionary adaptation of gonad metabolism tends towards changing GP and maintaining RE independent of temperature. Cold adapted invertebrates tend to maintain the proportion of energy invested in reproduction, irrespective of temperature, while gonad productivity is reduced.

Clarke (1980b) concluded that while low environmental temperatures were no bar to fast absolute growth polar species grew slower than the related species of similar ecology and potential maximum size from warmer waters. He noted, as others have, that growth was often markedly seasonal, and since temperatures fluctuate very little at high latitudes, concluded that food was a major regulating factor.

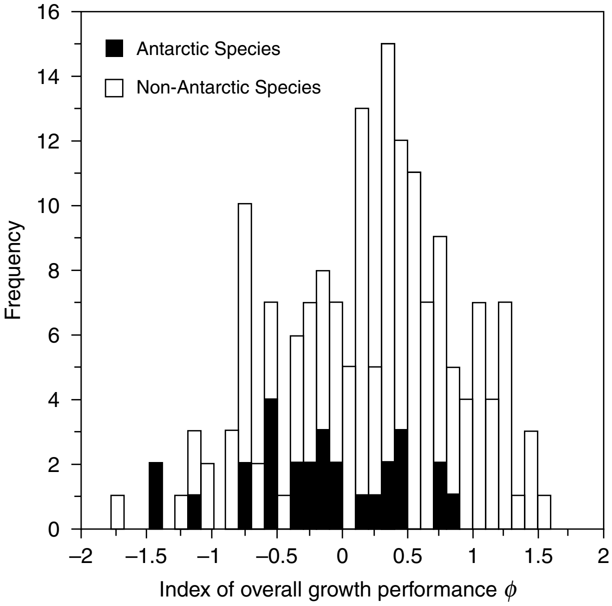


FIGURE 11.19 Frequency distribution of the index of overall growth performance in Antarctic ($N=28$) and nonAntarctic ($N=141$) benthic populations. The index is significantly smaller in Antarctic populations. (From Antz, W. E., Brey, T., Gallardo, V. A., *Oceanogr. Mar. Biol. Annu. Rev.*, 32, 241, 1994. With permission.)

11.17.4 SEASONALITY VS. NONSEASONALITY OF REPRODUCTION AND GROWTH

A question that has concerned Antarctic ecologists is whether reproductive and growth cycles are coupled or decoupled to/from the extremely seasonal conditions of the Antarctic, reflected especially by the short period of food input. Several Antarctic invertebrates have been found to exhibit strong seasonal oscillations in growth. While summer peak growth rates may well be in the range of comparable boreal species at other times, growth rates are extremely slow. Antz et al. (1997) surveyed the growth strategies of both Antarctic and nonAntarctic species (Figure 11.19). They analysed data from the literature and concluded that many different strategies have been realized in the Antarctic, from strict coupling to total decoupling of reproduction and growth.

11.17.5 LARGE SIZE

“Gigantism” is frequently mentioned as a characteristic of Antarctic benthic invertebrates and it has been noted in pycnogonids, sponges, isopods, amphipods, and freeliving nematodes (Arnaud, 1974, 1977; De Broyer 1977). It is postulated that slow growth, delayed maturation, prolonged gametogenesis, and embryonic development result in enhanced longevity and large size in Antarctic invertebrates. Arnaud (1974) tested this hypothesis in various groups of Antarctic invertebrates and concluded that while the phenomenon was real in some groups, it was lacking in others that were of “normal” size, or showed a tendency towards “dwarfism.” He found that the only Antarctic invertebrates that reached a large size were those that were not hampered by calcium problems, that is invertebrates requiring only small amounts of calcium (arenaceous foraminiferans, crustaceans and tubiculous polychaetes), or no calcium (hydroids, nudibranchs, ascidians, and many polychaetes). According to Arnaud (1977), species which are not limited by this factor reach a large size as a consequence of three favourable factors: (1) slow rates of development and growth; (2) low predation pressure on certain species; and (3) high availability of silica to siliceous organisms (e.g., radiolarians and hexactinellid sponges). When predation and interspecific competition is weak, organisms grow to an old age and large size. For example, the asteroid *Odonaster validus* may live for more than 100 years according to Pearse (1969), and the large rosellid hexactinellid sponges in McMurdo Sound may live much longer than this.

11.17.6 METABOLIC ADAPTATIONS

Antarctic organisms must be able to grow, reproduce, feed and evade predators at temperatures close to or even below 0°C. The first explanation of this was the concept of metabolic cold-adaptation (i.e., that polar poikilotherms are characterized by an elevated metabolic rate) (Clarke 1980, 1983, 1991). The concept of coldadaptation was attractive because it conveniently explained the frequently observed phenomena of slow growth, delayed maturation and prolonged gametogenesis. However, this concept has been

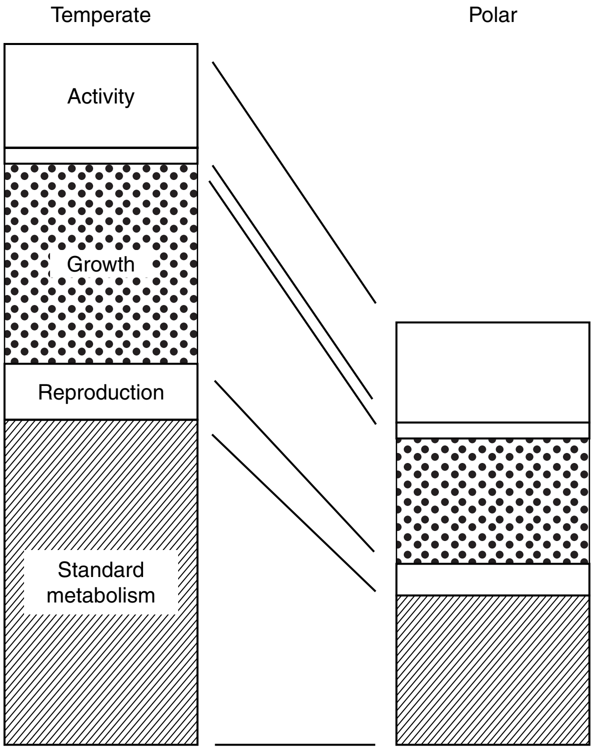


FIGURE 11.20 A diagrammmatic representation of the annual energy intake of a typical temperate-water marine invertebrate, and a typical polar marine invertebrate showing the effect of adaptation to cold water as proposed by A. Clarke (1980b). The relative sizes of the boxes representing the metabolism, reproduction, growth and moulting (unlabelled) in the polar rectangle are based on data for the Antarctic isopod *Serolis polita* (Luxmore 1982). The sizes of these boxes in the temperate-water species have been obtained from the literature for temperate-water species. The size of the box representing activity is arbitary, and is the same for both temperate and polar species. (From Clarke, A., *Antarctic Nutrient Cycles and Food Webs,* Siegfried, W. R., Condy, P. R., Laws, R. M., Ed., Springer-Verlag, Berlin Heidelberg, 571, 1985. With permission.)

challenged in the light of a growing body of biochemical and physiological data. Well controlled experiments on polar marine invertebrates (White 1975; Maxwell 1977; Ralph and Maxwell 1977b, 1977c; Maxwell and Ralph 1985) have demonstrated low, not elevated, metabolic rates at ambient temperatures. More recent experiments confirmed doubts about the validity of the concept (Peck 1989). Everson (1977a) concluded that in Antarctic invertebrates there is no detectable elevation of routine, and by inference, basal metabolic rate. Thus the concept that an elevated basal metabolic rate in cold water invertebrates resulting in less energy available for growth and reproduction cannot explain the slow growth rates that have been observed.

Clarke (1980b), in a reappraisal of the concept of cold-adaptation in polar marine invertebrates on the basis of a reduced basal metabolism, reduced growth, reduced reproductive effort, and on the assumption that the energetic costs of feeding, movement and other activities are comparable between different environments, advanced the view that polar adaptations tend towards an overall reduction in energy utilization (Figure 11.20). In comparing crustacean species living at temperate (10°C) and polar (0°C) environmental temperatures, it was found that the basal metabolism of polar species was reduced by 55%, growth by 40%, and reproductive effort by 30% in comparison with temperate species (Clarke 1979; Clarke and Lakhami 1979). Figure 11.20 depicts this in a diagrammatic form.

Clarke (1980b) points out that many of the features of the Antarctic marine benthos can be interpreted as the result of the evolution of typical K-adapted qualities, that is slow growth, protracted development, reduced effort, low basal metabolic rate, large yolky eggs, advanced newly-hatched juvenile stages, seasonal breeding, deferred maturity, increased longevity and large size. These qualities act together so as to adapt the species to cold temperatures and seasonal availability of primary production. Those organisms that have been selected for reduced annual energy intake will have been the most successful in colonizing the Antarctic benthos.

As we have seen, fish have evolved antifreeze compounds to avoid freezing at low temperatures. To date there have been a limited number of investigations on freezing avoidance in benthic invertebrates. Cziko et al. (2005) noted that in McMurdo Sound, in spite of the ubiquitous abundant growth of shallow-bottom anchor ice, starfish were always ice-free, suggesting that they may secrete an anti-ice growth compound to avoid being encased in ice. They found that most species of McMurdo Sound echinoderms they examined showed the presence of small amounts of thermal hysteris, equivalent to ~0.1–0.2°C freezing point depression and strong effects on the growth habit of single crystal ice. This ice-active compound is a heat resistant protein of about 6.5 kDa. And it is postulated that it plays a role in maintaining an ice-free microenvironment for the species that produce it.

12 The Fast Ice and Ice Shelves

CONTENTS

12.1 INTRODUCTION

Around the margin of the Antarctic Continent lies the fast-ice region. This is sea ice that either breaks out very late in the season or remains for two or more years, forming multiyear ice that may reach a thickness of several metres. It lies within the coastal area of the permanent pack ice zone as defined in Chapter 15. In addition there are the floating ice shelves formed by glacial ice outflowing from the ice-covered Antarctic Continent. Although such ice shelves extend to varying degrees at locations around the continent, the most extensive are the Ross Ice Shelf in the Ross Sea and the Filchner and Ronne Ice Shelves in the Weddell Sea.

12.2 THE COASTAL FAST ICE ENVIRONMENT

12.2.1 SEA ICE

The formation of the sea ice and its characteristics have already been discussed in Chapter 3. There, it was noted that there are two main types of sea ice: columnar or congelation ice, and frazil ice. The proportions of columnar and frazil ice can vary widely, although the former dominates the sea ice of the fast ice zone. However, in the inner Weddell Sea, ice-core data indicate that congelation ice accounts of only about 20% of the multiyear ice and 47% of the first-year ice, with fine-grained layers of frazil crystals making up most of the remainder.

12.2.2 ANCHOR ICE AND PLATELET ICE

Anchor ice and platelet ice have been discussed in Chapter 3 of Section 2. Where they are especially well-developed (e.g., in inner McMurdo Sound and under the McMurdo Ice Shelf [Knox 1986; Barry 1998]) they occur where the seawater becomes supercooled (temperatures below the in situ freezing point). Nucleation leading to frazil or platelet ice formation can occur when deep water cooled below freezing point is upwelled. In McMurdo Sound such conditions occur where water cooled by contact with the bottom of the shelf flows northward from underneath the McMurdo Ice Shelf (Barry and Dayton 1988) (see Figure 12.1). Ice platelets can range from 10 to 20 cm in diameter and 0.2–0.2 cm in thickness. Dayton, Robilliard, and DeVries (1969) have observed aggregations of platelets frozen to each other on the bottom in depths shallower than 33 m.

There is considerable variation throughout the McMurdo Sound region in the development of the platelet ice layer beneath the fast sea ice. In the early 1980s, in the middle of McMurdo Sound near the edge of the McMurdo Ice Shelf, the layer formed by small platelets was only 10–20 cm thick, while at White Island the layer of larger platelets was up to 5 m in thickness (personal observations). In some areas the tide cracks that develop along the margin of the land are filled with platelet ice to a considerable depth. There is also considerable variation in the occurrence of platelet ice round the Antarctic Continent. In many areas it has not been reported. However, the winter expedition of the *Polarstern* found extensive areas of platelet ice under the pack ice in the southern Weddell Sea (see Section 12.3).

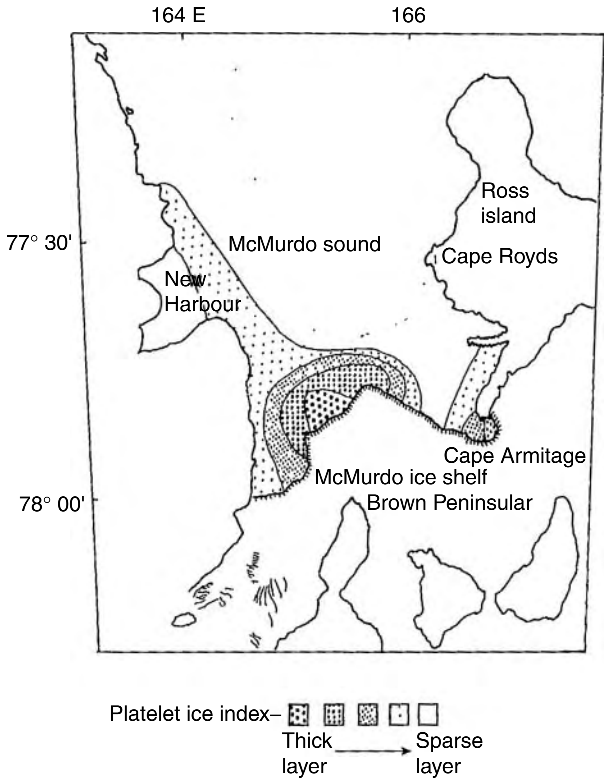


FIGURE 12.1 Platelet ice abundance index distribution during November 1984 in McMurdo Sound. Heavier dot pattern indicates greater platelet ice thickness indicative of cold water outflow from under the McMurdo Ice Shelf. (From Barry, J.P., *Polar Biol.*, 8, 367, 1988. With permission.)

Dayton, Robilliard, and DeVries (1969) consider that the anchor ice has considerable biological significance. When the anchor ice becomes detached due to currents, inherent buoyancy or a disturbance, it floats to the underside of the subice platelet layer carrying with it portions of the substratum, which in one instance was observed to weigh at least 12 kg. Epibenthic organisms such as asteroids, nemerteans, isopods, pycogonids, fish and algae entrapped within the anchor ice can thus be transported to the underside of the ice. This may act as an important distribution mechanism (Knox and Lowry 1977) when the sea ice breaks up to form pack ice which may drift a considerable distance before melting.

12.2.3 THERMOHALINE CHARACTERISTICS

The most extensively studied fast ice area is that investigated by Japanese scientists off Syowa Station (Hoshiai 1969, 1977, 1981a, 1981b, 1985; Fukuchi and Tanimura 1981; Wakatsuchi 1982; Fukuchi et al. 1984, 1985a, 1985b, 1986; Hoshiai 1985; Hoshiai and Tanimura 1986; Hoshiai et al. 1987; Tanimura et al. 1996). Fukuchi et al. (1985a) reported on data from five oceanographic stations in Lutzow–Holm Bay (1–5) in depths of 10, 25, 50, 160, and 675 m respectively. Temperatures varied from a maximum of −1.19°C to a minimum of −1.89°C while salinities varied from a maximum of 34.42 to a minimum of 33.52. Littlepage (1965) occupied a station on the fast ice over 290 m of water in McMurdo Sound during 1961. Values of temperature and salinity ranged from −1.4 to −2.5°C and 33.96 to 34.99. This temperature range was about 0.30°C lower than those recorded in Lutzow–Holm Bay, while the salinity range was about 0.50 higher. In contrast to the distinct seasonal variation observed for physical properties the levels of nutrient salts did not show clear seasonal trends. Phosphate-P, silicate-Si, and nitrate-N remained high throughout the studies in Lutzow–Holm Bay while levels of ammonium-N and nitrate-N generally were low.

In McMurdo Sound, Barry (1998) made an extensive study of the hydrographic patterns under the fast ice. During spring water temperature was nearly homogenous apart from some surface variations and very cold water near the bottom in the central sound. Temperatures below freezing point were observed at several sites, particularly where currents flowed northward from under the McMurdo Ice Shelf (see Figure 12.1), indicative of cooling by contact with the bottom of the shelf. Although summer temperatures near the bottom were near spring values (−1.9°C), the upper 100 m became highly stratified with relatively warm water near surface temperatures (−0.8 to −1.3°C), and a few values above zero in some isolated localities.

In spring the highest salinities were in the northern and eastern sound (34.86–34.89). Western sound waters were slightly less saline (34.73–34.77) due to dilution by meltwater input from beneath the shelf and/or glacial meltwater from the Koettlitz Glacier region. Salinity was strongly heterogeneous during the summer with a substantial halocline near the surface. In addition to dilution from sea ice meltwater, terrestrial and especially McMurdo Ice Shelf surface meltwater diluted the surface waters, especially in the western sound. During late January 1984, a 6-m surface layer of freshwater (0.2–0) was present at an isolated station in the western sound under permanent ice.

A number of studies of the fast ice environment have recorded the presence of a low salinity surface layer beneath the ice in late summer due to the melting of the ice (Hoshiai 1969; Watanabe et al. 1982; Iwanami et al. 1986; Matsuda et al. 1990). Often this layer is less than a metre thick and it may be concentrated in hollows on the underside of ridges in the ice and consequently may be missed in sampling through holes in the ice.

On the third winter cruise of the *Polarstern* a survey of the hydrographic conditions under the sea ice was carried out in November 1987 (Eichen et al. 1987). At that time most profiles showed a slight decrease in salinity close to the surface indicating that some melting had taken place (see Figure 12.7). At station 587 a temperature drop of 0.06°C occurred within 40–50 cm below the ice. At station 620, there was a layer of platelets some 60-cm thick below the solid ice. Within this platelet layer there was only a slight decrease in salinity (0.2). Nutrient levels in the upper low-salinity layer were much reduced with both nitrate and phosphate levels at the water surface under the ice near the limit of detection.

12.2.4 NUTRIENTS

There have been a limited number of studies of nutrient distributions in the waters of the fast ice zone. In the spring, the McMurdo Sound nutrient (NO_3^-, NO_2^-, PO_4^{3-}) distributions reflected the post winter pattern before the onset of the seasonal summer phytoplankton bloom Barry (1998). There were relatively homogeneous and high nutrient levels throughout the sound as a consequence of low productivity and winter replenishment by regeneration and mixing. Nitrate (30 μM) and phosphate (2.3 μM) concentrations were high while nitrite was usually low (<0.01 μM). On the other hand, in contrast to results obtained at Syowa station, nutrients (NO_2, PO_4) were low following the seasonal phytoplankton bloom and were near zero at isolated localities. Depletion was greatest near the surface where the water column stability was high. Nitrate levels were about 15% of the prebloom levels under the sea ice near McMurdo Station (3.9–5.4 μM) and were lower (0.1–1.6 μM) in the western sound. In contrast, nitrite concentrations were highest during the summer. Nutrient depression was probably due to a combination of phytoplankton utilization and dilution from low nutrient levels in glacial and sea ice meltwater.

Riaux-Gobin et al. (2003) described a coastal-to-offshore land-fast ice gradient in the distribution of nutrients. Nitrate, in very high concentrations, occurred in the platelet ice layer in the more coastal sites, apparently related to the high microalgal biomass in this layer, and it seemed to have been actively regenerated in this layer. Salicic acid also showed a coastal to offshore gradient.

12.2.5 CURRENTS

Inshore current systems have been extensively studied in inner McMurdo Sound. Mean currents in McMurdo Sound are the result of the additive effects of various driving forces including local and large-scale wind driven circulation, tidal rectification, and pressure gradient forces arising from variations in density. Barry and Dayton (1988) contrast their 1984 results with those of Lewis and Perkins (1985) in 1982 when northerly input from beneath the shelf dominated the southern sound (see Figure 12.18). They speculate that the differences were due to changes in the driving force of the Antarctic Coastal Current which flows west along the Ross Ice Shelf barrier and contributes strongly to net transport into McMurdo Sound through the southern extension (Cape Bird current) sweeping into McMurdo Sound. It is probable that global atmospheric anomalies such as ENSO (El Nino southern oscillation) is linked to these differences, as they have been linked by numerous authors to global scale variability in atmospheric pressure and associated zonal winds.

12.2.6 THE LIGHT REGIME

The light regime under the sea ice has been discussed in Chapter 3. Because the fast ice environment is located round the margins of the Antarctic continent at high latitudes the incident light regime has a very strong seasonal component, with a varying period of complete darkness depending on the latitude. Light penetration into the water column as discussed in Chapter 3 of Section 2 is determined by ice thickness, snow cover and the degree of shading by the sea ice microalgal community (see Figure 12.2). The most important variable however is the depth of the snow cover on the ice (Satoh et al. 1986; Grossi et al. 1987).

12.3 PRIMARY PRODUCTION

In this section, water column phytoplankton production will be discussed. Sea-ice microalgal and benthic microalgal production are considered on Chapter 3 and Chapter 11, respectively. An ecosystem model for the fast ice zone will be considered in Chapter 15.

Because of the thick layer of ice, often covered with snow drifts of varying thickness, in the coastal fast ice region light penetration in the water column is very low. Littlepage (1965) reported that only up to 0.5% of the incident light on

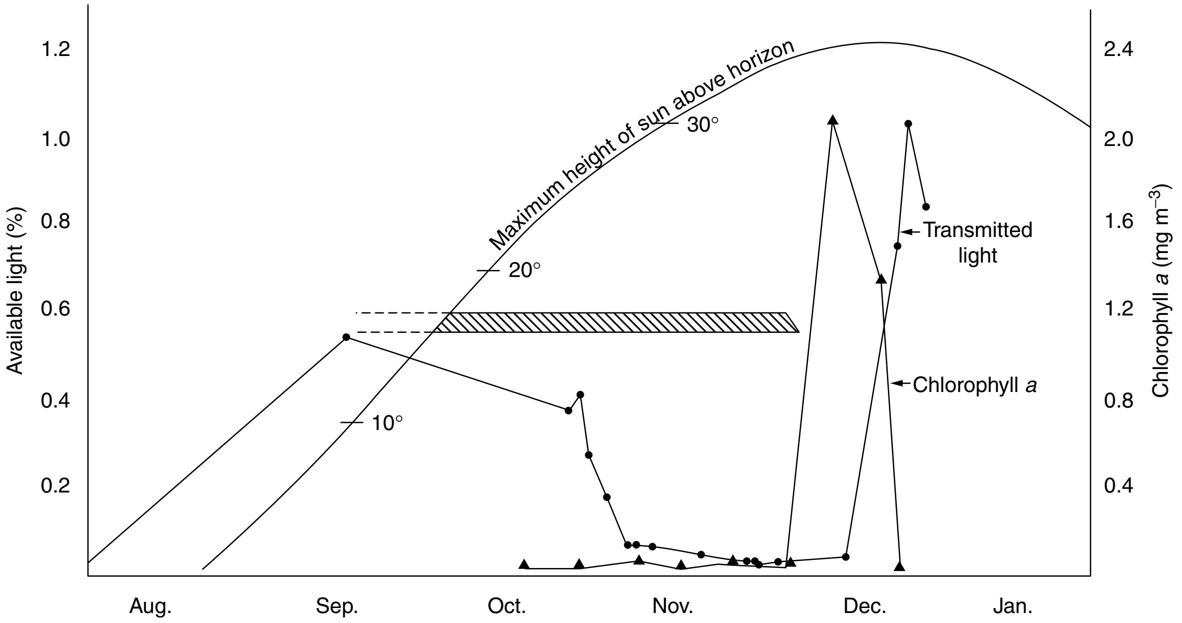


FIGURE 12.2 Profiles showing the percent transmitted light (circles) chlorophyll *a* (triangles) in the water column in relation to the maximum height of the sun above the horizon, the presence of sea ice (Aug. to Nov.-early Dec.) and the development of the sea ice microalgae (shaded area). (Adapted from Bunt, J.S., *Ant. Res. Ser.*, 1, 13, 1964a. With permission.)

the surface of the snow reached the surface of the water. However, with the development if the ice algal community, the amount of light is further reduced. Figure 12.2 illustrates this with data from McMurdo Sound. Total photosynthetically available radiation (PAR) was reduced to 10% of the surface downwelling irradiance in passage through the ice, and to less than 1% under the platelet ice layer. Absorption of light by the ice algae also affected the spectral composition of the light by strong absorption at 670 nm between 400 and 500 nm (Sullivan et al. 1984). In September–October the light penetration was between 4% and 6%, while in early November, as the ice algal community developed, the light transmission declined to reach hundredths of one percent. As the ice algal layer disintegrated in late December–January, the light penetration increased to one percent.

Bunt (1964a, 1964b) was the first to investigate in detail the water column phytoplankton under the fast ice. In the waters of McMurdo Sound, he recognized at least three distinct communities of algae. The first appeared to be composed entirely of a limited range of planktonic diatoms, with *Nitzschia seriata* as the numerically dominant species. In 1961, this community was evident in early December until it was overwhelmed suddenly by a second assemblage composed of diatoms and high concentrations of *Phaeocystis*. In the following summer, when the fast ice was thicker and more extensive, *Phaeocystis* did not make its appearance until the first week in January. The *Phaeocystis* bloom, which may persist for several weeks (personal observations at Cape Bird and in inner McMurdo Sound over several seasons) is replaced by a diverse assemblage of species typical of more northern Antarctic waters such as *Thalassiosira antarctica* and *Synedra pelagica*.

At Mawson Station in late December, Bunt (1960) recorded a maximum surface chlorophyll *a* concentration of 3.9 mg m^{-3} at 5 m, with an integrated stock (0–24 m) of 70 mg m^{-2}. At a deeper station on 28 January, the maximum chlorophyll *a* concentration of 2.15 mg m^{-3} at a depth of 75 m was recorded, with an integrated stock (0–100 m) of 152 mg m^{-2}. Off Cape Armitage in inner McMurdo Sound, Bunt (1964a, 1964b) studied the standing crop of phytoplankton beneath the fast ice. The peak chlorophyll *a* level recorded in early January at 5 m was 16 mg m^{-3}. On December 13, 1962, water from 5 m contained approximately 0.01×10^6 diatom cells l^{-1}. By January 16, 1963, this value had increased 36 times to 0.36×10^6 cells l^{-1}. Between January 2, 1983, when *Phaeocystis* first appeared, and January 6, the numbers of this species rose sharply to more than 10 l^{-1} (the numbers refer to individual unicells and not to colonies) and reached a peak of almost $3 \times 19\ l^6$ in a sample from 20 m in January. Figure 12.3 shows that at Syowa Station in the summer of 1967–1968, surface chlorophyll *a* levels closely followed the solar curve (Hoshiai 1969). Surface chlorophyll *a* increased in early December to reach a peak on December 22 of 6.13 mg chl *a* m^{-3} after which the levels declined to a low of 0.42 on January 20. A second peak of 2.64 mg chl *a* m^{-3} occurred on April 1. Chlorophyll *a* levels in deeper water increased later with single peaks of 4.8 mg chl *a* m^{-3} on January 4 at 2 m, 7.62 on January 11 at 4 m, 11.93 on January 29 at 6 m, and 10.99 on January 29 at 8 m.

Fukuchi et al. (1984, 1985a) measured chlorophyll *a* concentrations in the water column under the fast ice at Syowa Station at five stations (10–675-m depths) for a period of 13 months from January 1982 to January 1983. High

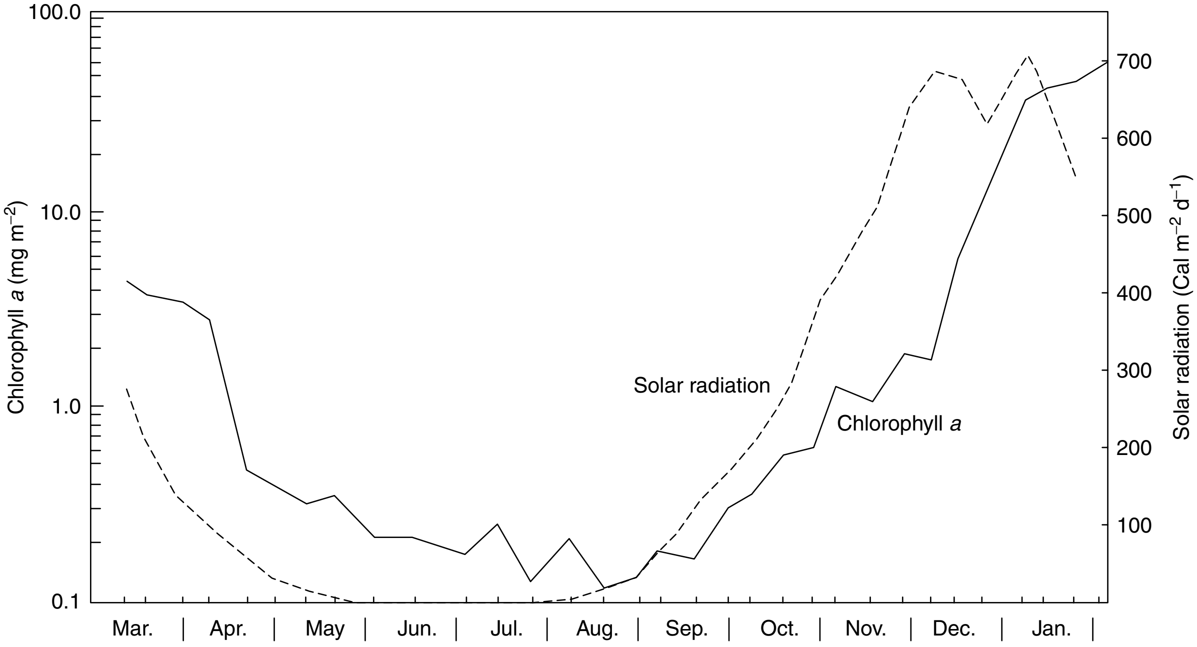


FIGURE 12.3 Seasonal variation of chlorophyll *a* beneath the sea ice and incident solar radiation at Syowa Station. (Hoshiai, T., *Ant. Rec.*, 35, 52, 1969a. With permission.)

chlorophyll *a* concentrations were recorded between December and March with peak values in late January: Station 1 (10 m) 7.01 mg m^{-3} at 6 m; Station 2 (25 m) 9.74 mg m^{-3} at 5 m; Station 3 (50 m) 11.3 mg m^{-3} at 5 m; Station 4 (160 m) 9.91 mg m^{-3} at 0 m. The maximum concentration recorded was 11.3 mg chl *a* m^{-3}. The peak levels were apparently caused by a slight decrease in the water temperature (> -1.73°C) and a slight decrease in salinity (<34.5). The average chlorophyll stock in the water column was 1.05–25 mg chl *a* m^{-3}, at least an order of magnitude higher than that reported from Antarctic open waters, such as 0.39 mg m^{-3} by ElSayed and Jitts (1973), 0.22 mg m^{-3} by Holm-Hansen et al. (1977) and 0.52 mg m^{-3} by Kundo and Fukuchi (1982).

Satoh et al. (1986) repeated Fukuchi et al.'s (1984) observations over the period February 1983 to January 1984. Figure 12.4 depicts the seasonal variation in integrated chlorophyll *a* stocks over this period at stations 1, 3, and 5. At all three stations there was a clear single annual peak of phytoplankton biomass over the period mid-January to mid-February. These peak biomass levels, however, were less than half of those occurring in 1983. Satoh et al. (1986) attributed this difference to less light penetrating into the water column due to the increased cover of the sea ice. This single phytoplankton bloom which is characteristic of high latitude fast ice locations contrasts to the three bloom (autumn, spring and summer) that occurred during the period from November 1972 to March 1973 in Arthur Harbour (64°46′ S, 64°06′ W) on Anvers Island (Krebs 1983) (Figure 12.5). While there are differences in the species composition of the three blooms the two dominant species *Porosira glacialis* and *Nitzschia* spp. were the same.

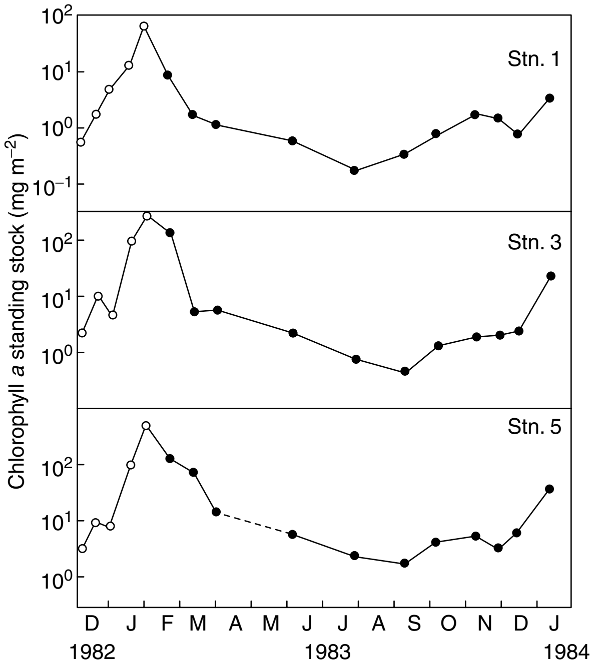


FIGURE 12.4 Seasonal variation of integrated chlorophyll *a* stocks from the water column under the sea ice off Soywa Station (Sta. 1, 12 m; Sta. 3, 38 m; Sta 4, 160 m; Sta. 5, 700 + m). Sta. 1 was sampled from 2 to 11 m; Sta. 3 from 2.5 to 35 m; and Stations 4 and 5 from 2.5 to 150 m. Open circles denote the stocks which were calculated from data cited by Fukuchu et al. (1985b). (From Satoh, H., Watanabe, K., Kanda, H., Takahashi, E., *Ant. Rec.*, 30, 19, 1986. With permission.)

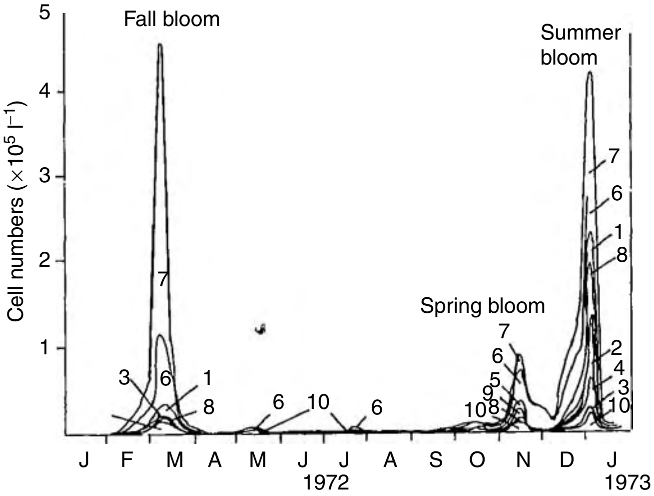


FIGURE 12.5 Phytoplankton species composition and cell concentrations at 6.1 m in Arthur Harbour, Anvers Island. 1. *Chaetoceros* spp., 2. *Charcotia actinochilus*, 3. *Corethron criophylum*, 4. *Eucampia antarctica*, 5. *N. glacei*, 6. *Nitzschia* spp., 7. *P. glacialis*, 8. *Rhizosolenia* spp., 9. *Thalassiosira* spp., and 10. Others. (From Krebs, W.M., *Micropaleont.*, 29, 267, 1983. With permission.)

The differences between the two locations can be attributed to the fact that the Arthur Harbour waters are ice free from spring to autumn and in the longer daylight hours.

Figure 12.6 illustrates an attempt to depict the annual microalgal production in inner McMurdo Sound (Knox 1990). The phytoplankton cycle is now well established with diatoms dominating early in the season (mid-November to mid-December), followed by the *Phaeocystis* bloom from mid-December to early January, and the subsequent diatom bloom in late January–February. The sea-ice microalgal production commences in spring, reaching a peak in mid-December and from mid-January the production is released into the water column with the melting of the sea ice. There may be a further smaller sea-ice microalgal production in the autumn after the sea ice has reformed. The production curve for the benthic microalgae is somewhat speculative. It is hypothesized that a spring peak of production occurs in early November before the growth of the sea ice microalgae reduces the light available to the algae. A second peak is hypothesized after the breakout and melting of the sea ice in February–March.

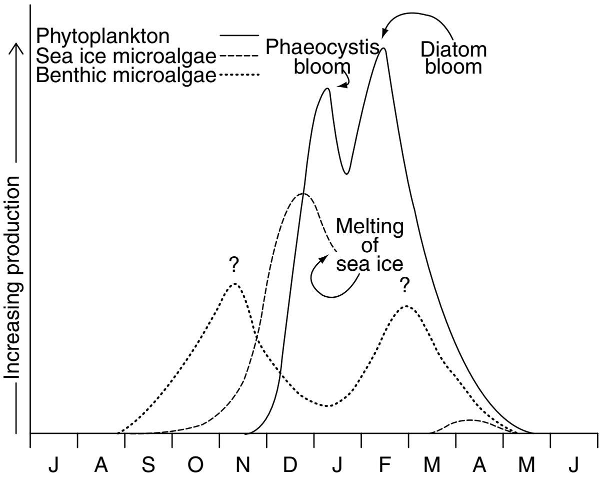


FIGURE 12.6 The seasonal cycle of microalgal production in inner McMurdo Sound. (From Knox, G.A., *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer-Verlag, Berlin Heidelberg, 115, 1990. With permission.)

In his study of the patterns of phytoplankton production in McMurdo Sound over the months of September to January, Rivkin (1991) found that the biomass, size distribution and production of the phytoplankton and bacterioplankton undergo distinct seasonal cycles (Table 12.1). As detailed by Knox (1990), the peak phytoplankton biomass in mid- to late December was largely due to the advection of phytoplankton from the Ross Sea. The size distribution of the phytoplankton was highly seasonal; nano- and picophytoplankton were dominant from August through November, while net phytoplankton were more abundant in December and January. During September and early October, bacterioplankton production was up to 35 times greater than concurrent autochthonous phytoplankton production. However, by late November autochthonous phytoplankton production was approximately 10- to 200-times greater than the bacterioplankton production (Table 12.1). The late austral winter and spring situation contrasts with most temperate and tropical environments where bacteria typically "bloom" with or after the phytoplankton bloom. It is therefore clear that the bacterioplankton in McMurdo Sound were utilizing organic material from sources other than autochthonous phytoplankton production. As detailed by Knox (1990), there is considerable input of phytoplankton and organic matter into McMurdo Sound from the Ross Sea during the late spring and early summer. Only a small proportion of the phytoplankton is consumed, and the rest sinks to the bottom where that which

TABLE 12.1
Daily Production by Bacterioplankton and Phytoplankton in McMurdo Sound[a]

Date	Production (mg C m^{-2} day^{-1})		Ratio of Phyto.:Bact. Production
	Bacterial	Phytoplankton	
Early Sep.	30–40	1.2–1.5	0.033–0.045
Mid-Sep.	40–60	1.6–1.5	0.030–0.045
Mid-Oct.	70–90	2.3–2.8	0.028–0.035
Mid-Nov.	0.9–2.4 0.4[b]	5.0–120	50–125
Early Dec.	2.6–18.7	200–500	30–75
Mid-Dec.	2.5[b] 1.3–8.9[c]	250–800	90–190
Late Dec.	11[d] 13–83[d]	1000–1500	50–90
Early Jan.	10[b] 23–240[c]	2000–2500	10–20

[a] Rivkin (1991).
[b] Kottmeier et al. (1987).
[c] Fuhrman and Azam (1980).
[d] Bunt (1964b).

Source: From Rivkin, R.B., *Am. Zool.*, 31, 5, 1991. With permission.

is not immediately consumed by the benthic herbivores is decomposed, releasing Dissolved organic matter (DOM) back into the water column where it would be utilized by the bacteria thus supporting the late austral winter and early spring bacterioplankton production.

In October–November 1987 during the third winter cruise of the *Polarstern*, brown discolouration of the water immediately below the pack ice was observed over an extensive area south of 70°S in the Weddell Sea. Examination of the water revealed that the brown colour was due to a dense diatom crop dominated by the genus *Thalassiosira* which is an important constituent of Antarctic spring phytoplankton blooms. It was found that the brown water was invariably associated with masses of platelets of 1–20-cm size and 0.1-cm thick (Figure 12.7). The *Thalassiosira* populations were suspended in the interstitial water between the platelets. Brown water was also encountered under ice in the absence of a layer of loose platelets. In such cases the brown water was maintained in position by what appeared to be a layer of loosely intermeshed ice crystals. The strong gradients shown in Figure 12.7 confirm the presence of a stabilized layer about 50-cm thick beneath the ice layer. The relationship between the chlorophyll gradient and low nutrient levels in this upper layer bears a striking resemblance to the situation observed in the open ocean in a "normal" water column during a declining diatom bloom; following nutrient depletion in the upper layer, in particular nitrogen depletion, the diatom population sinks out and the highest chlorophyll concentrations linger for some time at the pycnocline. Diatom populations suffering nitrogen depletion have a higher carbon to chlorophyll ratio than rapidly growing populations; the carotinid:chlorophyll ratio rises accordingly as can be seen in Figure 12.7.

Bunt (1964a) has studied primary production in the water column under the fast ice in McMurdo Sound, both by laboratory and incubation of samples taken on the eastern and western sides of the sound and in situ measurements under the ice off Cape Armitage. In early December the values for the eastern McMurdo Sound samples lay between

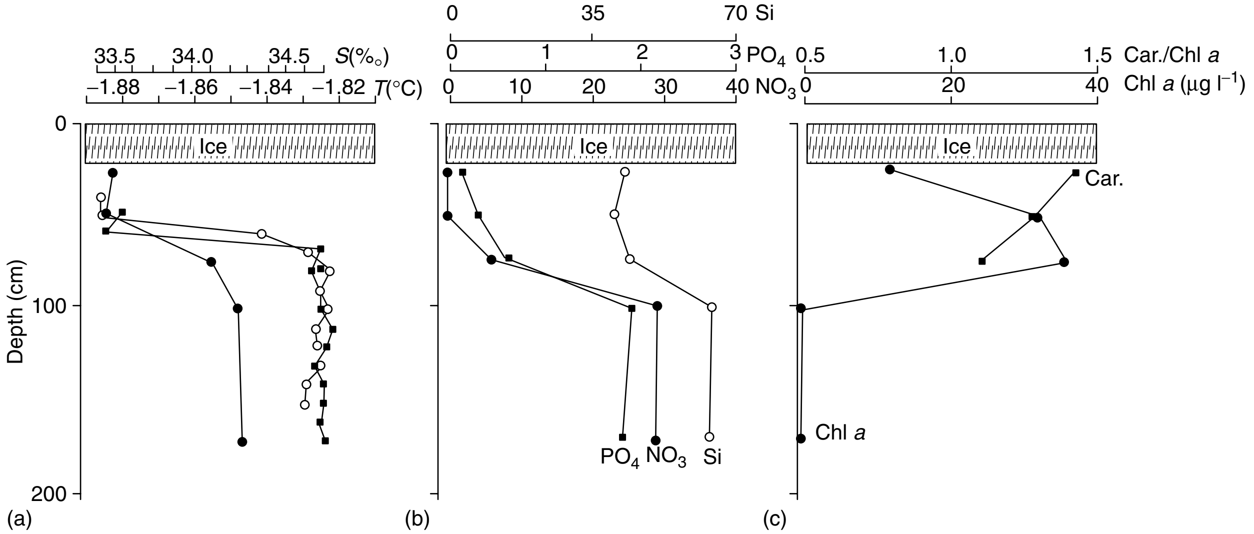


FIGURE 12.7 Profiles recorded from the under ice water layer from station 587 (76°06′ S, 28°27′ W) on November 12, 1986 in the Weddell Sea. (a) Temperature and salinity. (b) Nutrient concentrations: notice that nitrate had been reduced to the limit of detection in the uppermost water layer (Si = silica). (c) Chlorophyll *a* (g l^{-1}) depth distribution and carotenoid/chlorophyll (Car/chl *a*) ratios (R). (From Eiken, H., et al., *Ber. Polarforsch.*, 39, 182, 1987. With permission.)

0.3 and 0.4 mg C m^{-3} h^{-1}. With the appearance of increasing concentrations of microalgae, this figure rose sharply to a maximum mean of 1.78 mg C m^{-3} h^{-1} on 22 December 1961 and then began to decline. On the western side of the sound lower values were recorded and the peak was later in occurrence. Rates of C fixation varied between 0.010 and 0.056 mg C m^{-3} h^{-1} and represented only 1.6–6.8% of the values recorded in parallel samples incubated in the laboratory. This illustrates the effect of the ice cover in reducing light penetration to the water column below.

12.4 SEDIMENTATION AND RESUSPENSION

There have been a limited number of studies of sedimentation of particulate organic matter in the water column under the fast ice. Fukuchi et al. (1988) deployed a sequential, multiple-sampling sediment trap, set at depths of 5, 57, and 120 m respectively in Breid Bay off Syowa Station (70°11.54′ S, 24°18.68′ E) over the period December 28, 1985 to February 13, 1986. Over this period, the approximate chlorophyll concentrations (5–6 mg m^{-3}) and standing stocks (300–400 mg m^{-2}, 0–200 m) were high. Other recent studies in Breid Bay (Fukuda et al. 1985; Taniguchi et al. 1986; Ohno et al. 1987) have found that the summer phytoplankton bloom differs greatly in timing and magnitude from summer to summer. In the summer of 1985–1986, the bloom had already started on December 28, 1985, and had not yet terminated when the deployment terminated in mid-February 1986. Figure 12.8 is a schematic representation of the bloom and sedimentation process. The moored chlorophyll buoy and sampling in its vicinity indicated a patchy phytoplankton distribution and advective water movements. A single diatom species, the widespread *T. antarctica* dominated the sediment trap samples. The similarity in pigment flux and volume flux (Figure 12.8c) suggests that the pigment flux was largely due to the sinking of cells of this species. Fukuchi et al. (1988) estimated sinking rates for *T. antarctica* of 6.5–19.4 m day^{-1}. Evidence from this study and those in other localities (e.g., Bodungen et al. 1986 in Bransfield Strait) suggest that this species is not subject to heavy grazing pressure and that it may form a more important source of food for benthic than for planktonic animals.

Matsuda et al. (1987) studied the seasonal variation in downward flux of particulate matter under the fast ice in Kita-no-ura Cove (69°00′ S, 39°35′ E) in Lutzow–Holm Bay. A marked seasonal variation in the particulate organic carbon (POC) flux was observed (Figure 12.9), with larger fluxes in the summer (max: 136 mg C m^{-2} day^{-1}) and smaller ones in the winter (minimum: 1.5 mg C m^{-2} day^{-1}). Chlorophyll *a* flux varied much more than that of POC (maximum 4500 g m^{-2} day^{-1} in the summer, min: 3 g m^{-2} day^{-1}) suggesting direct input of sea ice microalgae and/or phytoplankton to the benthic community in the summer.

A complicating factor in the flux of particulate organic matter to the sediments is sediment resuspension. Such resuspension has been studied by Berkman et al. (1986) during the period March to July 1981 in McMurdo Sound. The sedimentation pattern during this period is shown in Figure 12.10a. Throughout the period there was suspended matter in the water column and material from the sediments (sponge spicules, benthic foraminiferans, diatom frustules and gastropods) in the 10-m-from-bottom collecting cone suggested a benthic origin for much of this suspended matter. The presence or absence of sea ice may affect the magnitude of the resuspension (Figure 12.10b), e.g., the bulk of the sedimentation in late June coincided with intense wind activity, (up to 35 m s^{-1}). When sea ice was present, anchor ice and currents caused less extreme peaks of resuspension. Viable phytoplankton cells were present in the resuspended sediments during the winter. The resuspended detrital material may provide a viable food resource for plankton herbivores and epifaunal suspension feeders during the austral winter.

12.5 ZOOPLANKTON

There have been a limited number of studies of the zooplankton under the fast ice near the Antarctic coast (e.g., Bunt 1960; Hicks 1974; Zverva 1975; Fukuchi and Sasaki 1981; Fukuchi and Tanimura 1981; Krebs 1983; Fukuchi et al. 1985b; Knox 1986; Tanimura et al. 1986; Forster 1989; Tucker and Burton 1990; Knox et al. in press). These studies have been carried out in the vicinity of shore stations in McMurdo Sound and near Mawson, Syowa, Molodezhnaya and Mirny. The most detailed study is that of Tanimura et al. (1986) of the zooplankton under the fast ice near Syowa Station in a water depth of 10 m. Thirteen groups of zooplankton were recorded. In order of abundance they were Copepoda, Polychaeta, eggs, the larvae of benthic animals other than Polychaeta, Appendicularia, Foraminifera, Siphonophora, Ostracoda, Euphausiacea, Chaetognatha, Mollusca, Amphipoda, and Isopoda. The seasonal change in the total numbers is shown in Figure 12.11a. In January 1982, the number of zooplankters was 3×10^3 individuals m^{-3}, but by late March it had decreased to 0.7×10^3 individuals m^{-3}. A peak number of 5.0×10^3 individuals m^{-3} was recorded in June. Numbers decreased gradually over the ensuing months but remained above 1×10^3 individuals m^{-3}. In the early December the number began to increase and again reached 3×10^3 individuals m^{-3} in the following January.

Among the 13 zooplankton groups, five constituted more than 99% of the total numbers. The copepods, including nauplii, were by far the most dominant, contributing 84.5% of the total numbers. Polychaetes, including the larvae of benthic species, were ranked next in abundance (5.2%). The larvae of benthic animals other than polychaetes and eggs contributed 2.9 and 5.1% respectively. The final group in order of abundance was the Appendicularia (1.5%). Figure 12.11b depicts the seasonal change in these five

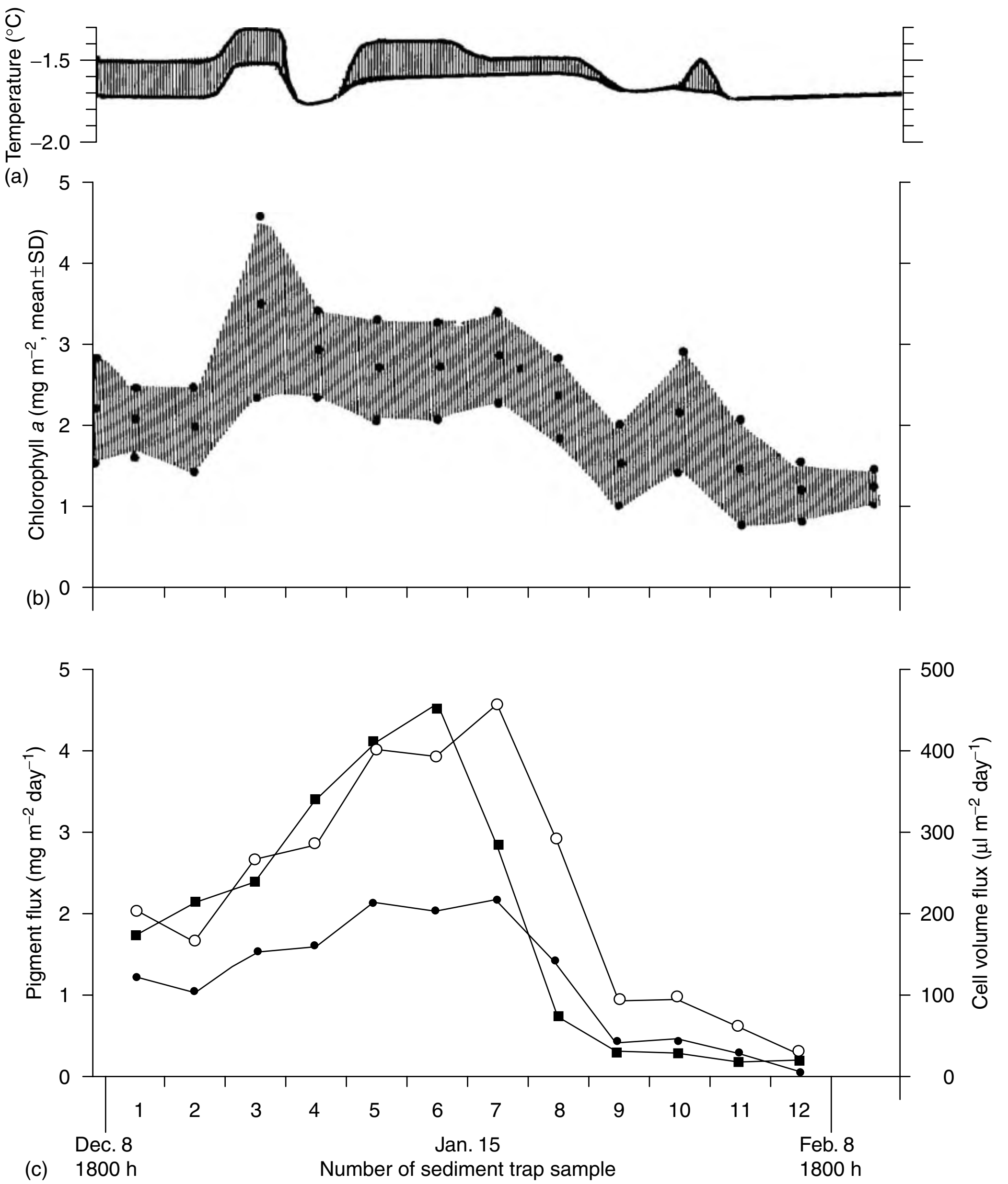


FIGURE 12.8 The bloom process and sedimentation in Breid Bay, December 1985 to February 1986. Serial numbers of sediment trap samples (1–12) correspond to 3.5 day intervals. (a) Temperature (*T*) and salinity (*S*); and (b) chlorophyll *a*; (c) pigment flux (amount settling) and cell volume. (From Fukuchi, M., Hattori, H., Sasaki, H., Hoshiai, T., *Mar. Ecol. Prog. Ser.*, 44, 279, 1988. With permission.)

groups. The polychaetes, mainly the pelagic species *Pelagobia longicirrata* and spionid larvae, occurred throughout the year and were abundant between September and February. *Fritillaria borealis* was the dominant appendicularian with the greatest abundance between September and February. The various larvae of benthic animals other than polychaetes, consisting mainly of lamellibranch veligers, gastropod veligers, echinoderm larvae, bryozoan larvae and ascidian larvae, were numerous between November and January. Eggs, which largely could not be identified, were present in considerable numbers from mid-October to early December. Total copepod numbers decreased during the late summer of 1982, but thereafter numbers increased abruptly from March to June and declined gradually from June to October. They remained low from late October 1982 to January 1983.

A total of 11 species of copepods excluding harpacticoids were identified; *Calanus propinquus, Ctenocalanus vanus, Microcalanus lygmaeus, Stephus longipes, Euchaeta* sp., *Scolecithricella glacialis, Metridia gerlachei, Paralabidocera antarctica, Oithona frigida, Oithona similis* and *Oncaea curvata*. The seasonal change in the abundance of these 11 species and the harpacticoids and nauplii (as a whole) is shown in Figure 12.12. Of the three cyclopoid copepods, the dominant species throughout the year were *O. similis* and *O. curvata*, except in the summer months when

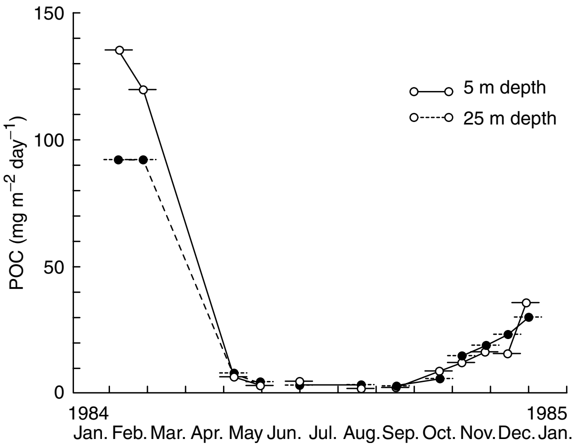


FIGURE 12.9 Seasonal variation of particulate organic carbon (POC) under the fast ice in Lutzow–Holm Bay. (From Matsuda, O., Ishikawa, S., Kawaguchi, K., *Proc. NIPR Symp. Polar Biol.*, 1, 23, 1987. With permission.)

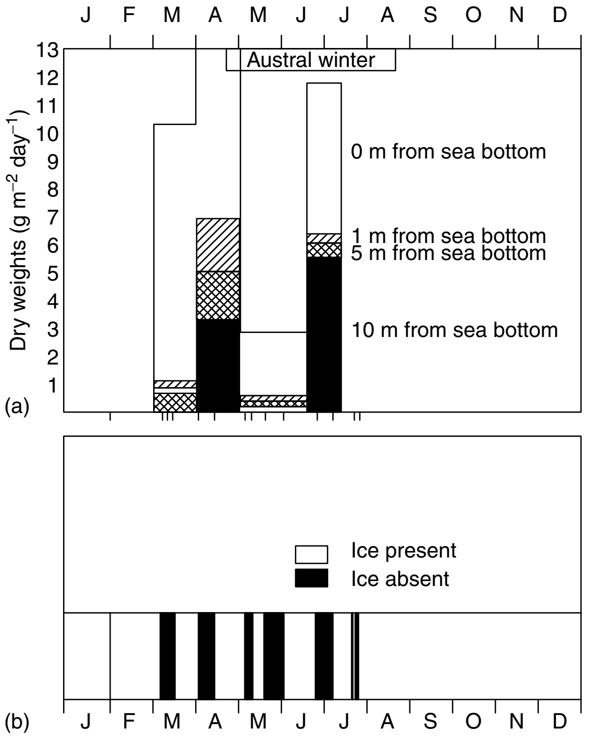


FIGURE 12.10 (a) Dry weights of suspended matter collected in cones placed at 0, 1, 5 and 10 m from the sea bottom in inner McMurdo Sound during the austral winter. (b) The periods when sediment resuspension was influenced by wind-generated waves (ice absent), or by anchor ice and currents (ice present). (From Berkman, P.A., Marks, D.S., Shreve, G.P., *Polar Biol.*, 6, 1, 1986. With permission.)

P. antarctica was dominant. The latter species was not present during the rest of the year. The harpacticoids were present throughout the year and were most abundant in mid-June. Copepod numbers, in contrast to Antarctic oceanic waters where numbers increase in the summer and decline in the late autumn, (Mackintosh 1934; Hardy and Gunther 1936; Foxton 1956, 1966), have their peak of abundance in the winter season with a maximum in mid-June.

Fukuchi et al. (1985b) studied the seasonal changes in the biomass and composition of the zooplankton community under the fast ice near Syowa Station over the period May to December 1982. Average biomass was 13.5 g wet wt 1000 m^{-3}, with a maximum of 25.5 g in August. Figure 12.13 shows the seasonal changes in the number of total zooplankton and that of the three dominant groups, copepods, ostracods, and chaetognaths. Copepods were the dominant group with their numbers varying from a high of 97.7% of the total numbers in June to a low of 50.3% in early December. Amongst the copepods, calanoids were the most numerous, comprising as much as 85–99% of total copepods. Chaetognaths, principally *Eukrohnia* spp. (82–100%) were scarce in May, but increased to more than 1000 individuals 1000 m^{-3} in July–September and November–December. Ostracods showed a similar pattern. The seasonal changes in the zooplankton community is summarized in Table 12.2. It is of interest that the maximum biomass and numbers occurred during the July–September period. There were some major differences in the species composition at Tanimura et al.'s shallow water station (10 m) and Fukuchi et al.'s deeper water station (660 m). Although the peak of copepod numbers occurred during the winter at both sites, ostracods and chaetognaths were numerically more abundant at the deeper water station.

I have studied the summer distribution of the zooplankton beneath the fast ice at a station (water depth 540 m) on the edge of the McMurdo Ice Shelf some 17 km from McMurdo Station (Knox 1986; Knox et al. in preparation). The zooplankton samples were numerically dominated by Copepoda with the numbers generally being higher in January than in December. The small euphausiid *Euphausia crystallorophias* was common with higher numbers in January. A second euphausiid, *Thysanoessa macrura*, was sparsely present. Cnidaria, especially the siphonophoran, *Pyrostephos vanhofferii*, were abundant in all samples. Pteropods were present on all occasions, the most common species being *Limacina helicina*. Larval fish, especially *Pleurogramma antarcticum*, were recorded from all samples after, and including, January 4. Less abundant members of the zooplankton included a large mysid, amphipods, isopods, ostracods, chaetognaths, pelagic polychaetes and polychaete larvae. The zooplankton community differed from that found at Syowa Station in the absence of appendicularians and in the abundance of siphonophorans, pteropods, euphausiids and larval fish; the first two of the last four groups were present only in low numbers at Syowa Station, while the latter two groups were absent. The reason for this difference was probably due to the advection of water from the open water to the north in the Ross Sea under the fast ice and ultimately under the McMurdo Ice Shelf.

Bunt (1960) reported nine species of copepods, excluding hapacticoids, at Mawson Station; seven out of

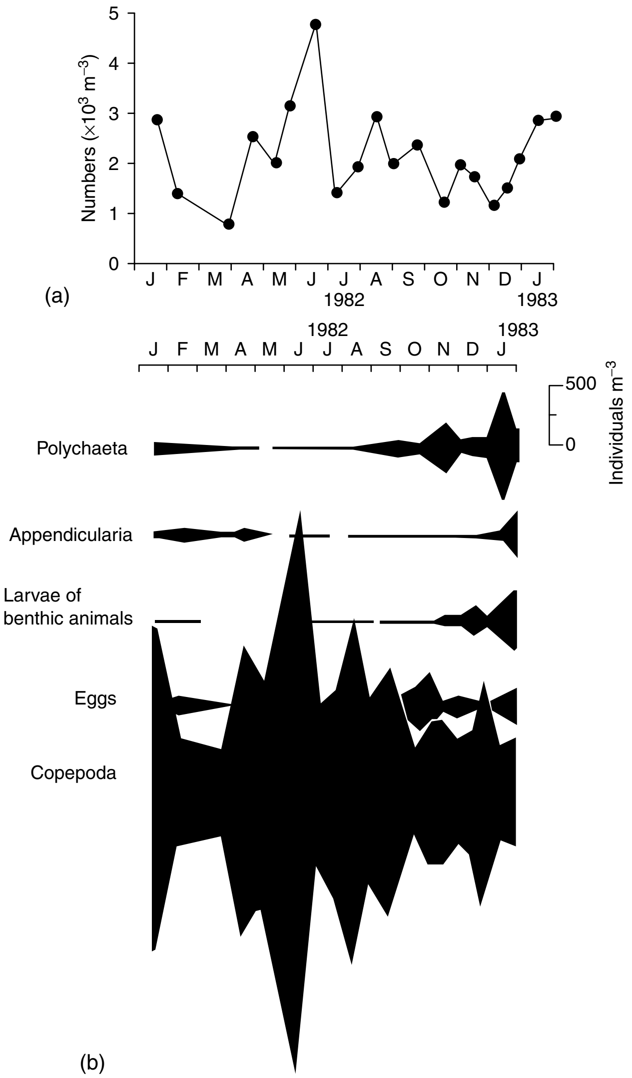


FIGURE 12.11 Seasonal change in (a) the total numbers of zooplankton collected beneath the fast ice off Syowa Station, and (b) the abundance of the major groups of zooplankton collected beneath the fast ice off Syowa Station. (From Tanimura, A., Fukuchi, M., Hoshiai, T., *Mem. Nat. Inst. Polar Res.,* Special Issue, 40, 212, 1986. With permission.)

these nine species occurred at Syowa Station and in McMurdo Sound. Zverva et al. (1975) reported 15 species from Mirny Station and 19 species from Molodezhnaya Station, excluding harpacticoids. All of the species were present at Syowa Station. Tucker and Burton (1990) recorded 12 copepod species from shallow water sites adjacent to Davis Station, seven of which were also found off Syowa Station. It would appear that there is a common copepod fauna in inshore coastal waters under the fast ice round the Antarctic Continent. Dominant species in all localities are *O. similis*, *O. curvata* and *P. antarctica*. While some of the species are found in the adjacent ocean many of the species are known to be associated with ice. It would appear that the sea ice algae form an important food source for these species, especially for nauplii and copepodite stages during the winter. Hoshiai et al. (1987) found large numbers of the development stages of *P. antarctica* and harpacticoids in the lower platelet ice layer of the sea ice during the winter at Syowa Station.

Siegel et al. (1992) investigated the epipelagic zooplankton in the northern Weddell Sea. The sampling area was divided into three zones, an Open Water Zone (OP), and Outer Marginal Ice Zone (OMIZ), and Inner Marginal Ice Zone (IMIZ) and a Closed Pack Ice Zone (CP). The abundance and diversity of the zooplankton increased from the inner CP area to the outer OP area. In the CP area a total of 14 species was recorded (9 copepods, 2 pelagic molluscs, 1 chaetognath and 2 euphausiids). *C. propinquus* was the most abundant copepod with a density of about 1000 m^{-3}. Other copepods present in lower numbers included *Calanoides acutus*, *Rhincalanus gigas* and *Rhynchonerella bougraini*. In terms of biomass the species with the largest biomass were *Euphausia superba* and *T. macrura*.

12.6 THE SYMPAGIC COMMUNITY

The sympagic community comprises the meiofauna that lives within the sea ice either permanently or at some stage of their life cycle. This in ice fauna consists of amphipods (Rakusa-Suszczewski 1972; Richardson and Whitaker 1979; Waghorn and Knox 1988; Hopkins and Torres 1989), foraminifera (Lipps and Krebs 1974; Dieckmann et al. 1991), polychaetes (Andriashev 1968). Investigations of the composition and abundance of the sympagic biota include Gunther et al. (1999b) in Drescher Inlet, Weddell Sea, Katbrjeweit et al. (1993), Schnack-Schiel et al. (1997, 1998) and Gradinger (1999) in the Weddell Sea, Swadling et al. (1997) and Swadling (2001) in east Antarctica, Gugliemo et al. (1998) in Terra Nova Bay, and Hoshiai et al. (1987) and Tanimura et al. (1996, 2002) off Syowa Station.

Studies on the reproduction of sympagic copepods (Berkman et al. 1991) revealed that they were capable of producing several generations per year with reproduction uninterrupted during the winter. Studies of the life cycles of the three dominant copepods, *Stephoa longipes*, *Drescheriella glacilis* and *P. antarctica*, have been carried out by Tanimura et al. (1984, 1986, 1996), Dahms et al. (1990), Kurbjeweit et al. (1993), Schnack-Schiel et al. (1995), and Swadling et al. (1997). The three common species differ in their relationship with the ice (Tanimura et al. 1996; Swadling et al. 1997) (Figure 12.14). *P. antarctica* overwinters in the sea ice as nauplei and undergoes two main growth periods that coincide with autumn and spring blooms of ice microalgae. Upon entering a pelagic phase from stage CIV in late spring this species remains closely associated with the under-ice surface (Hoshiai et al. 1987; Tanimura et al. 1996). The life cycle of this species is summarized in Figure 12.15. Before the onset of ice growth in April, the

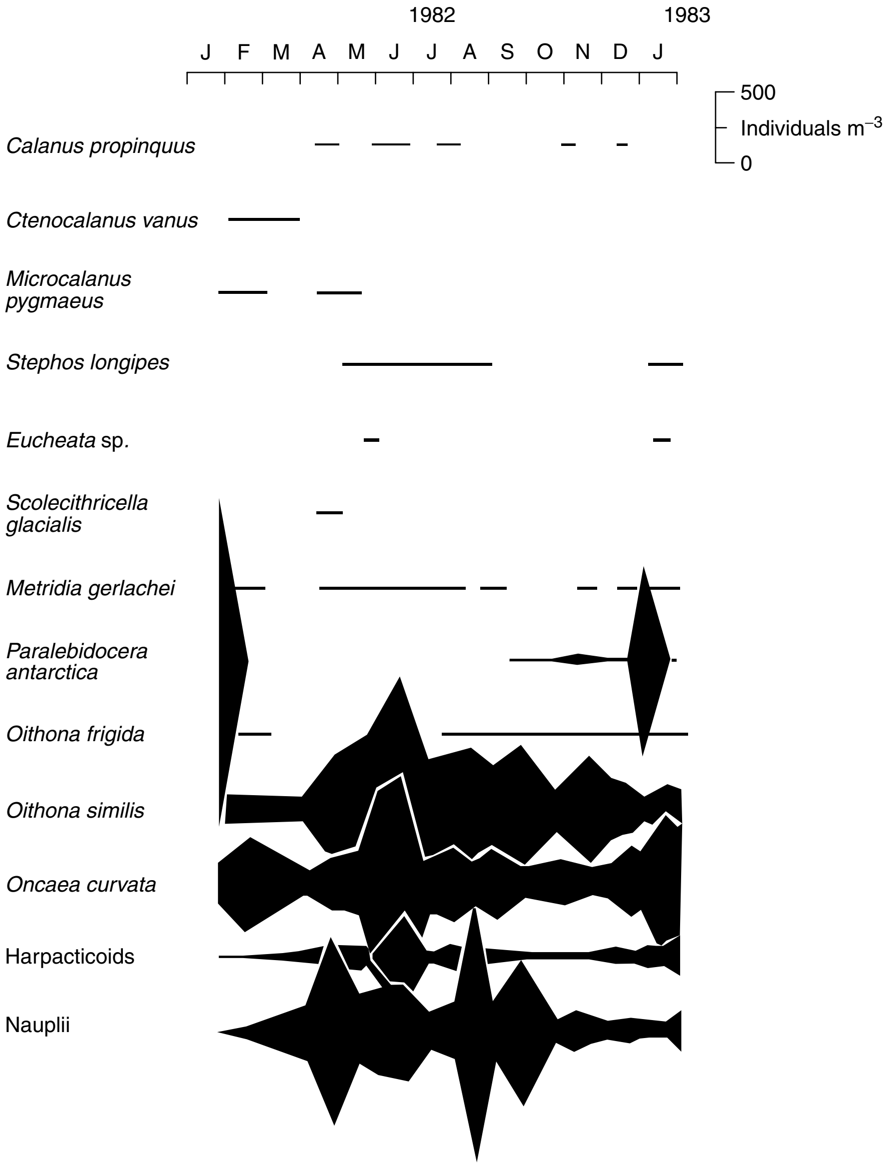


FIGURE 12.12 Seasonal change in the abundance of copepods collected beneath the fast ice off Syowa Station. (From Tanimura, A., Fukucho, M., Hoshiai, T., *Mem. Nat. Inst. Polar Res.*, 40, 212, 1986. With permission.)

young nauplii, which are the offspring of the previous generation, immediately enter the bottom part of the sea ice (possibly between growing ice crystals or brine channels) and develop into later naupliar stages of NIV and/or NV by the end of May. From June through to September, when the ice thickens, the population remains in the bottom part of the ice in naupliar stages. The population growth recommences when ice growth stops in October. The rapid development from the later naupliar stages to early copepodites (CI–CIII) takes place in the bottom of the ice by mid-November. From November through to December, the population gradually shifts their habitat from the sea ice to the water immediately below the ice. Maturation and mating takes place just beneath the ice as demonstrated by Tanimura et al. (1984) with the melting of the undersurface of the ice in mid-summer. This life cycle, as described by Tanimura et al. (1996) for populations of *P.antarctica* near Syowa Station, is similar to that observed for the population found in nearshore waters of the Vestfold Hills (Swadling 2001).

Drescheriella glacialis differs from the other two species in that it inhabits the sea ice throughout its entire life cycle, and reproduction occurs year-round (Dahms et al. 1990). However, *D. glacialis* occurred in high densities in coastal areas devoid of ice in the late summer, so that it must have a benthic or pelagic phase in its life cycle.

Kurbjeweit et al. (1993) has described the life cycle of *S. longipes* in the southeastern Weddell Sea. They found that *S. longipes* was the most abundant copepod within the upper 50 m of the water column. Abundance exceeded those in the upper ice water layer by 1–3 orders of magnitude and the

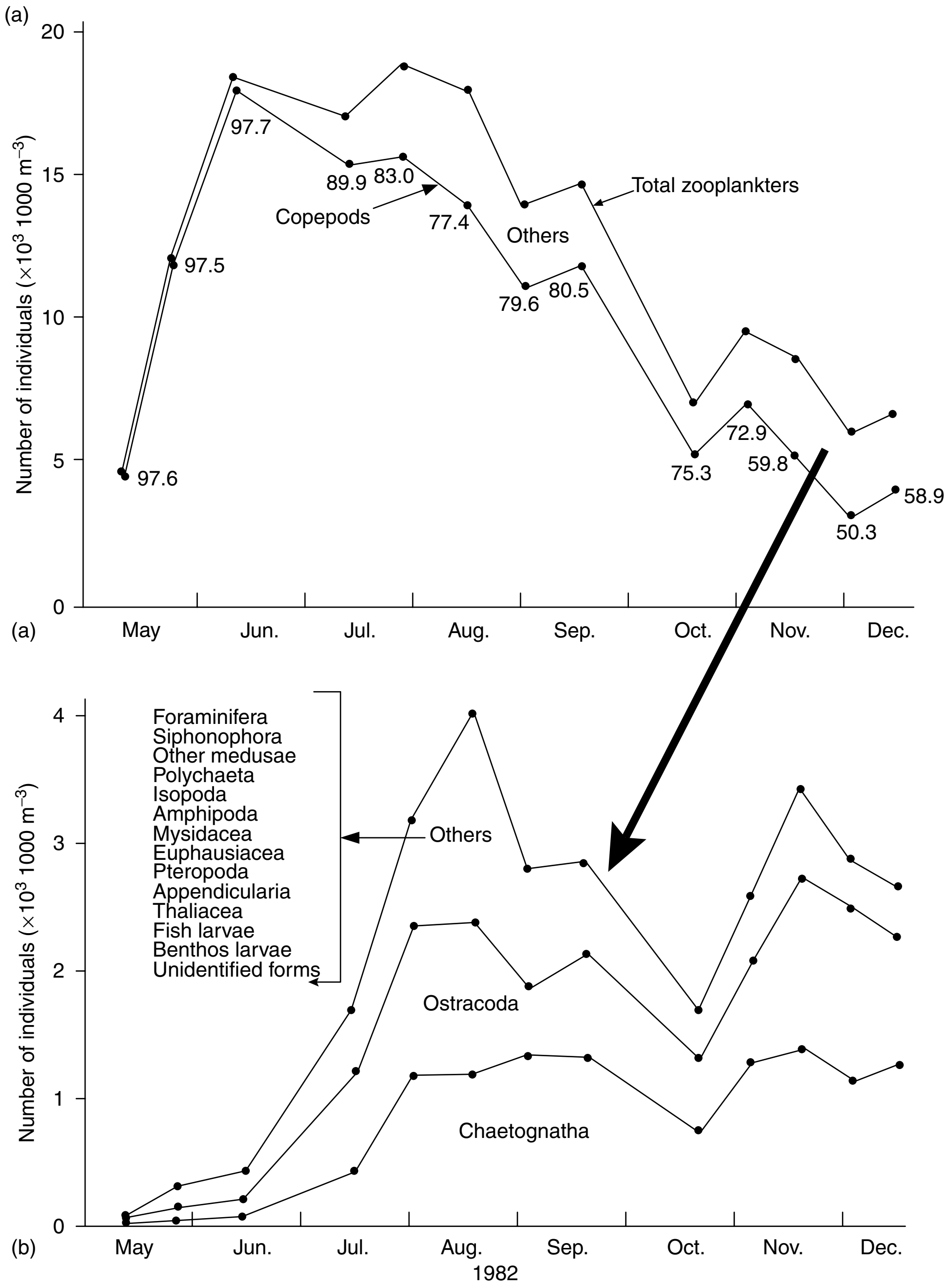


FIGURE 12.13 Seasonal change in (a) individual numbers of total zooplankton and copepods and (b) zooplankton other than copepods in a 0–660 m water column beneath the fast ice off Syowa Station. Numerals in the upper figure indicate the percentage of copepods. (From Fukuchi, Tanimura, A., Ohtsuka, H., *Bull. Mar. Sci.*, 32, 518, 1985b. With permission.)

water column below by 3–5 orders of magnitude, respectively. Nauplei and young copepodite stages (CI and CII) outnumbered all other metazoan groups within the ice. It has been found that *S. longipes* breeds in the upper layers of the water column and attaches its sticky eggs directly onto the frazil ice crystals thus facilitating their incorporation into the sea ice (Schnack-Schiel et al. 1998). Kurbjeweiy et al. (1993) has diagrammed a schematic representation of the abundance of the various development stage of *S. longipes* and the phytoplankton standing stocks within and below the sea ice. In January–February copepodites CI–CV migrate into the water column where they over winter on or near the bottom. By November–December, the adults are found beneath the sea ice where they lay their eggs.

In coastal waters off the Vestfold Hills, East Antarctic, Swadling (2001) found that *D. glacialis* and *P. antarcticus* accounted for at least 90% of the total sympagic meiofaunal abundance. Abundances were high, reaching 175 individuals l^{-1} (190,000 m^{-2}) for *D. glacialis* and 660 l^{-1} (901,000 m^{-2}) for *P. antarctica.*

TABLE 12.2
Different Phases of the Zooplankton Community Under the Fast Ice

Phase	I	II	III	IV
Month	May–Jun.	Jul.–Sep.	Oct.–Dec.	Jan.–Apr.
Season	Autumn–winter	Winter–spring	Spring–summer	Summer–autumn
Biomass (g wet wt 1,000 m^{-3})	Increasing (1.5–7.5)	Large (25.5–15.3)	Decreasing (15.2–8.7)	Increasing–decreasing (?8.7–15.0–7.5)
Numbers (no. 1,000 m^{-3})	Increasing	Large	Decreasing	Increasing–decreasing
% Copepods	98	77–83	75–50	?50–80–50

Source: From Fukuchi, M., Tanimura, A., Ohsuka, N., *Bull. Mar. Sci.*, 37, 518–528, 1985b. With permission.

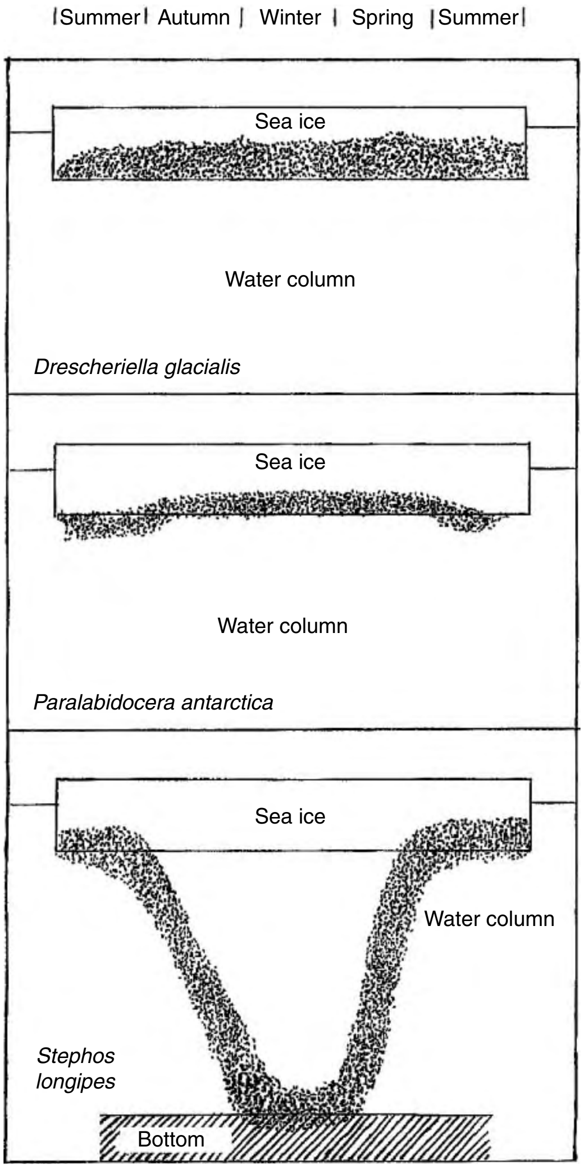


FIGURE 12.14 Schematic comparison of the relations with sea ice among three Antarctic ice-associated copepods, *D. glacialis, P. antarctica*, *S. longipes*. Stippled area indicates the main habitat through the life cycle in each copepod. (From Tanimura, A., Hoshiai, T., Fukuchi, M., *Ant. Sci.*, 8, 264, 1996. With permission.)

12.7 THE PLATELET ICE COMMUNITY

Gunther et al. (1999b) investigated the metazoan fauna of the platelet ice layers at Dreschler Inlet, Weddell Sea. The loose matrix of the platelets provides an extensive surface for algal growth at favourable light levels (Arrigo et al. 1993) and it is continuously flushed with nutrient-rich seawater (Dieckman et al. 1992; Arrigo et al. 1995). Arrigo et al. (1995) found that algal stocks of up to 37 g C m^{-2} can be attained within the platelet layers. Twenty eight metazoan species were found. The most abundant group was the Copepoda, of which almost 90% of the individuals belonged to three species: *D. glacialis*, *S. longipes* and *P. antarctica*. This contrasts with earlier studies (Smetacek et al. 1992; Arrigo et al. 1995; Grossman et al. 1996), which failed to detect these copepods in the platelet ice layers. Among the copepods the Harpacticoida was the largest group, represented by 26 species. Total abundance varied between 40 and 120 individuals l^{-1}. Figure 12.16 depicts the relative abundance of the three dominant copepod species. *D. glacialis* was the most abundant species (40%), followed by *S. longipes* (39%) and *P. antarctica* (9%). Most of the harpacticoid species were only found sporadically and in very low numbers.

Kurbjeweit et al. (1993) found that the calanoid *S. longipes* was present in the platelet layers of the Weddell Sea, in abundances that were 2 orders of magnitude higher than in the water column. *D. glacialis* and *S. longipes* were also found in slush-ice layers in the Amundsen and Belligshausen Seas (Schnack-Schiel et al. 1998) where they dominated the copepod meiofauna (110 individuals l^{-1} and 40 individuals l^{-1}, respectively).

12.8 THE CRYOPELAGIC COMMUNITY

In Chapter 3, an account was given of the cryopelagic community associated with the bottom ice microalgal assemblages. The dominant members of this community were copepods, amphipods, adult and larval euphausiids (principally *E. crystallorophias*), some fish (especially *Pagothenia borchgrevinki*), larval and juvenile fish (larval and *P. antarcticum* and the larvae and juveniles of some benthic species), and the larvae of some benthic invertebrates.

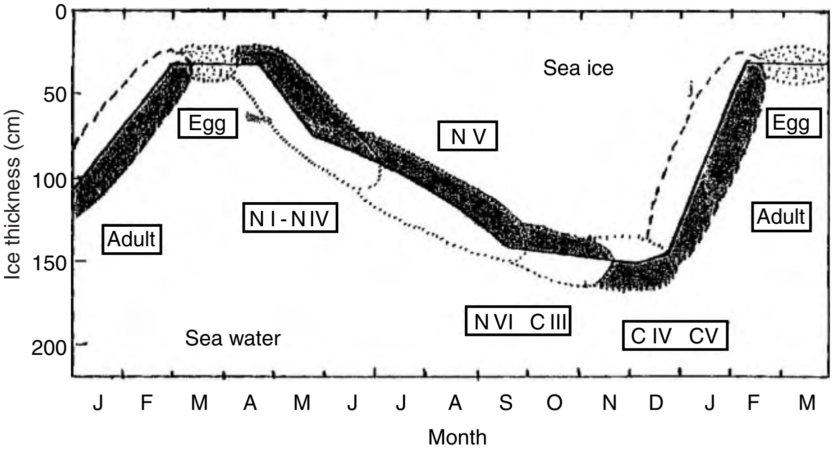


FIGURE 12.15 Schematic diagram of *P. antarctica* life cycle in the ice-covered area near Syowa Station. Hatched area indicates the main habitat of *P. antarctica*. Solid line denotes the seasonal change in ice thickness. (*Source*: Tanimura A., Hoshiai, T., Fukuchi, M., *Ant. Sci.*, 8, 263, 1996. With permission.)

Tanimura et al. (1984) collected the zooplankton at the sea ice–water interface off Syowa Station in January 1982. A dense monospecific swarm of the calanoid copepod *P. antarctica* (primarily adults with a density of 2–6$\times10^4$ individuals m^{-3}) was observed during the day. At night the swarm disappeared from the whole of the water column and the zooplankton community in the 0-m layer consisted of *P. antarctica* (13.1–39.5%), the calanoid copepods *O. similis* (14.1–39.5%) and *O. curvata* (11.4–34.2%), harpacticoid copepods (1.1–3.3%), copepod nauplii (2.7–34.2%), polychaete larvae and chaetognaths. It was postulated that the disappearance of the swarm at night was due to its entering the interstitial water of the loose lower layer of the sea ice. In their study of the meiofauna of the sea ice in the fast ice zone off Syowa Station Hoshiai and Tanimura (1986) found that in addition to the copeods *C. vanus*, *O. similis* and *O. curvata* which were temporary members of the meiofauna, the copepod *P. antarctica* and harpacticoids (3 species) were present continuously throughout the winter in the bottom layer of the sea ice with a maximum abundance of 21.8×10^4 m^{-2} in September. Nauplii of *P. antarctica* appeared in the sea ice in late March and reached a maximum density of 7.1×10^4 m^{-2} in July. Copepodites appeared in late September and at the stage of copepodite IV they migrated into the water column (Hoshiai et al. 1987). It therefore appears that the nauplii feed and grow in the sea ice habitat. Hoshiai et al. (1989) investigated the gut contents of the nauplius, copepodite and adult stages of *P. antarctica* from the sea ice and found diatom frustules and/or their fragments in the guts of the nauplius stages IV, V, and VI, and copepodite stages I, II, and III. Common species found in the guts were *Amphiprora kufferathii*, *Navicula glacei*, *Pinnularia quadratanea*, *Gomphonema* sp., and *Nitzschia cylindricus*, all members of the sea-ice microalgal assemblage. The tube-forming *Berkeleya rutilians*, although one of the dominant ice algal species, was not found in the guts of the copepodites. After shifting to the water column the gut

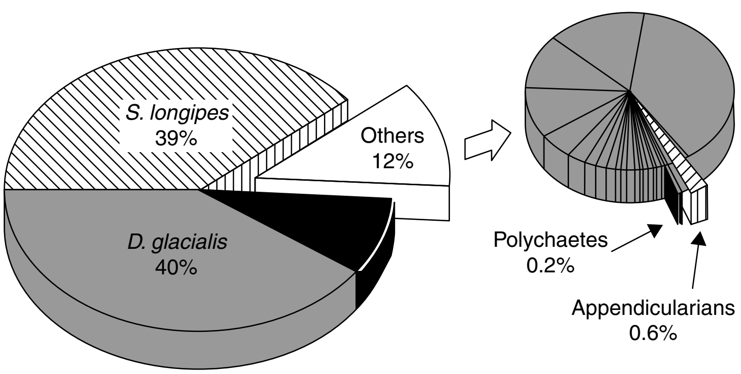


FIGURE 12.16 Relative abundance of dominant copepod species and higher taxonomic groups in platelet ice layers at Drescher Inlet, Weddell Sea. Data represent an average over all samples. (From Gunther, S., Gleitz, M., Dieckmann, G.S., *Mar. Ecol. Prog. Ser.*, 177, 84, 1999a. With permission.)

contents of *P. antarctica* reflected the species composition of the water column diatoms, which was very similar to that of the sea ice.

The largest member of the cryopelagic community is the small fish *P. borchgrevinki* that occurs singly or in schools in the surface layers beneath the ice. Studies of the diet of this species has given varying results depending on the locality and the season. Eastman and DeVries (1985) analyzed 38 specimens caught in November 1978 in McMurdo Sound and found low diet diversity with copepods and amphipods the most frequent prey. The prey items identified by Eastman and DeVries were as follows; copepods (in 61% of fish), the amphipod *Orchomeme plebs* (58%), hyperiid amphipods (21%), mysids (21%), fish (18%) and cephalopods (6%). Bradfield (1980) determined the dietary composition from the examination of the stomach contents of 156 *P. borchgrevinki* collected at the edge of the McMurdo Ice Shelf in the centre of McMurdo Sound. A list of the food items is given in Table 12.3. *P. antarcticum* larvae and the amphipod *Hyperiella dilatata* occurred in half the stomachs, with the latter occurring in the largest numbers. The most important food items in terms of biomass were *P. antarcticum*, *E. crystallorophias*, *O. plebs* and *H. dilatata*. Prey-size distribution and prey diversity suggested an opportunistic feeding strategy and it was concluded that *P. borchgrevinki* obtained its food from the ice algal community or in the top few metres of the water column below the ice.

TABLE 12.3
List of Items from the Stomach Contents of *P. borchgrevinki* from Inner McMurdo Sound During Summer

	Size (mm)
Invertebrates	
Polychaetes	
Harmothoe sp.	10
Molluscs	
C. antarctica	9
L. helicina	1.5
Crustaceans	
Small copepods	
C. acutus	4
M. gerlachei	
C. propinquus	
Large copepods	
Euchaeta	8
Antarctica	
E. eribi	
Amphipods	
Hyperiella macronys	6
O. plebs	12
E. antarcticus	10
Euphasiids	
E. crystallorophias	20
Vertebrates	
Fish	
P. antarcticum (larva)	50
Eggs	1.5

Source: From Bradfield, P., B.Sc. Project in Zoology, University of Canterbury, Christchurch, 1980.

Forster et al. (1987) collected specimens of *P. borchgrevinki* from below the sea ice 1.5 km off Pram Point McMurdo Sound over the period November 8 to 6 December, 1985. Numerically, the dominant prey was the pteropod *L. helicina* (83%), followed by the hyperid amphipod *H. dilatata* (5%). Other prey species in decreasing order of occurrence were *E. crystallorophias*, *Euchaeta antarctica*, other copepods, a decapod crustacean larva, chaetognaths, the amphipods *O. plebs* and *Epimiriella macronyx*, and unidentified juvenile fish. In volumetric terms, the dominant diet contributors were *O. plebs* (38%), *L. helicina* (17%) and chaetognaths (15%) (Figure 12.17). This contrasts to Bradfield's results in which the dominant food items were larval *P. antarcticum, E. crystallorophias*, and the amphipods *O. plebs* and *Eusirus antarcticus*.

In contrast, Hoshiai et al. (1989) found that the stomachs of *P. borchgrevinki* from under the fast ice near Syowa Station contained copepods, appendicularians, tintinnids, polychaetes and unidentified items. More than 90% of the food items were copepods, including nauplii. Species present were *C. vanus*, *S. longipes*, *O. similis*, *O. frigida*, *O. curvata* and *P. antarctica*, as well as a few harpacticoids. Most of the nauplii were *P. antarctica*. Because *P. antarctica* nauplii live and feed in the bottom sea-ice layer, this is evidence that *P. borchgrevinki* feed on the sea ice community meiofauna.

The McMurdo Sound fast ice ecosystem will be further considered in Chapter 15.

12.9 THE ROSS AND McMURDO ICE SHELVES

The Southern Ross Sea is overlain by the world's largest floating ice sheet (540,000 km^2, Zumberge and Swithinbank 1962), the Ross Ice Shelf or Ross Ice Barrier. Ice thickness varies from about 200 m near the barrier edge to 700 m in the southeastern area of the shelf. Along the cliff-like barrier edge, an average of 35 m rises from the surface of the water and about 165 m are submerged. The average depth of the water along the barrier is 567 m. The width of the shelf in places exceeds 1300 km. A number of banks shallower than 500 m exist beneath the Ross Ice Shelf, one lying to the south of Pennell Bank and trending northeast and another southwest of Roosevelt Island. Depressions exceeding 800 m are found along the ice shelf periphery, with a maximum sounding of about 1400 m near 165°E, 79°S.

The McMurdo Ice Shelf is that part of the Ross Ice Shelf opening into the McMurdo Sound (see Figure 12.1). It has a maximum width of about 40 km. To the south it is bounded

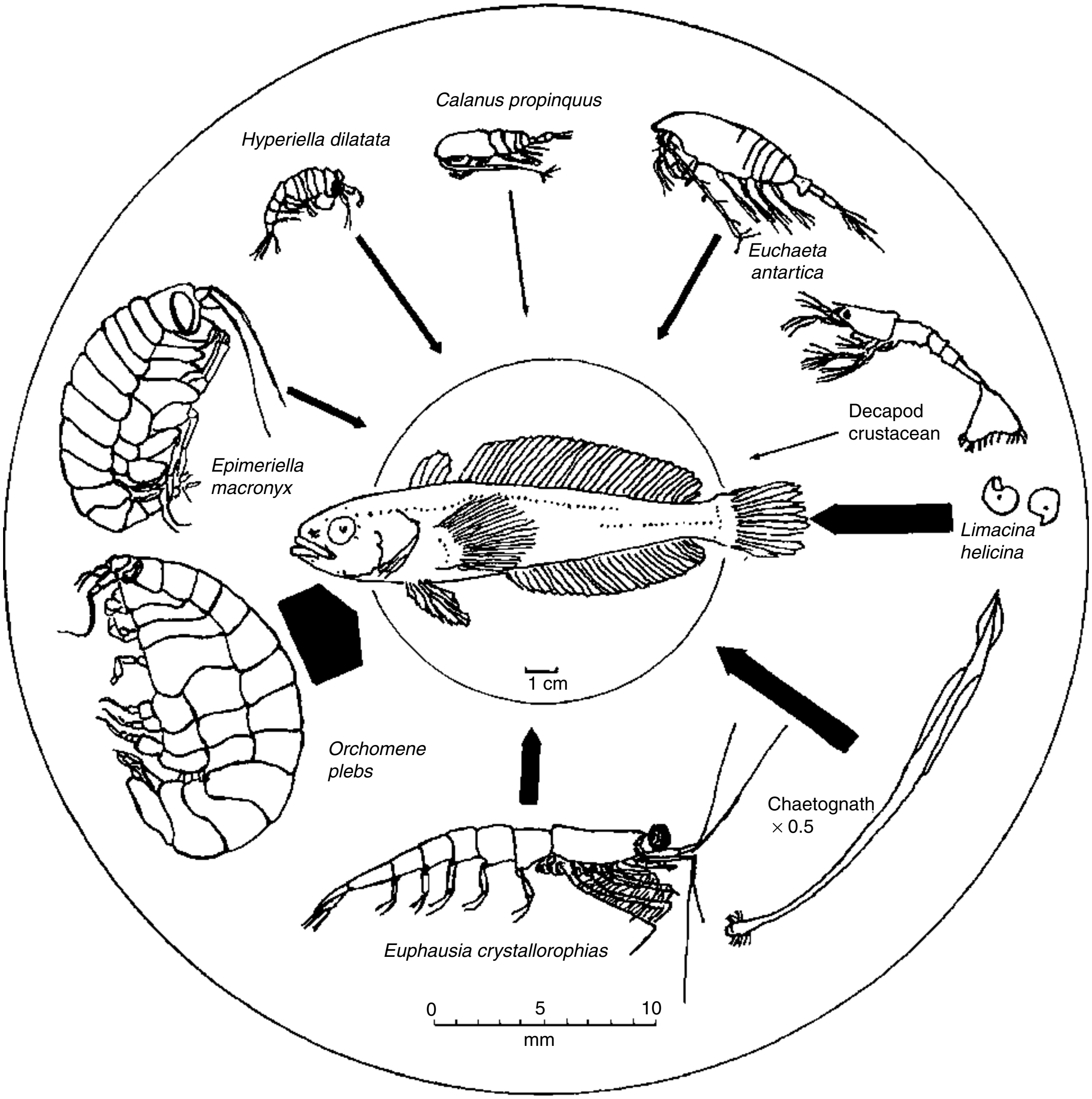


FIGURE 12.17 The dominant prey of the cryopelagic fish *P. borchgrevinki* collected from under the fast ice in inner McMurdo Sound in November–December. The arrows represent estimated proportionate volumetric contribution of each prey species. The prey are drawn to the same scale except for the chaetognath. (From Forster, B.A., Cargill, J.M., Montgomery, J.C., *Polar Biol.*, 8, 49, 1987. With permission.)

by White Island, Black Island and the Brown Peninsula. The Koettlitz Glacier descends onto the shelf in the southwestern corner. On the eastern side of the shelf, ice thickness varies from approximately 5 m at the seaward edge in McMurdo Sound to 70 m to the east of White Island (Littlepage and Pearce 1962). A narrow band of multiyear sea ice extends along the northwestern coast of White Island where a tide crack is developed along the coast. Extensive crack systems in the shelf occur off the northern end of White Island and in the Koettlitz Glacier Region. Along the southern coast of White Island there are large ice billows and domes.

12.9.1 CIRCULATION PATTERNS BENEATH THE SHELF

12.9.1.1 Ross Ice Shelf

Jacobs et al. (1970, 1978) suggest a possible circulation pattern beneath the Ross Ice Shelf. Modified circumpolar deep water reaches the ice shelf primarily over the broad central channel between 170°W and 180°, with a warm core centred around 300 m. This warm core flows beneath the ice shelf and undergoes cooling, dilution and lateral mixing. As the water flows beneath Ice Shelf it would be divided by the shallow bank lying to the southwest of Roosevelt Island. One branch would then turn east round Roosevelt Island to emerge with lowered salinity and temperature near freezing point. The other branch would travel in a large cyclonic gyre beneath the Ice Shelf. As the ice shelf thickens this water moves to deeper levels and melting near the Barrier edge would lower the temperature to near freezing point, after which any transfer of heat to the cold shelf ice would be accompanied by freezing, releasing salt to the Ross Sea Shelf water. Increase in salinity and density due to freezing would reinforce the cyclonic circulation.

In the summer, the prevailing wind blows from the east parallel to the ice barrier. The windinduced currents transport the low salinity (approximately 50-m) layer towards the ice shelf where it must descend. Directly off the shelf low salinities are found to a depth of 150 m. Because of the sinking of this low salinity layer near the barrier, diatoms live in abundance at subcompensation depths. Off Cape Crozier, the diatom *Trigonium arcticum* has been found in abundance on the sea bed in 300 m.

12.9.1.2 McMurdo Ice Shelf

Because of its possible biological significance, there has been considerable interest in the circulation and hydrology under the sea ice of McMurdo Sound and the McMurdo Ice Shelf. Circulation patterns are complex and variable (see reviews by Heath 1971, 1977; Raytheon 1983; Lewis and Perkins 1985). Based on observations carried out up to 1975 (Gilmour et al. 1960, 1962; Tressler and Ommundsen 1962; Littlepage 1965; Heath 1971, 1977; Gilmour 1975), Heath (1977) proposed a circulation pattern that has in large part been confirmed by subsequent studies (see Figure 12.18). All of these studies identified a strong tidal influence on the current patterns, with the currents being strongest when the tidal range is greatest.

In the outer sound, a strong southerly current—the Cape Bird current—passes round Cape Bird towards Cape Royds where it swings across the sound to join a northward flowing current on the west side of the sound. Estimates of the net movement of surface currents in the east sound from north to south vary from 2.5 km day^{-1} (Barry and Dayton 1988), to 6.5 km (Gilmour et al. 1962), 10.3 km (Littlepage 1965), and 4–12 km (Palmisano et al. 1988), with a mean of 6.8 km. These currents show considerable variation indicative of either seasonal or year-to-year variations. The majority of the studies have confirmed a northerly flow from under the shelf on the west side of the sound. Further north, this flow from under the shelf joins the northward flow of the water that originated from the Cape Bird current.

The most controversial aspect of the current flows is a northward flowing surface current on the east side of the sound, the Cape Armitage Current, which has been identified by a number of investigators (Evans 1965; Littlepage 1965; Car and Codspoti 1968; Heath 1971). Measurements made closer than about 2 km from the coast near Cape Armitage at the end of Hutt Point Peninsula indicated a flow out from under the shelf. Barry and Dayton (1988), on the other hand, consider that the flow along Cape Armitage is to the south. Heath (1971), on the basis of hydrological measurements, considered that the northerly outflow near Ross Island probably originated from water flowing under the Ross Ice Shelf from the Ross Sea to the west of Ross Island. Figure 12.18 depicts a hypothetical circulation pattern based on the information discussed above.

12.9.2 WATER CHARACTERISTICS UNDER THE ROSS ICE SHELF

Measurements of water characteristics at the Ross Ice Shelf Project site (82°22.5′ S, 168°37.5′ W) have been made by a number of workers (e.g., Jackson et al. 1978; Gilmour 1979; Jacobs et al. 1979; Michel et al. 1989). At this site, the ice thickness is 370-m thick and the water column under the ice measures 237 m. Within the water column, temperature and salinity increased from −2.16°C (the freezing point in situ) and a salinity of 34.39 at the ice–seawater interface to −1.86°C and 34.83 (Gilmour 1979; Jacobs et al. 1979). Mixed layers beneath the ice and near the bottom were separated by an inverse thermocline but the stratification was stabilized by a halocline. Temperature and salinity characteristics of the bottom boundary layer indicate that it is part of the highsalinity shelf water from the western Ross Sea. Forster (1978) advances the following tentative interpretation of the temperature and salinity fields found under the Ross Ice Shelf but at the same time points out that more data is needed. Water from the open ocean is found under the ice shelf as a bottom layer near the sea floor. The water is subsequently modified by net melting at the bottom of the ice shelf. This water then returns to the open ocean in the top layer just beneath the ice.

From the biological point of view there is considerable interest in the age of the water beneath the Ross Ice Shelf and the period of interchange with the open sea. Estimates based on tritium and ^{14}C properties of seawater have been made by Jackson et al. (1978) and Michel et al. (1979). The tritium concentrations in the upper 100 m of water at the RISP site are similar to a surface concentration of 0.5 TU reported by Jacobs (1977). The presence of a tritium concentration of 0.5 TU under the shelf indicates that this water has been renewed within the period since nuclear weapons testing (1957 through 1962) in the atmosphere.

Measurements of ^{14}C made in the surface waters of the Ross Sea in 1971 were on the order of −100 per mil, whereas krill collected at 77°44′ E in 1972 was found to have a ^{14}C of −107 per mil. Therefore, the ^{14}C value for the Ross Sea in the early 1970s was less than 100 per mil. The most recent measurements were made in McMurdo Sound. The sample from the east side of the sound had a ^{14}C value of −69 per mil, whereas the other samples had values of −106 to −1145 per mil. Tritium measurements showed similar trends. The water on the east side of the sound is derived from water from the Ross Sea to the east of Ross Island, whereas on the west side of the sound (Heald Island and Cape Chocolate) the water flows out from under the McMurdo Ice Shelf. The ^{14}C sample collected at the RISP site had a ^{14}C value of −74 per mil.

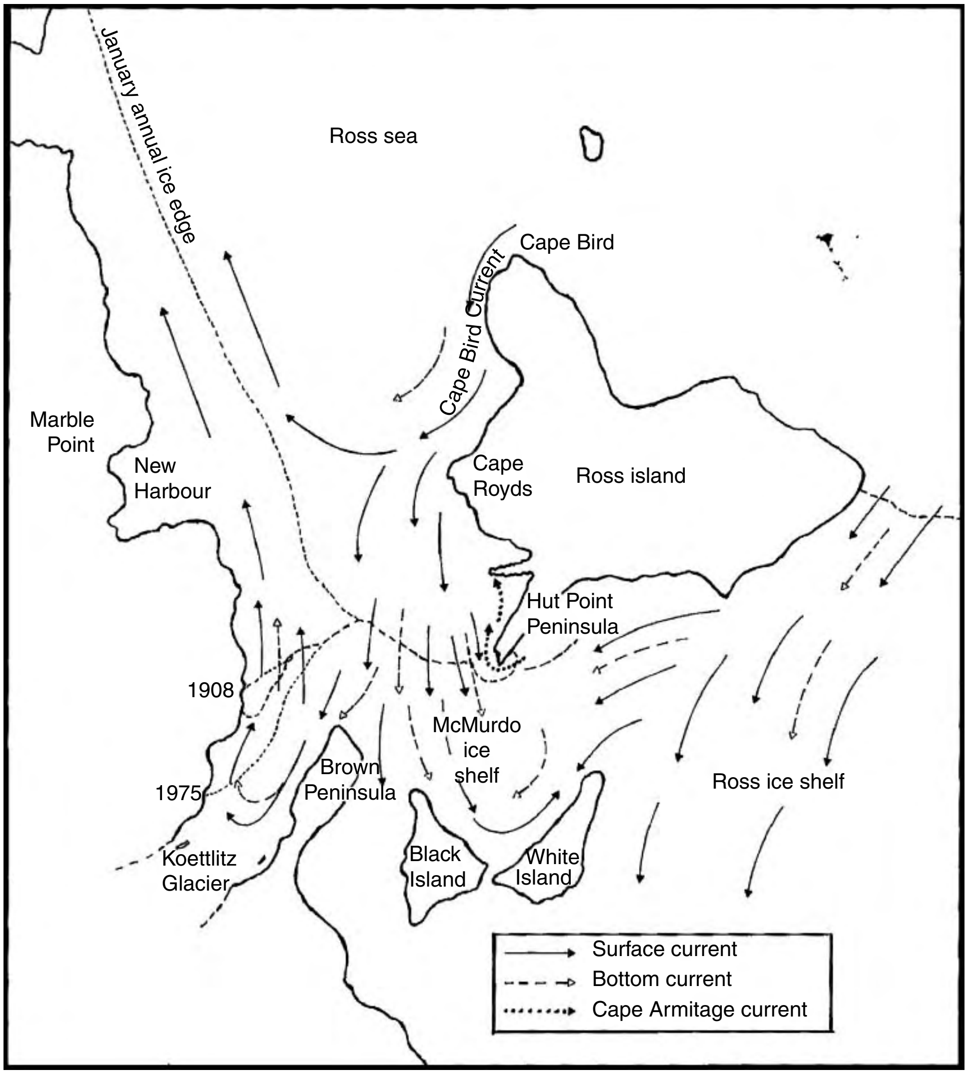


FIGURE 12.18 Water circulation patterns in inner McMurdo Sound and beneath the McMurdo Ice Shelf. (From Knox, G.A., *Mem. Nat. Inst. Polar Res*, Special Issue, 40, 345, 1986. With permission.)

Because this value is much higher than ^{14}C activities found in 1972, the water at a depth of 22 m at the RISP site must have been in the open Ross Sea.

12.9.3 THE MCMURDO ICE SHELF TIDE CRACK COMMUNITIES

Tidal rise and fall and the northward movement of the McMurdo Ice Shelf form tide cracks along the coast. Such tide cracks are particularly well developed along the west coast of White Island. The phytoplankton of the White Island tide cracks has been discussed in Chapter 3. Three species of copepod (a calanoid, *Paralabidocera grandispina*, a cyclopoid *Pseudocyclopina belgica*, and a harpacticoid, *Tisbe prolata*) were associated with the tide crack (Knox 1986; Wahgorn and Knox 1989). Two of these were described a new species (Waghorn 1979). Each species had marked peaks of abundance; from late November until mid-December *P. belgica* and *T. prolata* were most abundant while from mid-December till early January *P. grandispina* dominated (Figure 12.19). The species appeared to use different life history strategies to utilize the short spring–summer food abundance. *Paralabidocera grandispina* probably overwinters as nonadults (possibly as eggs in other Arctiidae) which develop through the adult stage during spring and summer. *Pseudocyclopina belgica* probably overwinters as late copepodites or adults. It appears to lay its eggs and complete some of its development during spring and summer. *Tisbe prolata* probably overwinters as late larval or adult stages and lays eggs in the summer which probably do not hatch until late summer. It seems that the tide crack is an important nursery for *P. grandispina* and *P. belgica* and that is a habitat for the older stages of *T. prolata*.

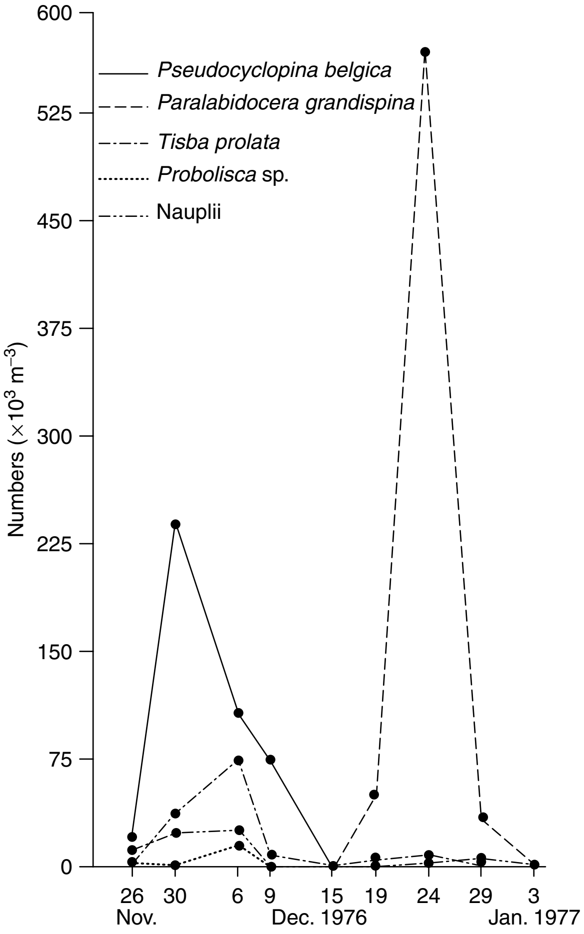


FIGURE 12.19 The succession of copepod species in a tide crack at White Island on the McMurdo Ice Shelf. (From Waghorn, E.J., Knox, G.A., *N. Z. J. Mar. Freshw. Res.*, 557, 1989. With permission.)

12.9.4 THE PLANKTON BENEATH THE MCMURDO ICE SHELF

The plankton in the water column at White Island (78°10′ S, 167°30′ E), McMurdo Sound has been studied over two summers (Knox 1986; Knox et al. in press). Since 1960, the University of Canterbury (Christchurch, New Zealand) Antarctic Research Unit had been observing and tagging an apparently isolated Weddell Seal population along the northwestern coast of White Island (Stirling 1965, 1972; Kooyman 1981c; Davis et al. 1982). This population was first recorded in the austral summer of 1958–1959 by Heine (1960) and since then there has been considerable speculation as to its origin, permanence and regulation of numbers (Littlepage 1965; Stirling 1972). Most observers believe that they have no contact with other Weddell seal populations in McMurdo Sound, and that they are unable to migrate the distance of about 20 km beneath the permanent ice to cracks in the sea ice at the edge of the ice shelf. They overwinter in situ by maintaining breathing holes in the tide cracks or pressure ridges.

The seals at White Island number between 20 and 30. In the summer of 1966–1967, a total of 20 seals were located; 5 adult males, 1 subadult male, 8 adult females, 3 subadult females, 2 male pups and 1 female pup. The seals that were captured were all in excellent condition, in fact the adults were among the largest that we had encountered in several years' study of the Weddell Seals in the McMurdo Sound region (Stirling 1969c, 1971a). This implied that there was an abundant food supply available to them at some considerable distance from the edge of the McMurdo ice Shelf. To investigate this, a research programme was initiated in the summer of 1976–1977 to investigate the tide crack community (Waghorn 1979; Rawlence et al. 1987; Waghorn and Knox 1989), the dynamics of the under-ice pelagic ecosystem (Knox 1986, 1990; Knox et al. 1992), the structure of the benthic community, and the population and feeding ecology of the fish (Zurr 1977; Bradford 1980).

Movement of the ice sheet away from the northwestern coast of White Island gives rise to an area of thinner fast ice that is probably only a few years old and averages about 3–5 m in thickness. Water column processes under the ice shelf (temperature, salinity, current speed and direction, light penetration and dissolved oxygen) were measured at weekly intervals over the summer of 1976–1977 through a hole in the fast ice over a water depth of 67 m (Knox 1986; Knox et al. 1990, Knox et al. in press). Seawater temperatures ranged from −1.91 to −1.96°C. Dissolved oxygen levels varied from 5.0 to 6.05 ml l^{-1} in early December to 4.65–4.8 ml l^{-1} in late January. Water current speeds of up to 0.13 m s^{-1} were recorded at a depth of 50 m and a predominantly northward flow was detected. Light levels under the ice were low with less than 1% of the incident light being transmitted to a depth of 3 m. No chlorophyll *a* was detected in the water column when measured by processing one litre of seawater.

Zooplankton were sampled using a WP2 freefall net. Zooplankton biomass values in the water column ranged from 12 to 447 mg wet wt m^{-3} and were similar to values recorded elsewhere from Antarctic coastal waters. Hicks (1979) measured zooplankton biomass at a series of stations in the seasonal sea ice off Pram Point near Scott Base on Ross Island. His stations were some 20 km north of the White Island station. His biomass values for 100-m sectional hauls ranged between 0.073 and 3.309 mg m^{-3}. These values are about two orders of magnitude lower than the values recorded at White Island and probably indicate that he was sampling either a different water mass or that the zooplankton production is highly variable from year to year, depending on ice conditions.

Thirty-two zooplankton species were recorded including an ostracod, 21 copepods (10 calanoids, 3 cyclopoids and 8 harpacticoids), 4 amphipods, 2 euphausiids (*E. crystallorophias* and *T. macrura*), a chaetognath, and 3 pteropods. Larvae of polychaetes and fish (*Prionodraco evarni* and *P. antarcticum*) were found on some occasions. The species composition of the zooplankton was similar to that found in the inner Ross Sea (Hicks 1974). Amongst the Copepoda, however, there were a number of species which have previously not been recorded from the region, but which are known to be associated with ice in other localities in Antarctica. Copepods were the most abundant animals but other common species were the pteropods, *Clione antarctica* and *L. helicina* and an ostracod, all of which have a circumpolar distribution (Baker 1954). The amphipods, *O. plebs* and *O. rossi*, and the euphausiid *E. crystallorophias* were occasionally caught in large numbers. The dominant copepods were *C. acutus, C. propinquus, Ctenocalanus citer, Euchaeta* sp., *M. gerlachei, Paralobidicera grandispina, O. similis, O. curvata* and *T. prolata*.

The absence of chlorophyll *a* in the water column at White Island during the study was puzzling, as it had been expected that phytoplankton from the blooms which occur in McMurdo sound following the breakup of the sea ice would have been carried under the McMurdo Ice Shelf towards White Island. The decreasing concentrations of dissolved oxygen over the summer, the low water temperature and the absence of detectable chlorophyll *a* in the water column at White Island support the hypothesis that during the 1976–1977 summer the water under the shelf at White Island had not originated directly from the southward flow of water under the shelf past Ross Island, but rather it was water from a northward flow from under the shelf. This water was probably derived from water moving south in the middle of the sound, and then turning north as it encountered grounded ice in the vicinity of Black Island (Knox 1986). The stock of phytoplankton in this water mass could have been consumed by the abundant zooplankton or sedimented to the bottom before it reached the vicinity of White Island.

The research at White Island was continued during the 1978–1979 summer through a hole in the ice over 75 m of water. The zooplankton was similar to that recorded during the 1976–1977 season but was more varied and more abundant in the early part of the season. This difference can be attributed to the earlier breakout of the sea ice in McMurdo Sound in the 1978–1979 summer season with earlier and enhanced plankton production in the sound. ATP levels reached a marked peak in early January following the peak in phytoplankton production which occurred in the sound (Figure 12.20). In this season, greater volumes of water were processed for chlorophyll *a* determinations. In order to obtain a reading, 16 l of water had to be filtered during November but later in the season this volume was reduced to 4 l. Nevertheless the amount of phytoplankton in the water column was very low.

12.9.5 THE BENTHOS BENEATH THE MCMURDO ICE SHELF

Littlepage and Pearse (1962) were the first to report the presence of animal life under the permanent ice shelves in McMurdo Sound. They collected benthic invertebrates belonging to 16 major taxonomic groups from 43 to 75 m at White Island (22 km from the ice edge) and from the Koettlitz Glacier (28 km from the ice edge). They reported that a number of the extremely common, shallowwater invertebrates found at McMurdo Sound were absent from White Island. Dayton and Oliver (1977) dived through a tide crack at White Island and reported a range of epifaunal plankton-feeding species which were also common at Cape Armitage, such as the sponges *Polymastia inagitata* and *Latrunculia apicalis*, the alcyonarian *Alcyonium paessler*, the actinarians *Artonidactis victrix, Isotealla antarctica* and *Urticinopsis antarctica*, the stoloniferan *Clavularia frankliniana*, the hydroids *Lampra* spp. and *Halecium arboreum*, and the large bivalve *Laturnula elliptica*. Bruchausen et al. (1979) captured a single cryopelagic fish *Pagothenia borchgrovinki* in a trap lowered through a crevasse near Minna Bluff, 80 km from the shelf edge. The ice thickness and water layer at this point were approximately 175 m and 500 m respectively. It is also of interest that Heywood and Light (1975) caught four specimens of the same species in a large periglacial lake, lying an Ablation Valley in King George Sound (70°49′ S; 68°25′ W). King George Sound is covered by shelf ice 100–500 m thick.

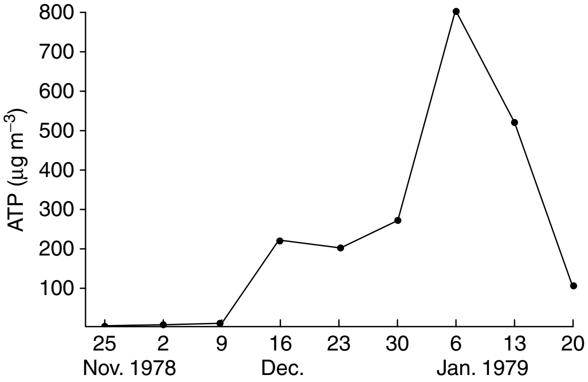


FIGURE 12.20 Summer distribution of ATP in the water column beneath the McMurdo Ice Shelf at White Island. (From Knox, G.A., *Mem. Nat. Inst. Polar Res., Special Issue*, 345, 1986. With permission.)

During the two seasons that the University of Canterbury Antarctic Research Unit worked at White Island, benthic collections were made through the ice holes with an orange peel grab. Analysis of the samples has revealed a rich benthic fauna (Knox 1986; Knox and Ensor in press). A total of 307 species have been recorded from this somewhat limited aereal sampling. The number of species in each taxonomic group were Foraminifera (32), Porifera (25), Hydroida (8), Alcyonaria (3), Actinaria (5), Stolonifera (1), Scleractinaria (3), Platyhelminthes (1), Nemertinea (2), Polychaeta (88), Pycnogonida (12), Ostrocoda (20), Cumacea (3), Tanaidacea (6), Amphipods (13), Isopoda (14), Brachyopoda (1), Amphuneura (1), Gastropoda (23), Bivalvia (10), Bryozoa (23), Echinoidea (1), Asteroidea (5), Ophiuroidea (6), Holothuroidea (1), Ascidacea (1), Acarina (3) and Pisces (4), a total of 307 species. A number of these have not been identified to species level and a number will prove to be new species. The species composition is similar to that found at similar depths near the northern edge of the McMurdo Ice Shelf. However some differences are apparent. The thick layer of sponge spicules, mollusc shells, and debris that is characteristic of much of the benthic area in eastern McMurdo Sound were not found at White Island. The bottom was composed of pebbles and cobbles with relatively coarse sediment between them. The most common epifaunal species were particle-feeding sponges, alcyonarians, bryozoans and hydroids, suggesting that the major food source was plankton and detritus. Detrital feeding amphipods were abundant.

In addition to the benthic invertebrates, collections of benthic fish were made (Zurr 1977). Two notothenoid fish *Trematomus centronotus* and *T. bernacchii* were common. *Trematomus centronotus* was caught early in the season, whereas more *T. bernacchii* were caught later. The *T. bernacchii* were significantly larger than the *T. centronotus* and were predominantly old females. Castellini et al. (1984) caught fish at White Island throughout 1981. Between March and August, four species of fish were captured: *T. centronotus* (37 specimens), *T. bernacchii* (10), *T. loenbergii* (2) and *T. hansoni* (1).

12.9.6 CIRCULATION AND PRODUCTION BENEATH THE MCMURDO ICE SHELF

Circulation patterns have briefly been touched upon in Section 12.3.1. Here, we will attempt to relate the circulation patterns to the production of the underice benthic communities. The benthic area off White Island, as we have seen, has a substantial biomass of benthic invertebrates and fish, the latter being sufficiently abundant to support year round the resident Weddell seal population. White Island is ice locked and the marine community there represents a unique ecosystem, since there is little or no primary production in its vicinity due to the thick ice and low light levels. Consequently the ecosystem must be supported by energy flux from the open sea. As little or no phytoplankton has been found in the water column during the period of summer phytoplankton bloom in the open waters of McMurdo Sound, the energy input must be through detrital material, bacteria and the abundant zooplankton in the water that moves past the island.

There is still debate as to the exact pattern of water movement under the shelf. Based on an examination of the available data on current flows within McMurdo Sound, Knox (1986) has hypothesized the circulation pattern depicted in Figure 12.18. This proposed pattern is supported by the available information on the distribution of the phytoplankton, zooplankton and benthic invertebrate communities in the inner sound. Dayton and Oliver (1977) have drawn attention to the contrasts between the soft-bottom benthic assemblages on the east and west sides of McMurdo Sound. In their studies Dayton and Oliver recorded 37 species and 2828 individuals in a core ($0.018\ \mathrm{m}^{-2}$) in 20 m off Cape Armitage on the east side of the sound and 50 species and 176 individuals in a similar core taken in 40 m of water on the west side of the sound. The infaunal assemblages of the east sound have higher densities than almost any other area in the world's oceans, whereas those in the west sound have very low densities, similar to deep sea habitats. In addition, there is a decreasing north–south infaunal gradient along the west sound (Dayton and Oliver 1977). One obvious hypothesis to explain such patterns is that there are differences in the amount of primary production available to the benthic communities.

However, phytoplankton pigment concentrations do not show consistent east–west sound differences. Dayton, Watson, and Palmisano (1986) sampled a range of sites in the east and west sounds and found no consistent differences; within site and between site differences reflected advection and local differences in ice and snow cover. Advection of phytoplankton from the open water is especially important in the east sound (Palmisano et al. 1986). In contrast to the chlorophyll data of Knox (1986) and Knox et al. (in press), Dayton, Watson, and Palmisano (1986) recorded chlorophyll *a* values of $0.62 \pm 0.15\ \mathrm{mg\ m}^{-3}$ at White Island and postulated that this was due to advection of phytoplankton from the north. However, since the samples were taken in the vicinity of the tide cracks, it was possible that it was the tide crack phytoplankton that was being sampled. Southerly sites sampled in the west sound by Dayton, Watson, and Palmisano (1986) at Marshall Valley, Garwood Valley, and Heald Island have either extremely low values or no chlorophyll in the water column. The other possible contributors to the primary production base are the ice algae and the benthic microalgae. Palmisano and Sullivan (1983a) found no consistent differences in the biomass and productivity of the ice algae in the east and west sounds. In contrast the benthic microalgal biomass and production showed considerable differences, with high values in the east sound and low values in the west sound (Dayton, Watson, and Palmisano 1986; see Chapter 11 of Section 4.1). In the 1982–1983 summer, I sampled water column production processes at three sites across the sound: station A, 1.5 km south of Scott Base (water depth 340 m); station B, approximately 1.0 km north of the edge of the McMurdo Ice Shelf and 22 km from Cape Armitage (water depth 350 m); and station C, approximately 2.0 km north of the Dailey Islands on the west side of the sound (water depth 210 m). Station A was sampled five times from mid-November to late February, while stations B and C were sampled in early December and early January.

At Station A there was no chlorophyll present in the water column on the first and second samplings on November 29 and December 6. Significant chlorophyll levels were recorded on December 23, coincident with a *Phaeocystis* bloom being advected under the ice. Very high chlorophyll levels were recorded at station B on January 5 1983 following the breakout of the sea ice in the outer part of the inner sound. As expected, low chlorophyll levels were recorded on both occasions at station C. Zooplankton samples were dominated by copepods with numbers increasing over the season. The first two samplings at station A (November 29 and December 6) revealed a very sparse fauna. Juveniles of the euphausiid, *E. crystallorophias*, were present throughout the sampling period with adults occurring late in the season. Numbers increased as the season progressed. Amphipods and ostracods were generally present and were most numerous in the later samples. Pteropods were present in all samples and on several occasions occurred in large numbers. Larval fish were present in the latter part of the season. There were some significant differences between the three stations. Station B in the middle part of the sound had the richest fauna, both in terms of species and numbers, on all occasions. Station C on the west side of the sound had the sparsest fauna.

Thus the circulation pattern depicted in Figure 12.18 is supported by the biological data. The inshore surface current moving round Cape Armitage and up the coast of Ross Island is derived from Ross Sea water advected under the Ross Ice Shelf, with the addition of water advected under the McMurdo Ice Shelf in the center of the sound returning northward along the coast of White Island. Some of this water which advects under the McMurdo Ice Shelf returns as the northward flowing current along the coast of the west sound.

Castellini et al. (1984) have made some preliminary calculations of the minimum energy flow to White Island necessary to support the seal populations found there. An adult Weddell seal consumes about 15 kg of fish per day (Kooyman 1981c). Of the 25–30 resident seals, about 10 are young animals and it is assumed that they consume half an adult's amount of food. This yields a total of 2×10 kg fish per year taken in the immediate area. Although the fish population density may vary, the seals have been at White Island for over 25 years which indicates a fairly consistent food supply. Assuming the fish population to be relatively stable, the maximum sustainable yield equations (Wilson and Bossert, 1971) predict that the seals are not removing more than 50% of the fish. This suggests that the fish biomass is at least 4×10^6 kg. If the fish population requires about eight to ten times its biomass to survive (Gulland 1970), then at least 3.6×10^6 kg of zooplankton are brought into the area from the open sea via undershelf currents. However, a primary component of the fish diet are detrital feeding, scavenging amphipods which occur in large numbers at White Island. In addition, other benthic invertebrates are consumed. Part of the energy input therefore passes through other consumers before being consumed by the fish. Thus the energy influx must support the benthic invertebrates which as we have seen occur in considerable numbers off White Island, although not as abundantly as further north off Cape Armitage.

Castallini et al. (1984) also calculated from data in Holm-Hansen et al. (1977) that a section of open water in the Ross Sea equivalent to the area fished by the Weddell seals at White Island (20 km shoreline, 4 km offshore) would yield 3.9×10^7 phytoplankton produced each year. Using a 10% estimate (Gulland 1970; Knox 1970) for the biomass for each successive consumer level this primary production would result in about 3.9×10^6 zooplankton and 3.9×10^5 fish produced in the area each year. This is the same stable fish biomass figure arrived at above by using estimates the food consumption patterns of seals. Castellini et al. calculated the primary productivity that could maximally be produced in the White Island tide crack (20 km crack by 1 m wide) would produce only 20–25 kg of fish—a minimum amount relative to the 2.0×10 kg necessary to support the seals. Holm-Hansen and Huntly (1974) concluded that seals remove about 1.3% of the total annual production in the Antarctic seas. The calculations by Castellini et al. (1984) for the White Island area predict that the seals are removing 0.5% of the energy flowing into the area each year.

12.9.7 LIFE BENEATH THE ROSS ICE SHELF

From the water below the Ross Ice Shelf at the RISP site, Lipps et al. (1977, 1978, 1979) and Bruchhausen et al. (1979) observed a number of invertebrates and fish. Large numbers of amphipods (*O. plebs*, *O. rossi* and *Orchomene* sp.) were trapped and observed by television and one large isopod (*Serolis trilobitoides*) was captured. Two fish species (*Trematomus* cf. *T. loennbergii* and *Gymnodraco acuticeps*) and two large crustaceans were seen on the television screens. The sediments showed no signs of animal activity, no bioturbation, and no faecal pellets (Ronan et al. 1978). Meifaunal bivalve, gastropod, ostracod and foraminiferan skeletons were found but no living infauna was detected. These findings indicated that a significant biological community, apparently without unique forms, exists as far south as 450 km from the open sea.

Azam et al. (1979) studied the microbial life beneath the Ross Ice Shelf at the RISP site. Bacterial numbers as estimated by epiflourescence microscopy were $1.2\times10^6\ \mathrm{l}^{-1}$ in the 66-m sample and somewhat lower in the deeper samples (8.7×10–$9.5\times10\ \mathrm{l}^{-1}$). These bacterial densities are similar to those reported from the deep sea. The total microbial biomass in the water samples from 20 to 200 m, as estimated from the measurement of ATP, was between 0.14 and 0.5 ng ATP l^{-1}. These values are two to three orders of magnitude lower than those from seawater in the Ross Sea (Holm-Hansen et al. 1977). Microbial heterotrophic activity was measured as rates of assimilation and respiration of several isotopicaly labelled substrates and also by microautoradiography. D-glucose assimilation and respiration of samples incubated at 0°C yielded turnover times of the order of 5×10^5 h, thus 10^3–10^4 times less activity than in the Ross Sea around McMurdo Sound (Holm-Hansen et al. 1978). These studies and autoradiographic observations confirmed that the bacteria were metabolically active. Assimilation of thymidine, uridine, and adenosine triphosphate occurred at extremely low rates similar to those in deep sea populations. Occurrence and metabolic activity of bacteria were also examined in the sediments. Epiflourescence microscopy revealed the presence of 8.7×10^7 and 1.6×10^8 bacteria g sediment^{-1} (dry weight) in the top 2 cm of the two samples examined. In one case, 3.9×10^7 bacteria were found per g (dry weight) at 8–10-cm depth in a core.

Water samples were examined for small microplankters. Many small unidentified organisms were seen, with the largest numbers of 1.1×10^4 cells l^{-1} being found in the 200 m sample. A few naked dinoflagellates were seen. Larger phytoplankters occurred at between 10 and 200 cell ml^{-1}, with the greatest abundance at 20 m; abundances were more than one order of magnitude lower at 100 and 200 m. The phytopkankton consisted mainly of pennate diatoms together with a few centric forms. While no protozoans were seen in the sample at 20 m, the skeletal remains of simple nassellarian radiolarians were found in the deeper samples. Metazoan forms observed included naupliar and postnaupliar copepods of the family Oithonidae. Two specimens of another segmented metazoan, probably a polychaete larva, were found in the sample at 20 m.

Thus, although in low abundance, several components of what might constitute a planktonic food chain were found in the waters under the Ross Ice Shelf. With the data available, it cannot be determined whether the microbial organisms represent an indigenous population, or if they represent remnants of populations from the Ross Sea.

13 Ice-Edge Processes

CONTENTS

13.1 INTRODUCTION

In 1971, El-Sayed (1971a) reviewed the biological aspects of the pack ice ecosystem. He concluded that, “despite the valuable information we now have concerning the taxonomy, distribution and abundance of marine organisms in the pack ice zone, there are still enormous gaps in our knowledge of the biomass and relative abundance of these organisms. …Further our data is poor with regard to the relationships between the trophic levels and the flow of energy through the Antarctic pack ice.” Apart from isolated observations, particularly of phytoplankton on blooms (Burkholder and Mandelli 1965; El-Sayed 1971b; El-Sayed and Taguchi 1981) it was not until recently that multidisciplinary research programs have been directed at understanding the quantitative relationships of the flora, fauna and energy flow in the pack ice ecosystem. The Group of Specialists on Southern Ocean Ecosystems and Their Living Resources stressed, early in their deliberations, the importance of pack ice zone studies, and particularly studies of processes occurring at the edge of the retreating ice. The group recommended that such investigations be included in the BIOMASS Program.

The marginal ice-edge zone is an oceanographic front that transitions from dense pack ice (those waters completely covered with ice) to waters completely free of ice (Dunbar 1983). It is a dynamic zone responding rapidly to physical forcing such that the transition from 10/10 ice cover to open water may be abrupt or occur over hundreds of kilometres. The position of the ice-edge can vary widely, with mesoscale features occurring over a period of days and large-scale changes occurring seasonally. Furthermore, significant interannual variations occur (Niebauer 1980; Zwally et al. 1983a) in connection with global variations in air-sea interactions.

The U.S. National Academy of Sciences Committee to Evaluate Antarctic Marine Ecosystem Research recommended that an intensive study of the marginal ice zone be undertaken (National Academy of Sciences 1981). A workshop was held in Woods Hole in April, 1981 at which proposals for such a study were discussed. Further meetings resulted in the development of a project called the Antarctic Marine Ecosystem Research at the Ice-Edge (AMERIEZ). Two major hypotheses provided the focus for the studies recommended:

1. The pack ice-edge is associated with an oceanographic front that enhances biomass and productivity. This kind of enhanced productivity is similar to that found in association with other ocean fronts, such as upwelling along continental shelves and divergences. A combination of physical and chemical factors, including vertical water column stability, enhanced

light levels, and the physical presence of ice as a substrate, interact to control the enhanced productivity.

2. The seasonal ice margin constitutes an ecological interface between two biological communities—one associated with the open ocean, the other with the pack ice—and the advance/retreat of the ice-edge is a factor importantly reflected in the life history of associated organisms. The ice and associated open-water communities differ with respect to species composition, life-history patterns and rates of organic matter transfer.

Work carried out to date in both the Arctic and Antarctic seas has demonstrated that rapid gradients in ice, water properties, and atmospheric states, as well as in the composition of the biological communities take place at the ice-edge (e.g., Alexander 1980; Stirling 1980; Ainley and Jacobs 1981; Clarke and Ackley 1981a, 1981b; Dunbar 1983; Stirling and Cleator 1981; Buck and Garrison 1983; Johanssen et al. 1983; Muench 1983; Garrison et al. 1984; Miller et al. 1984; Smith and Nelson 1985a,b 1986 1990; Comiso and Sullivan 1986; Fraser and Ainley 1986, Wilson et al. 1986; Buck et al. 1987; Smith et al. 1987, 1988; Ainley et al. 1988; Sullivan et al. 1988, 1990a; Sakshaug and Skjoldal 1989; Comiso et al. 1990; Cota et al. 1990; Kottmeier and Sullivan 1990; Smith and Sakshaug 1990; Veith et al. 1992). The ice-edge zone has frequently been reported to be a region of increased phytoplankton biomass and productivity, both in the Southern Ocean (e.g. Hart 1934; Ivanov 1964; El-Sayed and Taguchi 1981; Nelson and Gordon 1982; Smith and Nelson 1985b,1986; Fryxell and Kendrick 1988; Smith et al. 1988; Fryxell 1989; Sullivan et al. 1990), and in northern polar seas (e.g., McRoy and Goering 1974; Alexander 1980; Alexander and Niebauer 1981). Additionally, the marginal ice-edge zone has been noted as being associated with elevated abundances of marine birds and mammals in the Bering Sea and other parts of the Canadian Arctic (McRoy and Goering 1974; Dunbar 1983; Stirling and Cleator 1981), and in the Southern Ocean (Siniff et al. 1970; Zenkovitch 1970; Laws 1977a, 1977b; Ainley and Jacobs 1981). There is, thus, a growing body of evidence that ice-edge phenomena may be of great importance in the overall biomass, production and nutrient and sedimentation cycles of the Southern Ocean (Nelson and Gordon 1982; Jennings et al. 1984; Fraser and Ainley 1986; Johnson and Smith 1986; Smith and Nelson 1986; Ainley et al. 1988; Nelson 1989; Nelson et al. 1989).

13.2 THE ICE-EDGE HABITAT

The location of the ice-edge is controlled by the combined effects of the upper ocean circulation and the local winds that advect ice from one location to another and by thermodynamic processes such as freezing and thawing which create or destroy ice in situ. The nature of the ice-edge varies greatly. Often there is a sharply delineated boundary between complete ice cover and open water over a very short distance (often less than one kilometer), although at other times a considerable area of loose pack (often many tens of kilometers) separates the consolidated pack from the open ocean. The ice-edge itself can be extremely complex with a hierarchy of scales varying from bands 110 km across (Muench and Charnell 1977; Martin et al. 1983; Muench et al. 1983; Wadhams 1983), through mesoscale features (10–100 km) possibly connected with ocean eddies (LeBlond 1982; Johanssen et al. 1983; Wadhams and Squire 1983), up to basin scale features. Associated with the ice-edges are complex oceanographic structures with a wide range of temporal and spatial scales that have been described both in the Arctic and Antarctic (e.g., Gordon and Huber 1982; Johannessen et al. 1983; Muench, et al. 1983). Significant regional variations in the character of the Antarctic ice-edge have been reported. In regions where the underlying currents flow northward, the sea ice is advected into lower latitudes as ice "promontories". With summer melting, this ice injects significant quantities of melt-water to the north. Because of its low salinity, this melt-water is confined to a surface layer that overlies a denser layer. The best developed of these ice "promontories" occurs in the western Weddell Sea where a strong western boundary current transports water from the coast of the Antarctic Peninsula towards Bransfield Strait and the eastern Scotia Sea (Gordon et al. 1981).

The boundary region between the Weddell Sea cyclonic and the eastward circumpolar flow of the West Wind Drift is an extremely dynamic region marking the boundary between the two current regimes and temperature-salinity properties. This boundary is a frontal zone corresponding to the maximum northern extent of the Weddell Sea pack ice. The front can be sharp and well defined with evidence of mesoscale features, such as eddies. In addition to the role of frontal zones in influencing the position and nature of the ice-edge, vertical transfer processes with the redistribution of heat and salt are also important to the thermodynamic balance which ultimately determines the ice-edge position.

The ice floes at the ice-edge structurally undergo three distinct stages (AMERIEZ 1983):

1. A formation stage where the ice initially grows and agglomerates into floes;
2. A metamorphic stage characterized by temperature changes, snow deposition and removal, ice ridging, and rafting;
3. A decay stage where wave action and top, bottom and lateral melting all contribute to erode the floes and distribute both organic (algae, bacteria, protozoa, invertebrates, detritus), and inorganic substances (freshwater, nutrients, etc.) into the ocean.

Each of these three physical phases is also characterized by the diversity and types of species and the amount of biological activity present.

In the formation stage, several types of sea ice algal communities (Chapter 3, Section 3.3.1) have been observed that have roughly been categorized into *bottom communities* and *interior communities* (Ackley et al. 1979; Garrison and Buck 1985b; Horner 1985a, Garrison et al. 1986; Horner et al. 1988). Sea ice bottom communities are of two types; those associated with congelation of columnar ice and those in structurally weak ice that may be attached to the undersurface of the floes as platelets and frazil billows beneath the intact ice cover. Interior communities are those formed by incorporation into the sea ice (both frazil and congelation or columnar ice) and which are somewhat removed from contact with the ocean water. Such communities develop in partial isolation under unique temperature, salinity, light and nutritional conditions.

During the "metamorphic" or second stage of ice floe development, the ice floe island community develops further. As pressure ridges form in the ice cover, the ridges act as snow fences. The loading of ice blocks can depress the floes so that local flooding saturates the snow cover at the base of the ridges. Such conditions produce an additional habitat, the *snow–ice surface* communities. Such communities are again characterized by a different set of temperature, salinity, light and nutrient conditions. Flooding caused by wave action can also produce a similar habitat. Temperature fluctuations can also create additional habitats by melting the snow cover and leading to melt accumulation on low spots under the snow cover.

Finally, in the decay phase the ice warms, increasing its water content by internal melting, and developing an interconnected pore space throughout the floe and eventually a semi-open connection with the water below. The "pore water" develops a rich algal, bacterial and protozoan community. In the latter stages of this structural development zooplankton may enter the labyrinth system and graze on the rich communities found there. Floe breakup leads to local isostatic imbalances and the development of lagoons and pools at the bases of the ridges, some of which may be periodically flushed by wave action. These form another habitat that is particularly rich in algae and associated microbial populations.

13.3 ICE-EDGE PHYTOPLANKTON BIOMASS AND PRIMARY PRODUCTION

As discussed in Chapter 3, the Southern Ocean as a whole is considered, based on sampling to date, to be a region of low productivity. However, it is also well known that Antarctic waters may exhibit occasional, periodic phytoplankton blooms. The conclusion that the Southern Ocean is only moderately oligotrophic seems paradoxical since there are large concentrations of phytoplankton consumers, especially krill, and since the primary production supports large stocks of birds, seals and whales. In addition, there are substantial deposits of diatoms on the Antarctic continental shelf (DeMaster 1981) indicating high surface productivity. This all suggests that a large source of primary production has been missed in most previous investigations of the Southern Ocean; it is highly probable that the missing link is the occurrence of ice-edge phytoplankton blooms which can often produce massive amounts of phytoplankton over very short periods. Examples of some recent studies of ice-edge phytoplankton biomass and production are given below.

The first of these is the study carried out in the western Ross Sea off the Victoria Land coast (Smith and Nelson 1985a, 1985b) (Figure 13.1a). Ice conditions along the transect were variable. Heavy ice (virtually 100%) was encountered near the coast (station 36), while station 37 was at a distinct boundary between heavy ice and broken ice. Ice cover in the middle part of the transect (stations 38 and 39) ranged from 20% to 60%, while stations 40–43 were in open water. Sections of temperature, salinity and density clearly showed the influence of the melting pack ice. A layer of low salinity water was present on the surface and it extended about 250 km from the dense ice pack at station 37, with a sharp halocline and pycnocline at a depth of 20–30 m. Further offshore from this feature, surface salinity and the depth of the mixed layer increased markedly.

Phytoplankton biomass, as measured by chlorophyll *a*, particulate carbon and biogenic silica distributions was tightly coupled to the region of melt-water influence, being embedded in the melt-water lens. Dominant species in the bloom were the pennate diatom *Nitzchia curta* (generally considered to be an ice algal species), which constituted up to 85% of the total cell numbers, and the congeneric species *N. closterium*. While the phytoplankton biomass was substantially greater in the bloom (stations 36–41) than seaward of it (stations 42 and 43), the major compositional ratios of the surface phytoplankton did not change appreciably indicating that the bloom was dissipated by both vertical and lateral processes. The decrease in stratification away from the melt-water input allowed for more active vertical mixing. The two zones were sharply discontinuous and separated by an abrupt change in water color. Concentrations of particulate organic matter within the blooms euphotic zone were much greater than outside the bloom. The particulate carbon values were extremely high, resembling the concentrations found in hyperproductive upwelling areas such as those off the coast of Peru (Hobson et al. 1973). Concentrations of biogenic silica in this bloom were the highest yet reported from the world's oceans, averaging approximately three times higher than concentrations reported off the coast of northwest Africa (Krebs 1983). The data suggested the bloom was initiated by seeding of the water column by the release of ice algae.

The second example is the November 1983 AMERIEZ cruise to the Weddell Sea. This cruise undertook several approximately north–south transects through the marginal ice zone (Smith and Nelson 1986). Selected results from one such transect are shown on Figure 13.2. All transects through the open water at the ice-edge showed a pronounced phytoplankton bloom. Phytoplankton biomass, as measured by chlorophyll *a*, increased from background levels ($>0.1\ \mu g\ l^{-1}$) in areas of virtually complete ice cover to more than $9.0\ \mu g\ l^{-1}$. The distribution of biogenic silica (a measure of diatom biomass) showed a similar pattern with the region of high concentration ($>1.0\ \mu mol\ SiO_2\ l^{-1}$)

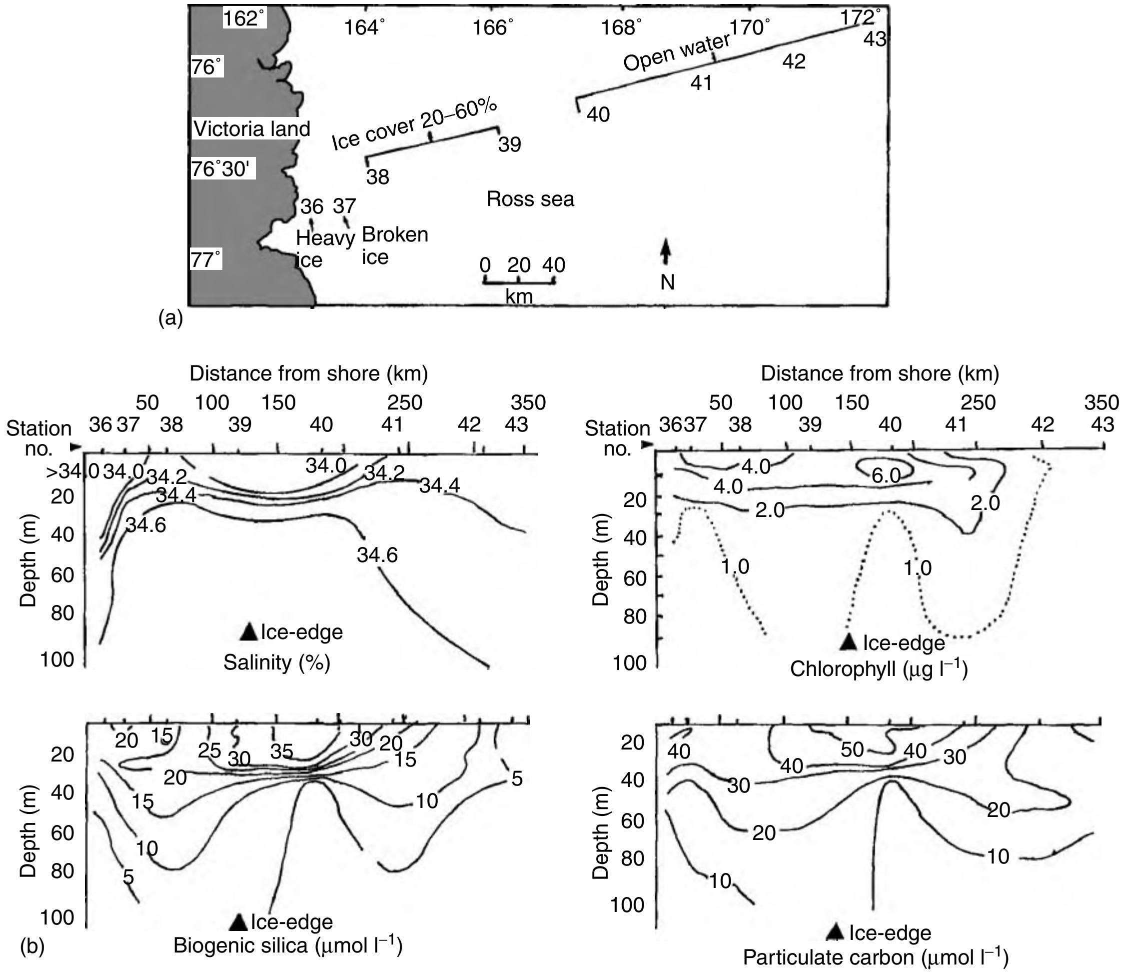


FIGURE 13.1 (a) The location of the transect study across a receding ice-edge in the Ross Sea, showing ice conditions along the transect. (b) Vertical sections of salinity, chlorophyll *a*, particulate carbon and biogenic silica along the transect depicted in (a). (From Smith, W.O., Jr., Nelson, D.M., *Science*, 227, 163, 1985. With permission.)

coinciding almost exactly with the high chlorophyll region. This relationship strongly suggested that the phytoplankton biomass in the bloom area was dominated by diatoms, of which *Thalassiosira gravida* was the dominant species, in spite of the high numerical abundance of very small *Phaeocystis* cells. The phytoplankton biomass was strongly influenced by water mass characteristics and physical fronts, which were distinguished by large changes in surface salinity and dissolved silicic acid concentrations. The region of enhanced phytoplankton biomass was limited to a region that had salinity less than 34.2, and the seaward extent of the bloom was limited by a hydrographic front which was best defined by silicic acid distribution. Primary productivity as measured by photosynthetic ^{14}C incorporation was centered in the high biomass region where the vertically integrated primary productivity was ca. 750 mg C m^{-2} day^{1}. Bacterioplankton cell production coincided closely with the distribution of chlorophyll *a* and primary production rates.

More recently Smith and Nelson (1990) have summarized rates of primary production, specifically NO_3^- uptake, and NH_4^+ uptake by phytoplankton in the marginal ice-edge zone of the Weddell Sea in the austral spring of 1983 and autumn 1986 (Figure 13.3). In spring chlorophyll *a* concentrations averaged 3 µg l^{-1}, primary productivity 490 mg C m^{-2} day^{-1}, and surface phytoplankton growth rates 0.30 doublings day^{-1}. In autumn these rates were all much lower, averaging 0.14 µg l^{-1}, 126 mg C m^{-2} day^{-1}, and 0.14 doublings day^{-1}. During both seasons NH_4^+ was consistently the preferred source of *N*, but because of the much greater availability of NO_3^- in the euphotic zone (21–26 µM NO_3^- vs. 0.4 µM NH_4^+ during both seasons), NO_3^- uptake rates generally equalled or exceed those of NH_4^+. Vertically integrated ratios (the ratio of NO_3^- uptake to the sum of NO_3^- plus NH_4^+ uptake) averaged 0.52 (range from 0.35 to 0.70) in spring and 0.72 (range from 0.60 to 0.84) in autumn.

Smith and Nelson (1990) have tabulated the available information on *N*-uptake by phytoplankton in high latitudes (Table 13.1). The data indicates that marginal ice-edge zones may be characterized by ratios higher than those elsewhere in

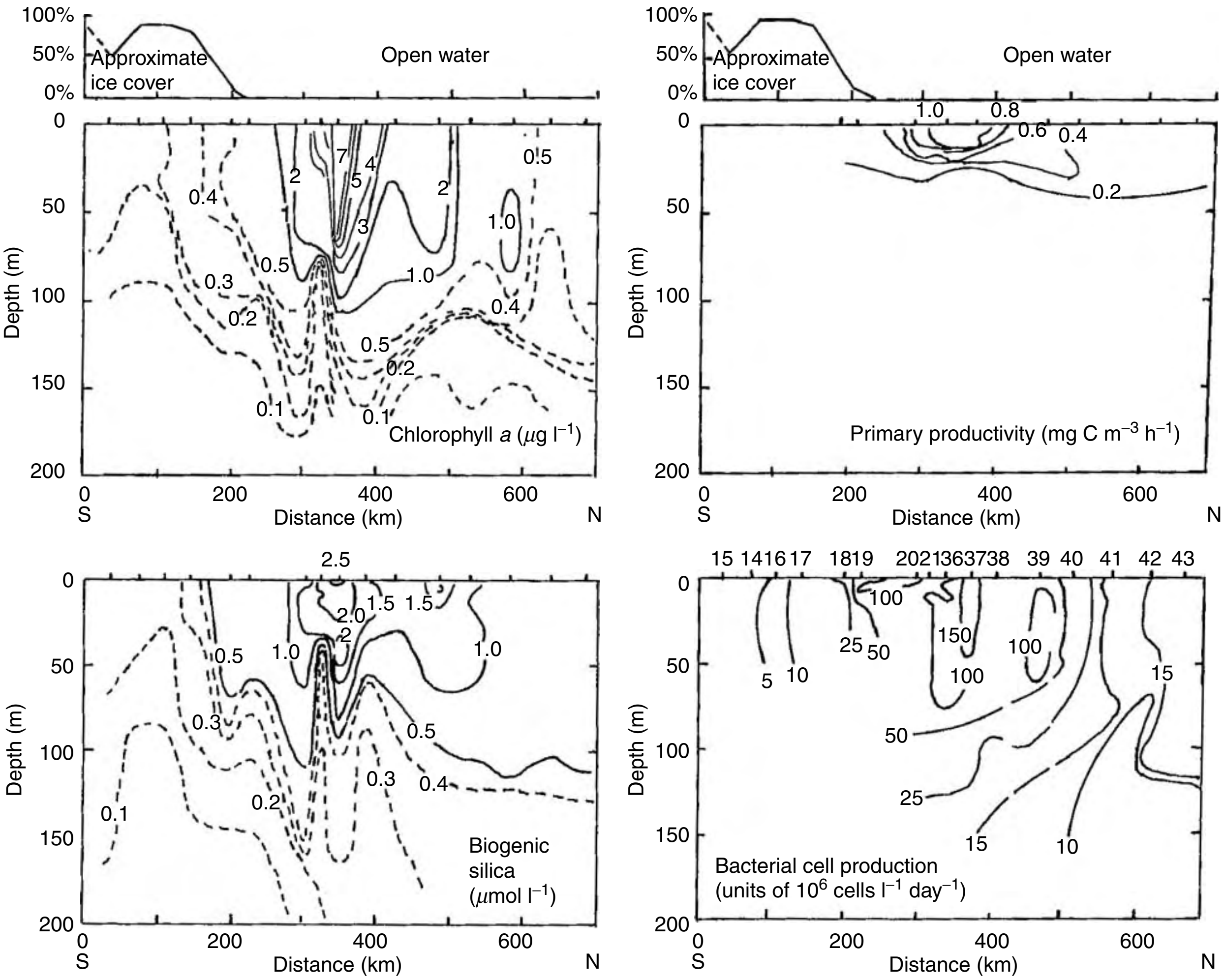


FIGURE 13.2 Vertical sections of chlorophyll *a*, primary production, biogenic silica and bacterial cell production along a north–south transects across the ice-edge in the Weddell Sea in November 1983. (From AMERIEZ, *A Research Plan for Antarctc Marine Research in the Ice-Edge Zone (AMERIEZ),* AMERIEZ Steering Committee, Washington, DC, 35, 1984. With permission.)

polar regions, indicating that nitrate-*N* ("new"-*N*) is the dominant source of *N* in these zones. Smith and Nelson (1990) note that in 1983 they observed sharply elevated relative preference indices for NH_4^+ whenever ambient NH_4^+ concentration was less than 0.3 μM, and they interpreted this as evidence that Antarctic phytoplankton growing at NH_4^+ concentrations less than 0.3 μM have an ability to increase their rate of NH_4^+ uptake in response to increased availability.

The overall spatial extent of the Weddell Sea ice-edge bloom was about 250 km, remarkably similar to that of the bloom in the Ross Sea. However, although the average chlorophyll *a* concentrations were similar in the two studies (3.1 vs. 3.7 μg l^{-1}), the concentrations of particulate carbon, nitrogen and biogenic silica were much lower in the Weddell Sea. The two areas also differed in that the extraordinarily high carbon to chlorophyll and biogenic silica to carbon ratios found in the Ross Sea were not present in the Weddell Sea, where the ratios were more typical of oceanic phytoplankton (Parsons et al. 1977). The differences may be due to the fact that the Ross Sea study took place in late January when the ice cover was near a minimum while the Weddell Sea study took place in November when ice cover was near maximum.

Japanese scientists (e.g., Tanimura 1981; Fukuchi and Tanimura 1982; Watanabe and Nakajima 1982; Watanabe et al. 1982; Fukuchi et al. 1984, 1985a, 1985b; Fukuda et al. 1986; Fukui et al. 1986; Taniguchi et al. 1986; Ohno 1987) have reported high values of surface and integrated chlorophyll *a* concentrations in the pack ice and fast ice regions of the Indian Ocean sector. In a study of the distribution of chlorophyll *a* along 45°E in the Southern ocean in February–March, Watanabe and Nakajima (1982) recorded the highest levels of chlorophyll *a* close to the edge of the fast ice and in a polyna (0.69 mg chl *a* m^{-2}). Low surface salinities (<33.9) were associated with the high phytoplankton standing stocks. Fukuchi et al. (1984) recorded very large integrated chlorophyll *a* stocks (466.5 mg chl *a* m^{-2}, 0–150 m) from the fast ice region of the eastern part of Lutzholm Bay.

In a study of the distribution of water column physical properties, chlorophyll *a* and nutrients off MacRobertsons Land (65–70°E, 61–69°S) in December, Fukui et al. (1985) recorded high chlorophyll *a* levels near the edge of the pack

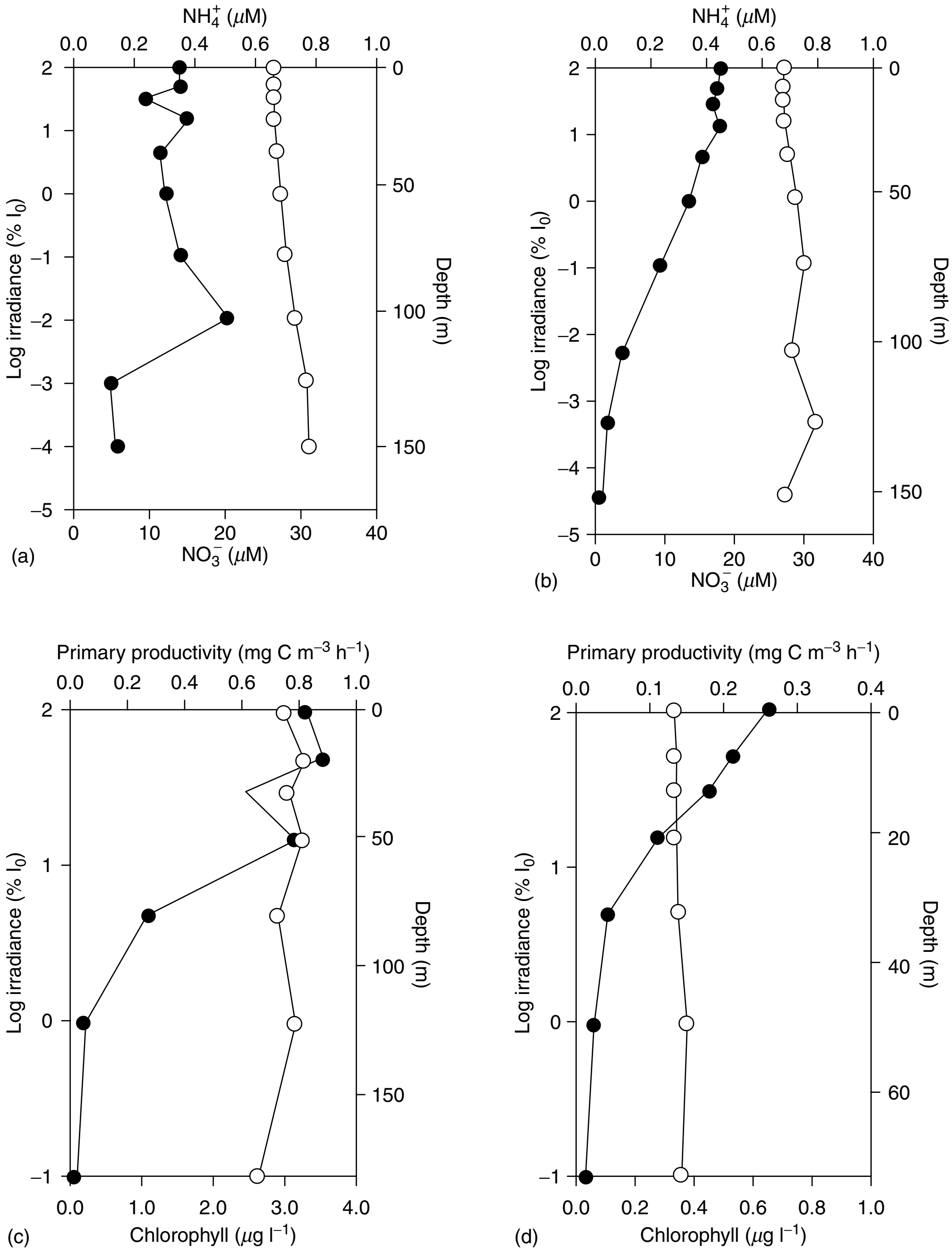


FIGURE 13.3 Measurements of nutrients, chlorophyll *a* and productivity in the upper 150 m in the Weddell Sea ice-edge zone. Sampling depths were based on penetration of radiation. The depth axis represents the mean depth associated with the light depths. (a), (b) Mean NH_4^+(•) and NO_3^-(○) in (a) spring 1983 and (b) autumn 1896. (c), (d) Mean chlorophyll *a* concentrations (○) and primary productivity rates in (•) (c) spring 1983 and (d) autumn 1986. (From Smith, W.O., Jr., Nelson, D.M., *Limnol. Oceanogr.*, 35, 251, 1990. With permission.)

ice (Figure 13.4). From Figure 13.4a it can be seen that the edge of the pack ice had retreated towards the coast from 63–64°S in mid-December to 67–69°S in January–February. The ice-edge zone was characterized by low surface salinities, 33.6–33.8 in December and 33.4–34.2 in January February (Figure 13.4a). A maximum integrated chlorophyll *a* value of 200 mg chl *a* m^{-2} (0–200 m) was recorded in a bloom at the ice-edge in Prydz Bay in January (Figure 13.4b). In the upper layers of this bloom (030 m) inorganic nutrients were depressed; <1.0 μg-at P l^{-1}, <20 μg-at Si l^{-1}, and <16 μg-at N l^{-1}. Tanimura (1981), Fukui et al. (1986) and Watanabe and Satoh (1987) have all suggested that these high chlorophyll concentrations were associated with the release of ice algae to the water column in spring and summer.

TABLE 13.1
Summary of Mean *f*-ratios and Mean Total Primary Productivity from Studies of Polar Regions that Reported *f*-ratios

	Season	*f*-ratio	Primary Productivity (mg C M^{-2} day^{-1})	Source
Pelagic studies				
Scotia sea	Spring	0.54	520	Olson (1980) and El-Sayed and Weber (1982)
Ross sea	Summer	0.42	515	Olson (1980) and El-Sayed et al. (1983)
Scotia sea	Summer	0.37	149	Gilbert et al. (1982) and El-Sayed and Weber (1982)
Baffin bay	Summer	0.53	227	Harrison et al. (1982)
Scotia sea	Summer	0.22	—	Rönner et al. (1983)
Antarctic peninsula	Autumn	0.42	—	Probyn and Painting (1985)
Scotia sea	Summer	0.22	—	Koike et al. (1986)
Mean[a]		0.39	353	
Ice-edge studies				
Scotia sea	Summer	0.48	114	Gilbert et al. (1982) El-Sayed and Weber (1982)
Ross sea	Summer	0.65	962	Nelson and Smith (1986) and D.L. Wilson et al. (1986)
Bering sea	Spring	0.74	—	Muller-Karger and Alexander (1987)
Farm strait	Summer	0.62	426	W.O. Smith and Kettner (1989) and W.O. Smith et al. (1987)
Weddell sea	Spring	0.52	489	W.O. Smith and Nelson (1990)
Weddell sea	Autumn	0.72	126	W.O. Smith and Nelson (1990)
Mean[a]		0.62	423	

[a] Means are simple arithmetic means and are presented to show trends rather than absolute values of the two regions.

Source: From Smith, W.O., Jr., Nelson, D.M., *Limnol. Oceanogr.*, 35, 809, 1990. With permission.

Comiso et al. (1990) using CZCS satellite data in the Weddell Sea marginal ice-edge zone and adjacent areas during the austral summer–autumn transition detected large areas of elevated phytoplankton pigment concentrations. Phytoplankton blooms, about 200 km wide and extending several hundred kilometres along the ice-edge, were observed. The data indicated that phytoplankton blooms are not simply a spring/summer phenomenon since large areas of elevated pigment concentrations were observed through the middle of March, a period in which the ice was generally advancing. In general blooms were in relatively shallow waters (less than 500 m), which may in some manner enhance residence time, stratification, and/or micronutrient flux. Phytoplankton growth occurred as far south as 77°S, indicating that even in the middle of March surface irradiance levels were sufficient to promote phytoplankton growth. These data indicate that estimates of ice-edge phytoplankton production will need to be revised upwards to take into account phytoplankton production in the late summer-early autumn.

13.4 POTENTIAL CAUSES OF PHYTOPLANKTON BLOOMS

According to Smith and Nelson (1986) the following sequence takes place during the initiation, development and decay of an ice-edge phytoplankton bloom:

1. Melt water produces a stable environment with light levels favourable to phytoplankton growth.
2. A bloom begins, and because the water column biomass is low, the phytoplankton comprises mainly those species released from the ice.
3. Ice melt continues, further increasing water column stability.
4. Some species grow in the stable surface layer, and their contribution to the overall phytoplankton assemblage increases with time. Although they may be considered ice algal species, most of their growth occurs in the water column.
5. As the low-density melt water degrades by vertical and lateral flow, vertical mixing increases, and the phytoplankton bloom dissipates by physical processes. Thus, the production and degradation of the vertical stability produced by melting sets the dimensions of the bloom.

The possible mechanisms involved in the above sequence will now be examined in more detail.

13.4.1 WATER COLUMN STABILITY

The primary mechanism proposed for the initiation and development of a bloom is the stable layer of low salinity

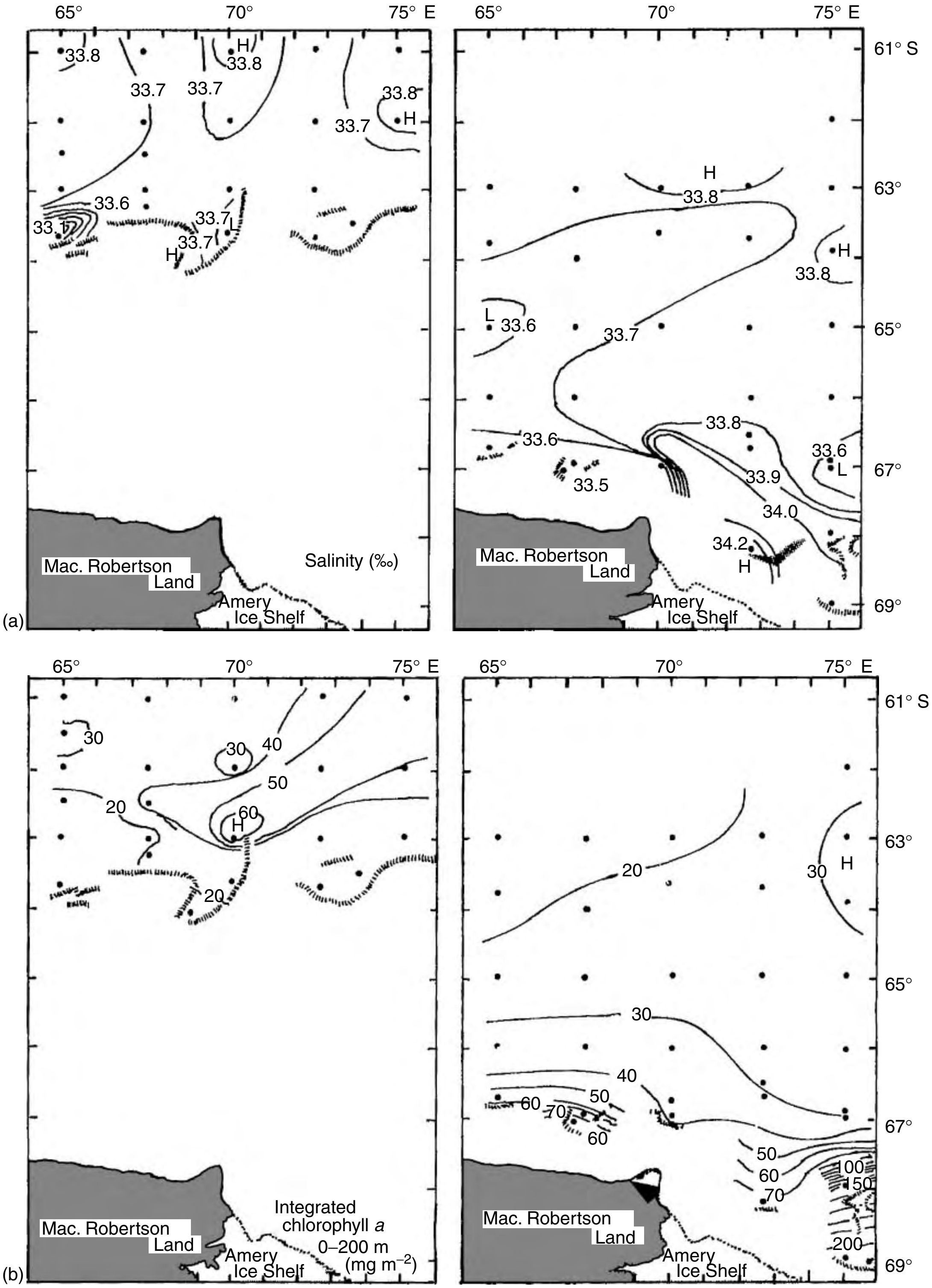


FIGURE 13.4 Surface distributions of (a) salinity, and (b) chlorophyll *a* off MacRobertson Land in mid-December 1983 (on the left) and January–February 1986 (on the right). The hatching represents the edge of the pack ice. (From Fukui, F., Otomo, K., Okabe, S., *Mem. Nat. Inst. Polar Res.*, 44, 43, 1986. With permission.)

(hence low density) water produced at the surface by the melting of the pack ice. Seasonal sea ice typically has a salinity of 5–10 in contrast to the 20–35 in the surface waters. Because storms are infrequent and thermal stratification rarely occurs, the water column the Southern Ocean usually has a deep mixed layer. The introduction of relatively fresh water from the melting ice greatly reduces surface density and causes vertical stability. A low-density layer is formed above the high-salinity water with the two layers separated by a discontinuity layer, through which mixing is negligible. The discontinuity layer is usually formed at between 10 and 50 m in depth thus ensuring that the surface phytoplankton would not be transported to greater depths. This in turn, allows the phytoplankton to grow in a well-illuminated environment. If the water were deeply mixed the average light intensity encountered by the phytoplankton cells would be low. In all of the investigations of phytoplankton blooms to date, a stable surface layer of low salinity water has been implicated and it would appear to be a major factor.

13.4.2 ICE-EDGE UPWELLING

A second potential mechanism is ice-edge upwelling that can occur as a result of complex interactions between atmosphere, ocean and ice (Roed and O'Brien 1983). However, while such ice-edge upwelling has been observed in the Arctic (Johannsen et al. 1983) it has not been identified so far in the Antarctic. In temperate and tropical systems the upwelling of nutrient rich water supports rapid phytoplankton growth in the euphotic zone. In the Arctic, such upwelling replenishes nutrients depleted by phytoplankton growth (Smith et al. 1987). In the Antarctic, however, nutrients are generally well above the concentrations needed for plant growth (El-Sayed 1970a; Gilbert et al. 1982) so that any nutrients brought to the surface by upwelling would not increase phytoplankton production. Thus it would appear that in the Antarctic upwelling is not a mechanism contributing to the formation of ice-edge phytoplankton blooms.

13.4.3 DECREASE IN TURBULENCE

A third possible mechanism contributing to bloom formation is a decrease in turbulence within the mixed layer caused by reduced wind stress due to the presence of ice. The decreased wind stress enhances primary production in nutrient-rich waters by decreasing turbulence within the mixed layer depth (Nelson et al. 1981), so that the phytoplankton cells are not mixed rapidly between euphotic and subphotic depths. Because the ice's effects on wind drag reaches tens of kilometres from the ice-edge (Overland et al. 1983), a bloom caused by reduced wind stress would be less extensive than one initiated by ice melt which may extend some 250 km (Smith and Nelson 1985a, 1986).

13.4.4 RELEASE OF ICE MICROALGAE

A further potential mechanism for initiating ice-edge phytoplankton blooms is the release of ice microalgae into the surface waters from the melting ice floes. As we have seen in Chapter 3 the algal biomass in sea ice can be extremely high (Whitaker 1977a; Ackley et al. 1979; Palmisano and Sullivan 1983a; Garrison et al. 1986). However the ice algal concentrations, in spite of their abundance, are of a magnitude that could not account for the chlorophyll *a* concentrations typical of ice-edge phytoplankton blooms. Furthermore, some of the ice algal species may sink very rapidly and thus have a short residence time in the euphotic zone. Johnson and Smith (1986) have examined the sinking rates of phytoplankton assemblages in the Weddell Sea marginal ice zone. Sinking rates, as determined by chlorophyll *a* levels, ranged from 0 to 2.73 m day^{-1} (mean = 0.89) and were similar to those reported from tropical (Bienfang 1985), temperate (Bienfang and Harrison 1984), and subpolar regions (Bienfang 1984). Despite apparently low sinking rates, passive sinking of phytoplankton has been shown to have a large impact on the composition of phytoplankton communities (Trimble and Harris 1984). Diatoms make up the overwhelming proportion of the biogenic material in sediments beneath the bloom in the Ross Sea as discussed above (Smith and Nelson 1985a,b), and sediment accumulation rates indicated that a large proportion (ca.80%) of the surface siliceous production was being delivered to the sediments (Nelson et al., unpublished, quoted in Johnson and Smith 1986). Material collected by sediment traps in the region of the Ross Sea bloom consisted primarily of single phytoplankton cells that apparently had not been ingested by herbivores (Dunbar, et al. 1985). Furthermore there is a strong taxonomic correlation between species found in the ice-edge bloom (Smith and Nelson 1985a) and those in the sediments (Truesdale and Kellog 1979). Johnson and Smith (1986) estimated that from 8% to 12% of the daily production was lost from the euphotic zone by passive sinking, a percentage similar to Biefang's (1984) estimate for a subarctic system.

A number of workers (e.g., Fukuchi et al. 1984; Sasaki and Watanabe 1984; Sasaki and Hoshiai 1986) have noted the increase that occurs in chlorophyll *a* concentration in the summer due to the release of ice algae from the melting ice at the bottom of the sea ice. As Sasaki and Hoshiai (1986) point out, there are three possible fates for the ice algae once they are released into the water column: (1) as discussed above, they may sink through the water column to be deposited on the bottom; (2) they may be consumed by animals living in the water column and their digested faeces sink to the bottom; and, (3) the released ice algae may actively grow within the water column and contribute to phytoplankton blooms. The relationships between the ice algal species and those of the water column phytoplankton community have been discussed in Chapter 3. The phytoplankton bloom in the Ross Sea (Smith and Nelson 1985a) was dominated by a single diatom species *N. curta* that is considered to be an ice algal species. The dense bloom in the Weddell Sea, off the Ronne Ice Shelf, reported by El-Sayed (1971b) was dominated at the surface by the diatom *Thalassiosira tumida*, a widespread dominant of Antarctic phytoplankton communities. In the Weddell Sea the phytoplankton blooms at the ice-edge (Smith and Nelson 1986; Nelson, et al. 1987) consisted of chain-forming species such as *Euchampia antarctica*, *Corethron criophilum*, *Rhizosolenia hebetata* and *T. tumida*, while beyond the ice-edge, the early spring bloom was dominated by the gelatinous colony formers *T. gravida* and the prymnesiophytye *Phaeocystis antarctica* (Fryxell et al. 1984; Fryxell and Kendrick 1988).

McMinn (1996) investigated the role of sea ice microalgae on the spring phytoplankton bloom in Ellis Fjord, eastern Antarctica. In the pack ice of the Southern Ocean the same microalgal species are usually found in both the ice and the water column, suggesting a closely coupled system (Garrison and Buck 1985b). However in fast ice environments the two communities are usually quite distinct (Bunt and Wood 1963; Krebs 1983; Palmisano and Sullivan 1983a). Dominant taxa in the interior ice community in Ellis Fjord included *Nitzschia cylindrus*, *Navicula glacei* and a dinoflagellate cyst. McMinn (1996) found that the spring increase in water column algal abundance appeared to be solely due to sea ice input with little subsequent net phytoplankton growth. McMinn's investigation, together with others from the fast ice environment (Bunt and Lee 1970; Plamisano and Sullivan 1985b) suggests that algal inoculation from the fast ice is not significant.

13.5 A MODEL OF ICE-EDGE BLOOM DYNAMICS

Figure 13.5 from Sullivan et al. (1988) schematically illustrates the two dimensional relationships among light, ice distribution and vertical stability. Phytoplankton growth under the ice is extremely low because of low in situ light levels and a deep mixed layer, whereas in the vertically stable area immediately seaward of the ice-edge, phytoplankton growth can approach the maximum possible for the prevailing temperatures ($\sim$0.8 doubling day^{-1}, Eppley 1972). With distance from the ice-edge the vertical stability is degraded by lateral flow and increased vertical mixing, and as a consequence phytoplankton growth can again become limited by light in the deep mixed layer.

Sullivan et al. (1988) point out that ice-edge "bloom" dynamics have two major components, each with different time scales and fundamentally different forcing functions. The first component is Lagranian and involves active growth and decay of the phytoplankton population at the ice-edge; it occurs over weeks and is controlled by factors that influence growth (light and vertical stability) and losses (grazing, sinking, vertical mixing, and advective processes.). The second is Eulerian in nature and involves the movement of the bloom over large geographic areas with the receding ice-edge; it occurs over months and is in large part controlled by ice dynamics, which in turn are largely a function of atmospheric effects. As a result, the temporal and spatial extent of the bloom is controlled by the relative rates of these processes.

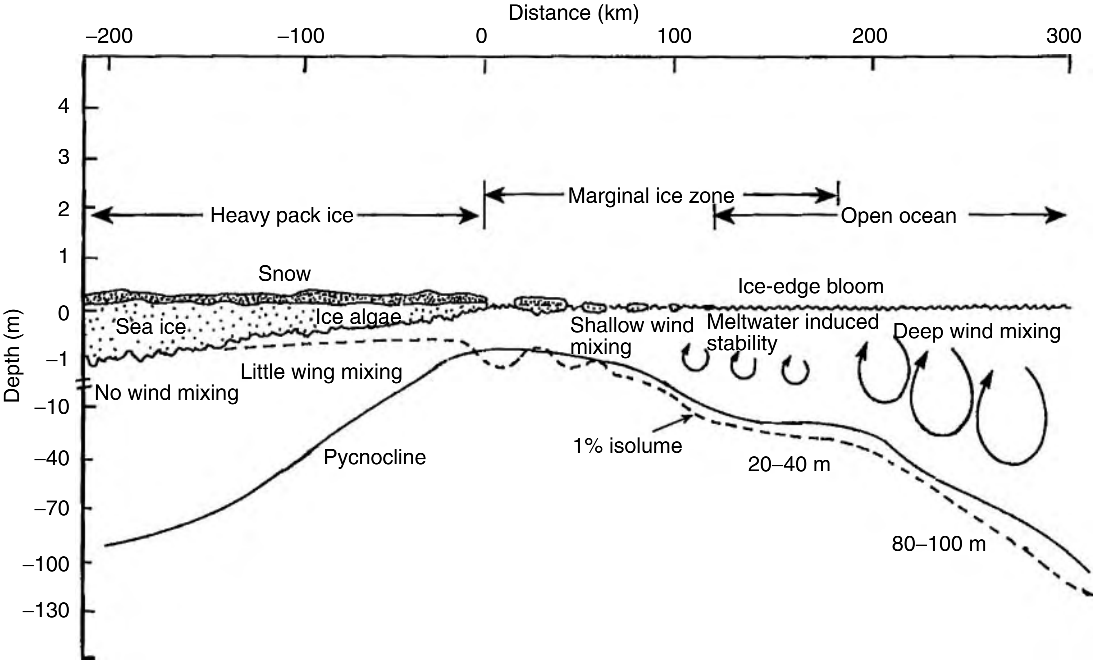


FIGURE 13.5 Schematic model of the conditions necessary for the development of an ice-edge phytoplankton bloom. (From Sullivan, C.W., McClain, C.R., Comiso, J.C., Smith, W.O., Jr., *J. Geophys. Res.*, 93, 12487, 1988. With permission.)

13.6 BACTERIOPLANKTON

Miller et al. (1984) investigated the vertical and horizontal distribution, activity and growth rates (μ) of bacteria during the November–December 1983 AMEREIZ cruise (Figure 13.6). Data on growth rates of the bacteria in the water column extend along a transect 120 nautical miles into the pack to 160 miles north of the ice-edge. There was a four-fold increase both in bacterial numbers and cell biomass over the transect. Bacterial cell numbers and biomass integrated throughout the water column to a depth of 150 m ranged from an average of 7×10^{12} cells m^{-2} (100 mg C m^{-2}) at the southernmost stations to an average of 33×10^{12} cells m^{-2} (400 mg C m^{-2}) to the north. The maximum bacterial growth rates (measured by 3-trimethylated thymidine incorporation) occurred in the upper 50 m of the water column in the region most recently uncovered by the receding ice (Figure 13.6). These were located in the low salinity surface layer. The growth rates steadily declined by two orders of magnitude to the south and by one magnitude to the north. Growth rates ranged from 0.02 doublings day^{-1} deep with the pack ice to 0.4 doublings day^{-1} just north of the ice-edge zone, declining to 0.03 doublings day^{-1} further north. These growth rates fit within the range calculated for other Southern Ocean regions (Fuhrman and Azam 1980; Hanson et al. 1983a, 1983b). Ice-edge bacterioplankton will be considered further in Chapter 14.

13.7 ICE-EDGE MICROHETEROTROPHS

It is only comparatively recently that the abundance and role of microheterotrophs has been studied in the ice-edge zone (Buck and Garrison 1983; Garrison et al. 1984; Heinbokel and Coats 1984, 1986; Garrison and VanScoy 1985; Garrison and Buck 1985a, 1989a, 1989b). Table 13.2 presents a summary of the occurrence and numerical abundance of the major planktonic forms encountered in the Weddell Sea ice-edge zone (Buck and Garrison 1983). Heterotrophic flagellates were the dominant component of the protozooplankton comprising 24–75% of the total protozoan biomass during AMERIEZ 83 and 62–67% of the biomass during AMERIEZ 86. Naked (nonloricate flagellates) were usually dominant among the heterotrophic flagellates, followed by dinoflagellates and choanoflagellates. Heterotrophic flagellates, principally *Gyrodinium* spp., *Amphidinium* spp., and *Gymnodinium* spp. are considerably larger than the naked or loricate flagellates. Although a variety of ciliates were present, nonsheathed oligothrichs (i.e., *Strombidium* spp.) dominated the ciliate biomass both during the 1983 (spring) and 1986 (autumn) AMERIEZ cruises. Tintinids were rare in the spring cruise but made up a significant fraction of the ciliate biomass during the autumn cruise.

During both AMERIEZ cruises protozooplankton biomass increased with increasing phytoplankton and bacterioplankton biomass and productivity and bacterioplankton biomass and production in transects across the ice-edge (Table 13.3). In the spring 1983 cruise the protozooplankton biomass in the area of the ice-edge to open water was four times that of the ice covered waters, while in the autumn 1986 cruise the open water biomass was three times that of the ice covered stations.

The abundance of microheterotrophs in the upper water column for stations under heavy ice cover (stations 5 and 6) and along a transect across the ice-edge zone (stations 15–21)

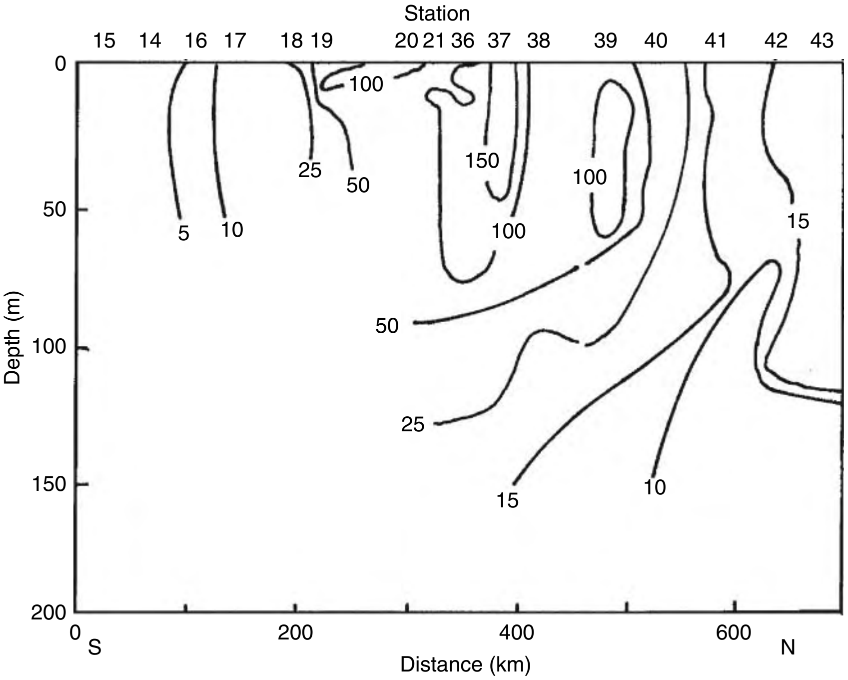


FIGURE 13.6 Bacterial cell production rates in units of 10^6 cell l^{-1} day^{-1} across an ice-edge zone in the Weddell Sea. (From Miller, M.A., Kempin, D.W., Manahan, D.T., Sullivan, C.W., *Ant. J. U. S.*, 19, 103, 1984. With permission.)

TABLE 13.2

A summary of the Occurrence and Numerical Abundance of the Major Protist Forms in the Ice-Edge Zone of the Weddell Sea

Taxon	Abundance (cells 1^{-1})	
	Mean	Range
Pyrmnesiophyceae		
(*Phaeocystis antarctica*)	1×10^{6}	3×10^{3}–4×10^{6}
(Motile cells)	2×10^{4}	1×10^{3}–9×10^{4}
Bacillariophyceae (diatoms)	5×10^{5}	1×10^{4}–1×10^{6}
Prasinophyceae	1×10^{4}	~0–3×10^{4}
Misc. flagellates	8×10^{4}	3×10^{3}–2×10^{5}
Cryptophyceae	5×10^{4}	1×10^{4}–1×10^{5}
Dinophyceae (dinoflagellates)	2×10^{4}	5×10^{3}–6×10^{4}
Archaeomonads	2×10^{4}	2×10^{3}–7×10^{4}
Chrysophyceae (*Distephanus speculum*)	3×10^{4}	~0–5×10^{3}
Choanoflagellata (choanoflagellates)	2×10^{4}	1×10^{3}–2×10^{6}
Siliceous cysts	9×10^{5}	—
Ciliata		
(Ciliates)	5×10^{3}	1×10^{3}–9×10^{3}
(Tintinnids)	3×10^{3}	3×10^{3}–3×10^{3}

A lower range ~0 means that the organisms were recognizable in a qualitative examination of the sample but were too rare to detect in quantitative counts; in such cases an abundance of 0 was used in calculating the group mean.

Source: From Buck, K.R., Garrison, D.L., *Deep-Sea Res.*, 30, 1261, 1983. With permission.

is shown in Figure 13.7 (Garrison et al. 1984, 1986). The abundance of microheterotroph biomass was concentrated in the upper 50 m; abundance dropped rapidly below approximately 50–60 m. Garrison et al. (1984) have tabulated data on the abundance and biomass of heterotrophs in the ice-edge zone in comparison with that in the sea ice (Table 13.4). While the concentrations of heterotrophic flagellates and choanoflagellates were greater in the sea ice than in the water, heterotrophic dinoflagellates and tintinids were not found in the sea ice and the abundance of ciliates was very much greater in the water.

13.8 ICE-EDGE ZOOPLANKTON AND NEKTON

There have been limited investigations of the ice-edge zooplankton. Brinton (1984) carried out zooplankton sampling along two transects across the ice-edge in the southern Scotia Sea in November–December 1983 using Bongo nets. Predominant organisms collected were pelagic tunicates, or salps (*Salpa thompsoni*) and euphausiid crustaceans. Amphipod crustaceans, the large gammarids *Cyphocaris* and *Parandaria*, and the smaller hyperiids *Vabilia* and *Cyllopus* commonly associated with salps, at varying abundances occurred throughout the upper water zone. During 1020 November the highest densities of salps were at the northernmost stations, 58–59°S, furthermost from the ice-edge within the maximum surface temperature gradient, 0.25–0.1°C. Torres et al. (1984) reported a mean salp biomass of 23.9 kg 100 m^{-2} for the upper 600 m. During sampling carried out from November 21 to December 2 the highest densities extended further south. Franz et al. (1987) have provided a preliminary report on an investigation of the ice-edge zooplankton carried out on the winter expedition of the *Polarstern* in early October and early December. The October crossing went from open water through the marginal ice zone into solid pack and then through a zone of ice floes into the coastal polyna. The total plankton biomass decreased with increasing percentage of ice cover and ice thickness but increased again slightly near the polyna (e.g., in the copepod *Onacea curvata*). In the northern part of the crossing larvae of the euphausiids *Euphausia frigida* and *E. superba* occurred in fair numbers up to 200 per 100 m^{-3}, but were absent in the south. Ostracods and polychaetes were more evenly distributed along the crossing. Fish larvae and appendicularians were virtually absent in early October. Chaetognaths and the copepods *Calanoides acutus* and *Rhincalanus gigas* (copepodids IV–V and adults) were prominent features of the open water sample in the north. When entering the marginal ice zone the abundance of chaetognaths dropped by an order of magnitude and the two copepod species were replaced by other copepods, *Metridia gerlachei* and juvenile *Calanus propinquus*. In the zone of heavy pack ice even those species

TABLE 13.3
Summary of the Mean Phytoplankton and Bacterial Production and Protozooplankton and Macrozooplankton during AMERIEZ 83 and AMERIEZ 86

	Values Integrated over Upper 100 m					
	Production (mg C m^{-2} day^{-1})		Biomass (mg C m^{-2})			
Cruise	PHYTO	BACT	PHYTO	BACT	PZOO	ZOO
AMERIEZ 83						
Ice covered	284.8	24.95	947	147.1	88.33	—
Ice-edge to open water	516.8	138	4372.3	384.1	426.77	—
AMERIEZ 86						
Ice covered	161.13	11.53	816.67	228.93	165.8	45.8
Open water	206.25	111.15	4989.5	394.95	551.85	213.6

BACT, bacterio-plankton; PHYTO, phytoplankton; PZOO, protozooplankton; ZOO, macrozooplankton.

Source: From Garrison, D.L., Buck, K.R., *Ant. J. U. S.*, 19, 136, 1985. With permission.

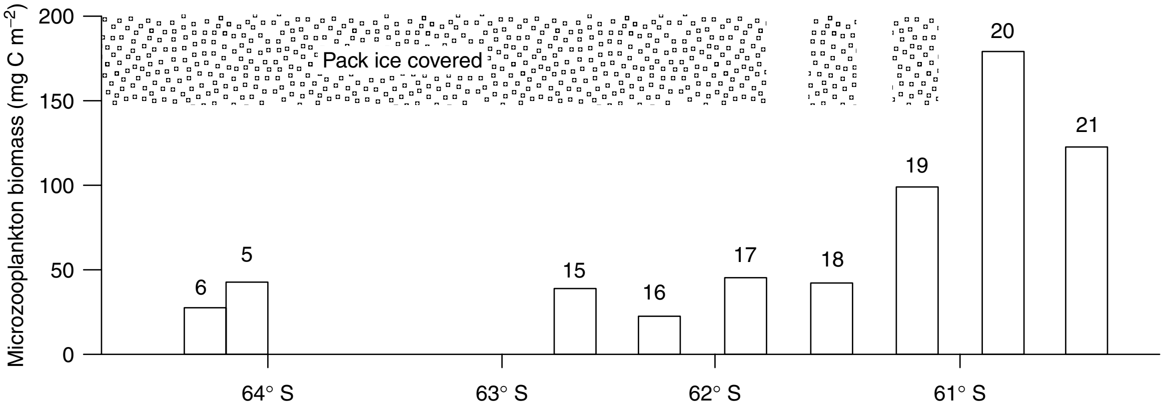


FIGURE 13.7 Microheterotroph biomass (in mg C m^{-2}) in the upper 50 m of the water column in the Weddell Sea in November 1983. Stations 5 and 6 were under heavy ice cover while stations 15–21 were along the transect across the ice-edge zone. (From Garrison, D.L., Buck, K.R., *Ant. J. U. S.*, 19, 136, 1985. With permission.)

TABLE 13.4
Average Concentrations of the Major Groups of Protists in Cells ml^{-1} in the Water Column in Relation to the Weddell Sea Ice-Edge

Taxa	Under-Ice Stations						Ice-Edge Stations			
	2	5	31	61	64	65	84	1	71	73
Choanoflagellata	246	21	15	39	215	151	818	155	80	1
Prymnesiophyceae	29	71	36	188	107	148	3107	2140	115	35
Bacillariophyceae	73	215	35	67	611	742	480	1245	1437	485

Source: From Garrison, D.L., Buck, K.R., Silver, M.W., *Ant. J. U. S.*, 19, 109, 1984. With permission.

were virtually absent. In all the copepods the ratio of adults to juveniles varied considerably. Also the numerous small copepod species *Oithona similis* and *Ctenocalanus citer*, as well as the eggs and nauplii of *Calanus propinquus*, decreased in density when entering the heavy pack ice.

In their investigation of the abundance and distribution of krill in the ice-edge zone of the Weddell Sea, Daly and Macaulay (1988) found that in the austral spring of 1983 the vertical distribution of krill under the pack ice was similar to that of the open water. Average krill biomass under the ice ranged from 1 to 68 g m^{-2}, and in the open water 10–100 g m^{-2}. However, the pack ice directly influenced the distribution and abundance of young krill. Juvenile *E. superba* were much more abundant under the ice than in the open water north of the ice-edge. Numerous observations were made of juvenile krill feeding on the sea ice microalgae on the undersides of the ice floes. In contrast to other trophic levels, krill did not increase in biomass at the ice-edge. Krill, however, may have been grazing phytoplankton that developed to the north of the ice-edge in an earlier stage of the ice retreat that was rapid at the time of sampling. The krill distribution may also have been part of a mesoscale patchiness, as krill are strong swimmers and swarms can move considerable distance when foraging for food (see Chepter 5 Section 4).

Torres et al. (1984) investigated the distribution of fish and salps in relation to the ice-edge in the southern Scotia Sea. The dominant fish in the upper 500 m were *Electrona antarctica* and *Gymnoscopelus braueri* (Myctophidae) and *Notolepis coatsi* (Paralepidae). Dominant fish in the lower 500 m of the water column were *Bathylagus antarcticus* (Bathylagidae) and *Cyclothone microdon* (Gonostomatidae). Mean fish biomass for the upper 1000 m of the study area was 327 g per 100 m^{-2}, a figure somewhat lower than that found by Frost and McCrone (1979) for the subarctic-transitional waters off Washington (450 g 100 m^{-2}) for myctophids only, but considerably higher than that found in tropical–subtropical systems studied by Maynard et al. (1973; 214 g 100 m^{-2}, Gulf of Mexico). Piscovorous fish were extremely rare in the study area.

There was a clear trend of increasing biomass moving from south to north away from the marginal ice zone, followed by a sharp drop in biomass north of 58°S. The biomass peak corresponded to the pronounced phytoplankton bloom found in the vicinity of 59°S. There was a marked increase with time in both fish and salp biomass in the southern part of the study area. The increase corresponded to an intensifying phytoplankton bloom at the retreating ice-edge. This suggested a gradual southward displacement of mobile micronektonic species in response to the increased production of ice-edge blooms and its associated increases in prey species. In the case of salps it suggested an increased population size through reproduction.

As a consequence of the research carried out through AMERIEZ new information on the impact of pack ice cover on the deeper-living (100–1000 m) mesopelagic micronekton community has been provided (Ainley et al. 1985). In ice-free waters throughout the world's oceans, a substantial fraction of the mesopelagic community migrates from 200 to 500 m daytime depths to, or near, the surface at dusk, returning to depth at dawn. Such organisms orient to a constant light level or ioslume, which move up and down in the water column with the setting and rising sun (Kampa and Boden 1954). In the Antarctic, where the diel light regimes differ markedly between winter and summer it would be expected that such vertical migration patterns would have radically different patterns through the austral seasons. Shading of the water column by pack ice would further complicate such patterns during periods of increasing day length through the contrasting light levels of open water and consolidated pack.

Salps and fish (*Electrona antarctica*, *Gymnoscopelus braueri* and *Notolepis coatsi*) are the dominant nektonic species in the open water zone with *Bathylagus antarcticus* and *Cyclothone microdon*. There is a clear trend of increasing biomass and diversity of the ichthyofauna (Torres et al. 1984), as well as a change in the seabird fauna moving northwards from the pack ice (Fraser and Ainley 1986) (see Section 13.8). At 58°S (the Weddell Scotia confluence) there was a sharp drop in fish biomass and seabird composition. The dominant diel distribution pattern of the fish was a vertical migration pattern (Torres et al. 1984).

Amphipods and crustacea dominated the crustacean component in open waters south of 59°S. Representatives of classical mid-water crustacean faunas (for example Pasiphaeidae, Opolaridae, Mysidacea, Panaeidae, Ostracoda) common in boreal, temperate and tropical waters, were not taken north of 59°S. No decapods, mysids or ostracods were captured in trawls reaching less than 310 m anywhere in the open-water transects, by day or night.

The myctophids, *E. antarctica* and *G. brauerii*, and krill were the main prey of seabirds in open waters, while the amphipods *Vibalia* and *Cyllopus* were most prevalent in seabird diets north of 58°S. Most of the prey were captured when they moved upwards into the surface waters at night as part of their diel migration cycle (Ainley and Boekelheide 1983; Ainley et al. 1983). Dietary changes occurred in the pack ice region. The above prey were captured with less regularity, and deep into the pack ice crustacea of the genera *Pasiphaea* and *Eurythenes* replaced myctophids as dominant items in the diet. The dominance of *Pasiphaea longispina* in the diets of the few seabirds that frequent consolidated pack, principally Snow Petrels, was unexpected as it had not been captured in trawls shallower than 310 m. The fact that two other deep-water species, the large amphipod *Eurythenes gyrllus* and the ostracod *Gygantocypris mulleri*, were also eaten by the pack ice seabirds indicated that an upward seasonal displacement of these mesopelagic crustacea had occurred. Thus these species that were unavailable to the birds became available at the surface in the pack ice. In the open water primary production extended to a depth of 110 m, but southward in the more concentrated ice phytoplankton chlorophyll became increasingly constricted to the surface until it was eventually confined to the ice itself, with extremely low concentrations in the water beneath. The reduction in light (the cue associated with vertical movement) encouraged mesopelagic species to reside at the surface.

13.9 ICE-EDGE VERTEBRATES

Beginning with the whalers, Antarctic voyagers have noted an increase in the abundance of vertebrates at the pack ice-edge (Marr 1962; Ainley and Jacobs 1981; Stirling and Cleator 1981). According to the authors of the AMERIEZ Research Plan (AMERIEZ 1981) the basis for this pattern could be due to (1) increased productivity due to upwelling at the ice-edge (Buckley et al. 1979), (2) enhanced productivity resulting from processes in the water column (Ainley and Jacobs 1981), (3) the release of ice algae and bacteria to seed the water column, (4) the rich community of prey organisms closely associated with or within the ice, (5) increased productivity and food web interactions as a retreating ice-edge exposes enriched water to sunlight (Hardy 1967), (6) an artifact forced on shipboard observers not capable of proceeding into the ice (Marr 1962), or (7) to an accumulation of organisms when they reach the sharp boundary of their preferred habitat (Ainley et al. 1988).

The vertebrate ice-edge community has rather low species diversity and includes six major species of birds, including Adélie Penguin (*Pygoscelis adeliae*) and Snow Petrel (*Pagadroma nivea*), and several species of mammals, including Crabeater Seal (*Lobodon carcinophagus*), Leopard Seal (*Hydrunga leptonyx*), Ross Seal (*Ommatophoca rossi*), and the Minke Whale (*Balaenoptera acutorostrata*). The open water community is much more diverse, has strong ties with the sub-Antarctic regions, and includes several species of birds, including Macaroni Penguin (*Eudyptes chrysocome*) and Cape Pigeon (*Daption capense*), Southern Fur Seal (*Arctocephalus gazelli*), Southern Elephant Seal (*Mirounga leonina bonina*), and the great whales.

13.9.1 SEABIRDS

Fraser and Ainley (1986) have reviewed the relationships of seabirds to the pack ice-edge. They point out that it is only comparatively recently that it had been recognized that most species of seabirds are constrained by specific oceanic characteristics, including temperature and salinity, water clarity, depth to bottom, depth of the mixed layer, and the presence or absence of ice, as well as feeding and flight characteristics (e.g., Brown et al. 1975; Pocklington 1979; Brown 1980; Zink 1981; Ainley and Boekelheide 1983; Kinder et al. 1983; Ainley et al. 1984). Recent studies (e.g., Zink 1981; Ainley et al. 1984) have shown that the ice-edge is a region of overlap between two distinct seabird communities, one associated with the pack ice and the other with waters generally free of ice but still under its influence (cold temperatures and icebergs) (Fraser and Ainley 1986). These two communities are each composed of four to five dominant species and up to five minor ones. The pack ice community comprises Emperor (*Aptenodytes fosteri*) and Adélie Penguins, and Snow and Antarctic (*Thalasoica antarctica*) Petrels. Penguins generally dominate in terms of biomass although Snow and Antarctic Petrels are more abundant. North of the ice-edge the Southern Fulmar (*Fulmaris glacialoides*), Cape Pigeon, Wilson's Storm Petrel (*Oceanites oceanicus*), and the Mottled Petrel (*Pterodroma inexpectata*) (Ainley et al. 1984) are the primary components. Southern Fulmars and Cape Pigeons dominate the community, both in terms of biomass and abundance. Except for the Antarctic Petrel, most of the species in the community north of the ice-edge tend to be associated with ice-free water (less than 20% ice coverage). This is especially evident among the major components, the Light Mantled Sooty (*Phoebetria palpebrata*) and Black-browed (*Diomedia melanophris*) Albatrosses. Most of the open water species have specialized foraging behaviours relying on dynamic soaring—taking advantage of air movement above the waves for support—which is difficult over the pack ice because the ice dampens sea swells (Ainley et al. 1984).

The presence of two distinct seabird associations in the pack ice and ice-free habitats is consistent with the hypotheses that seabirds are strongly tied by morphological and behavioural adaptations to specific water types or marine habitats. Fraser and Ainley (1986) discuss the factors that specifically determine the distribution patterns. One common explanation is that the increased abundance of seabirds at the ice-edge (Figure 13.8) is due to greater access to the ocean and its resources (Divorky 1977; 1980). This idea was developed from studies in the Arctic where the major seabird concentrations were associated with recurring polynas (Brown and Nettleship 1981). However, in the Antarctic in contrast to the Arctic where the pack ice has few internal leads and little open water (Zwally et al. 1983a), the pack ice has numerous leads and polynas (Ainley and Jacobs 1981; Zwally et al. 1983a). During the 1983 AMERIEZ cruise vast polynas were found in the Weddell Sea near 63°S yet the seabird densities were low. Fraser and Ainley (1986) pose the question: "If open water is so important to the seabirds and is available within the ice, why are they still concentrated at the ice-edge?"

Therefore the alternative hypothesis, the idea that ice-edge zones are biologically more productive, thus offering seabirds superior prey availability would appear to be more soundly based. Figure 13.8, based on data from the Weddell Sea, illustrates how low seabird numbers increased at each of four ice-edge stations (stations 3, 19, 12, and 20). Seabird numbers closely paralleled chlorophyll concentrations throughout much of the study area, including the ice-edge stations 10 and 12. At stations 3 and 12 where chlorophyll values were low, features of the water column suggested frontal discontinuities. There is a time lag between the ice disintegration with the release of ice algae to seed the water column and the surge in the productivity of the water previously covered by ice (Ackley et al. 1979; Alexander 1980). This suggests that seabirds should actually concentrate north of the retreating ice-edge. Figure 13.8c illustrates

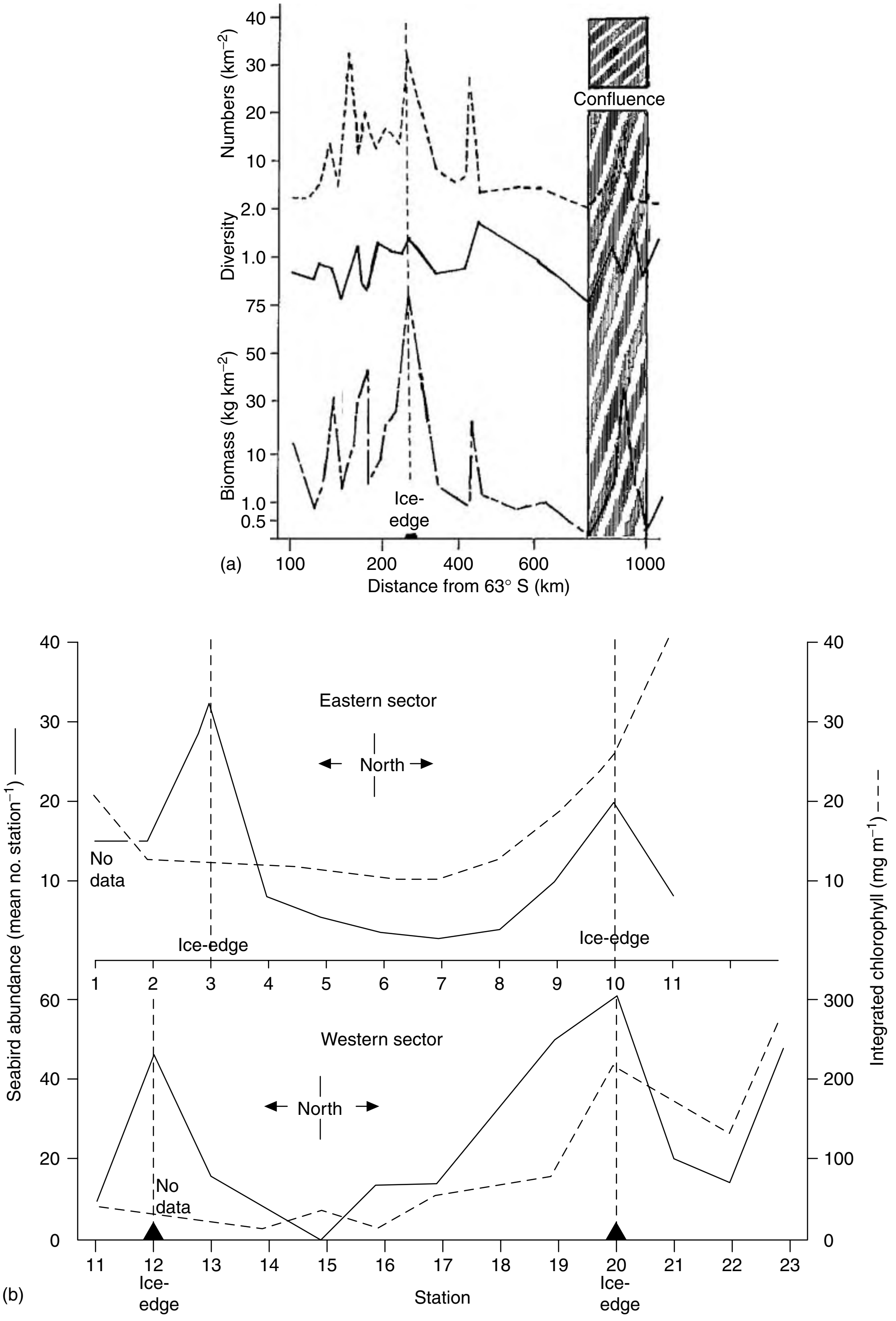


FIGURE 13.8. (a) A transect in the Weddell Sea illustrating changes in the density, species diversity (Shannon-Weaver diversity index), and biomass of the seabirds at the ice-edge and other locations. Note changes in scale to illustrate the patterns at the confluence (shaded area) of the Scotia and Weddell Seas (900 km north of 63°S). (From Fraser, W.R., Ainley, D.G. *Bioscience*, 36, 258, 1986. With permission.) (b) Seabird abundance and chlorophyll concentrations in the pack ice in the western Weddell Sea during the AMERIEZ cruise in November–December 1983 relative to the ice-edge (shown by vertical dashed line). Stations 6 and 15 represent the southernmost stations; north is plotted relative to these stations. No data was available for station 1 in the eastern sector and stations 11, 12, and 13 in the western sector. (From Fraser, W.R., Ainley, D.G., *Bioscience*, 36, 258, 1986. With permission.) (c) Transects from the Weddell and Scotia Seas illustrating the positions of peaks in biomass, species diversity and density of seabirds early in the season (thin lines) and two weeks later (thick lines). All distances are measured from 63°S. (From Fraser, W.R., Ainley, D.G., *Bioscience*, 36, 258, 1986. With permission.)

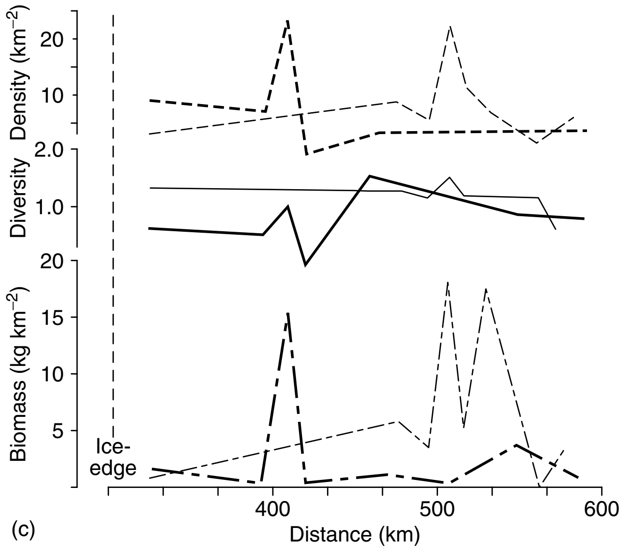


Figure 13.8 *(continued)*

how seabirds respond to the retreating ice-edge in the Weddell Sea. Peaks in their density, diversity and biomass were first recorded about 500 km north of the ice-edge at 63°S, but two weeks later they occurred 100 km south, a shift in tandem with the latitudinal displacement of the ice-edge, suggesting that seabirds were following the ice retreat. Pack ice surveys of seabird distributions (e.g., Zink 1981; Ainley et al. 1984, and others) have shown that seabird numbers peaked over intrusions of extremely thick, densely concentrated multiyear ice which were laced with floes showing both extraordinarily abundant algal and bacterial communities and advanced stages of decomposition. They were also the only sites within the pack ice where euphausiids, decapod crustaceans and other prey regularly occurred. Fraser and Ainley (1986) suggest that the birds were responding to the physical features of the ice, not to prey availability.

13.9.2 MAMMALS

A number of authors (e.g., Marr 1962; Laws 1977b; Mizroch et al. 1986) have noted that some species of baleen whales concentrate in the marginal ice-edge zone and follow the southward retreat of the ice, thus gaining access to their principal food the krill. Seals are also attracted to the ice-edge (Ribic et al. 1991).

Erickson (1984) has reported on studies of mammal distribution patterns in the pack ice during the 1983 AMERIEZ cruise. The overall composition of the seals observed was 77% Crabeater, 18% Leopard, 4% Weddell, and 0.4% Ross. The 18% Leopard Seals observed was several time greater than the normal abundance of this species in most censuses (Erickson et al. 1971; Condy 1976; Gilbert and Erickson 1977). The apparent explanation was that the AMERIEZ census coincided with the whelping period of the Leopard Seal when large numbers of females were hauled out on the ice tending their young. Leopard Seals were also distributed deeper into the pack ice than has been observed in other censuses taken later in the season (Gilbert and Erickson 1977). Crabeater Seal densities ranged from four seals per nautical mile at the ice-edge (60.5°S) to less than one seal per nautical mile at 100 nautical miles into the pack. The general pattern that emerges is one of increasing numbers of seals from deep within the pack ice to the ice-edge.

Although only four Minke Whales were seen by Erickson (1984), concentrations of Minke Whales have frequently been observed at the ice-edge. In the McMurdo Sound region in late January, I have observed groups of up to eight individuals at the ice-edge.

13.10 THE IMPORTANCE OF THE ICE-EDGE IN THE ECOLOGY OF THE SOUTHERN OCEAN

It is clear that in the past the importance of ice-edge blooms in the overall primary productivity of the Southern Ocean has been underestimated. Smith and Nelson (1986) have attempted to estimate the role of ice-edge blooms in the overall phytoplankton production in the Southern Ocean based on information from the Weddell Sea concerning the blooms spatial extent, its measured productivity, and its duration based on rates of ice retreat. Productivity was greatest within the bloom averaging 571 mg C m^{-2} day^{-1}. If the region's background production (i.e., that not influenced by the ice) is taken to be 134 mg C m^{-2} day^{-1} (Holm-Hansen et al. 1977), then the ice-edge bloom would

TABLE 13.5
Predicted Monthly Ice-Edge Production in the Southern Ocean, the Weddell Sea and the Ross Sea

	Southern Ocean		Weddell Sea		Ross Sea	
	Ice Cover[a] ($\times 10^6$ km^{-2})	Production ($\times 10^{12}$ g C day^{-1})	Ice Cover ($\times 10^6$ km^{-2})	Production ($\times 10^{12}$ g C day^{-1})	Ice Cover ($\times 10^6$ km^{-2})	Production ($\times 10^{12}$ g C day^{-1})
January	6.54	103.1	1.82	27.4	1.96	37.6
February	4.17	56.3	1.26	9.0	0.86	29.6
March	5.50		1.61		1.71	
April	8.00		2.32		2.90	
May	12.36		3.72		3.57	
June	15.81		5.47		3.95	
July	17.54		6.39		4.16	
August	19.82		6.60		4.41	
September	20.53		7.09		4.30	3.2
October	20.00	12.2	6.74	5.8	4.41	
November	17.72	54.2	6.21	9.1	4.20	6.1
December	10.88	157.3	3.37	50.2	3.22	29.2
Total		383.1		101.5		105.7

Area of ice cover estimated from Zwally et al. (1983). Aerial ice-edge production for the Weddell Sea calculated from W. O. Smith and Nelson (1985a) and for the Ross Sea from Wilson et al. (1986); Southern Ocean production is calculated using the average of these two values.

[a] Represents period ending on 15th of each month.

Source: From Smith, W.O., Jr., Nelson, D.M., *Science*, 227, 153, 1985. With permission.

supply approximately 3.4 times the daily production occurring before and after the bloom. The bloom follows the ice in the Weddell Sea, (60°S, 24°W) which retreats approximately 130 km per month from September through December (Zwally et al. 1983a). Since the blooms spatial extent was estimated to be 250 km, the bloom would last 1.9 months or 58 days at one point in this area. By multiplying the bloom's duration by the mean productivity, the ice-edge productivity was estimated to be 32.9 g C m^{-2}. Annual production in the Southern Ocean has been calculated to be 16 g C m^{-2} (Holm-Hansen et al. 1977); thus the ice-edge bloom may produce an amount up to two times the production over the rest of the growing season. This figure is similar to that calculated by Jennings et al. (1984) (556 mg C m^{-2} day^{-1}), which was based on apparent seasonal rates of nutrient depletion. Jennings et al. (1984) concluded that previous researchers had underestimated production by 25–67% because ice-edge production was not included.

Smith and Nelson (1986) made a similar calculation based on data from the Ross Sea study discussed above (Smith and Nelson 1985a, 1985b). In this case the mean productivity was 962 mg C m^{-2} day^{-1} (Wilson et al. 1986), more than seven times the productivity of the open water of the Southern Ocean. From data in Zwally et al. (1983a) the average rate of ice retreat at 76°S, 166°E is approximately 160 km per month during November and December when the ice-edge retreats most of its distance. Therefore the bloom at one point would last approximately 1.6 months or 48 days. From the available data Smith and Nelson calculated that the bloom would produce 45.6 g C m^{-2}, or nearly threefold more than the nonbloom production.

They further attempted to assess the impact of the ice-edge blooms on the total primary production of the Southern Ocean. Since the ice-edge blooms begin in regions with substantial ice cover, they used the progression of 15% ice cover as a convenient measure of the area uncovered by the ice retreat. Table 13.5 lists the mean monthly variations in area covered in the entire Southern Ocean, the Weddell Sea and the Ross Sea. It was calculated that the annual production associated with ice-edge blooms in the Southern Ocean is approximately 380×10^{12} g C. Of that the Weddell and Ross Seas produce approximately equal amounts (each producing approximately 25% of the Southern Ocean total). This can be compared with El-Sayed's 1978 estimate of 619×10^{12} g C for the Southern Ocean as a whole. This value is based on a productive area of 38.1×10^6 km^{-2}, whereas Smith and Nelson (1986) assumed that the ice retreats over 38.1×10^6 km^{-2}. Therefore, their calculations suggest that by including the ice-edge production from this smaller area, the estimate of annual production from the Southern Ocean is 990×10^{12} g C, an increase of more than 60%.

Smith and Nelson point out that the above calculations involve numerous assumptions, and therefore, some uncertainty. They note that we know little of the productivity of a reducing bloom, and that we have no information on the extent to which productivity within a bloom changes seasonally, or whether the spatial extent of the bloom varies.

Furthermore the contribution of the ice algae was not included in the calculations. Clearly a great deal more research is needed. Nevertheless, it is apparent that the ice-edge system potentially plays a major role in the ecological and biogeochemical cycles of the Southern Ocean. Because production at the ice-edge is potentially a large source of energy for herbivores, and is restricted both in space and time, grazers may have developed life-history strategies for exploiting the resources efficiently. Secondary consumers likewise are likely to have their migrations and reproductive cycles keyed into the availability of prey as a consequence of grazer activity.

14 Decomposition and the Roles of Bacteria and Protozoa

CONTENTS

14.1 INTRODUCTION

The most important generalization to emerge from the last two decades of intensive research on aquatic ecosystem energy flux is the conclusion that a large proportion of the energy moves through the detritus food web rather than through the more conspicuous grazer food web (Pomeroy 1974). The organisms involved in this detritus food web are comprised of bacteria, heterotrophic microflagellates (HMF) and heterotrophic ciliates. There has been an increasing appreciation of their role not only in the breakdown of organic matter and the regeneration of nutrients, but also as a potential food resource for larger consumer organisms. As a result of this work, it has been established that the standing stocks of planktonic microorganisms are far greater than originally inferred from early investigations, and that they may be comparable to the combined biomass of all other heterotrophs (Sorokin 1981).

In this chapter we shall consider the quantities and sources of organic matter (both dissolved and particulate) in both the water column and the sediments of the Southern Ocean. Information on the fate of this organic matter, including its remineralization to regenerate nutrients, is summarized. An account is given of the distribution, abundance, growth and production of both bacteria and heterotrophic protozoa, and recent information on their roles in what is now referred to as the microbial loop in the pelagic food web is critically examined. Bacteria and protozoa in ice edge systems and in the sea ice have been considered in Chapter 13 and Chapter 3, respectively.

14.2 QUANTITIES AND SOURCES OF ORGANIC MATTER

14.2.1 Introduction

One of the generalizations to emerge from research on oceanic ecosystems is that there is a large pool of nonliving organic matter (detritus) present at all depths of the water column, and that its organic carbon content may exceed that of the living microbial (primarily phytoplankton, bacteria and microprotozoa) and zooplankton components combined. Although it is convenient to classify the organic matter in the ocean into two categories—particulate organic matter (POM) and dissolved organic matter (DOM)—in reality it constitutes a continuum from organic matter in true solution, through macromolecules, colloids to small particles, and finally to large particles (Darnell 1967b; Figure 14.1). The differentiation between particulate and DOM is purely operational, depending on the size of the filter used. In the world's oceans, the dissolved organic carbon (DOC) is considered to average about $700\ \mu g\ l^{-1}$ (Williams 1975).

Darnell (1967a) defines organic detritus broadly as "all types of biogenic material in various stages of decomposition which represent potential energy sources for consumer species." Thus defined, organic detritus includes all dead organisms as well as secretions, regurgitations and egestions of living organisms, along with all the subsequent products of decomposition which further represent potential sources of energy, such as proteins or amino acids. It is sometimes convenient to distinguish coarse POM (that material retained by filters with apertures of 1 μm in diameter) and fine or subparticulate (sometimes called nanodetritus) POM (material that passes through such filters).

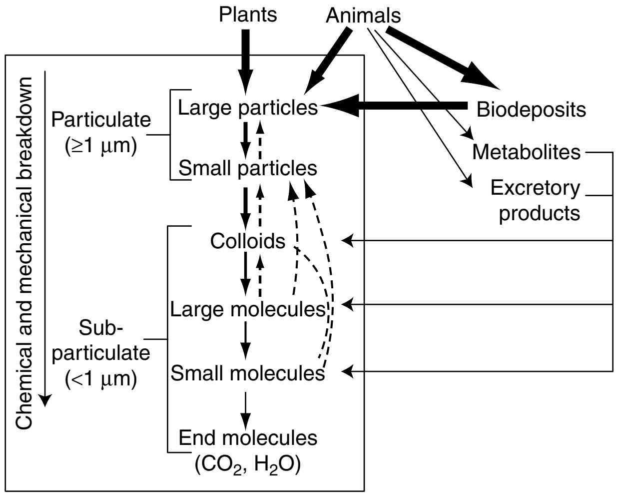


FIGURE 14.1 Schematic view of detritus formation and decomposition. (Modified from Darnell, R.M., *Estuaries*, Lauff, G.H., Ed., American Association for the Advancement of Science, Washington, DC, 376, 1976. With permission.)

14.2.2 Particulate Organic Matter (POM)

There have been a limited number of studies of POM in the waters of the Southern Ocean. The bulk of such studies have analyzed the filtrate from standard water samples for particulate organic carbon (POC). Such samples have included both living and dead plants and animals. Tanuoe et al. (1986) determined POC concentrations in water samples from the surface to deep water along three transects in the Pacific Sector of the Southern Ocean between 50°S and 65°S, and one in the Indian Ocean from 45°S to 62°S. In the Pacific sector, average POC concentrations ranged from 55.6 to $82.0\ \mu g\ C\ l^{-1}$ in the surface water layer (0–100 m), with the concentration decreasing with depth to 24.5–47.5 and $19.2–40.4\ \mu g\ C\ l^{-1}$ in the intermediate (125–300 m) and deep (300–1,500 m) water layers, respectively. These values are lower than those reported in most productive oceanic areas, but higher than those reported from other high latitude seas, and are comparable to those reported from the middle latitudes of the Pacific and Atlantic Oceans.

POM within the water column comes in a multiplicity of sizes and from a great variety of sources (Table 14.1). Dead phytoplankton cells, fragments from attached macroalgae, dead bacteria, dead protozoa, dead micro- and macrozooplankton, crustacea exuvia, and fecal pellets, especially those from copepods, euphausiids, and salps. Microscopic examination of organic particles in the open ocean has

TABLE 14.1
Principal Sources of Dissolved Organic Matter (DOM) and Particulate Organic Matter (POM)

Source of DOM	Source of POM
Phytoplankton exudation	Phytoplankton
Sea ice microalgal exudation	Bacteria
Benthic microalgal exudation	Protozoa
Benthic macroalgal exudation	Zooplankton
Autolysis of photoautotrophs	Crustacean exuvia
Release of DOM by microflagellates and ciliates	Thalacian houses
Excretion by zooplankton	Faecal pellets (especially those of copepods, euphausiids and salps)
Sloppy feeding by zooplankton	Macroalgal detritus organic precipitates from DOM

revealed two main types: amorphous particles typically greater than 100 μm maximum dimensions that clearly show remnants of previous cellular structure, and smaller amorphous particles which are clearly organic precipitates (Bowen 1984; Goldman 1984b; Biddanda 1985). There are a variety of mechanisms that bring about the conversion of DOM to particulate form, all of them involving the collection of surface-active material at a gas–liquid interface and compression of the interface. The surface of bubbles and the surface of the seas are sites of aggregation of surface-active molecules. Wave action is an important agent in the conversion process. In addition, inorganic particles frequently act as a focus for the condensation of DOM to POM.

In addition to the aforementioned smaller aggregates, larger particles—variously referred to as marine snow, fecal matter, agglomerates, conglomerates, macroflocs or large amorphous aggregates—are frequently encountered. Such large marine amorphous aggregates (generally referred to as marine snow) have been reported as a ubiquitous component of pelagic marine waters (Fowler and Knauer 1986; Herndl and Peduzzi 1988), and I have found them to be abundant in water samples from McMurdo Sound. Such marine snow aggregations are microhabitats for a rich detrital community of living phytoplankton (Beers et al. 1986), cyanobacteria, bacteria and protozoa (Caron et al. 1982; Goldman 1984b; Silver et al. 1984). Compared to the mean abundance of these groups of organisms in an equivalent volume of water, macroaggregates are enriched by factors ranging from 5 to 1,500 (Préslin and Aldridge 1983; Beers et al. 1986). Their high population density of heterotrophic bacteria and protozoa suggest that these macroaggregates may be major sites of remineralization of organic matter (Silver and Alldredge 1981).

Bacteria often form large quantities of extracellular POM which often brings about the adhesion of bacteria into clumps (Massalaski and Leppard 1979; Paerl 1974). Similar clumping can occur in some species of phytoplankton. Blooms of *Phaeocystis antarctica* in the Southern Ocean add large quantities of extracellular organic slime to the water column. As the *Phaeocystis* bloom decays, particulate matter in the water column adheres to the slime aggregates. Zooplankton contributions to the macroaggregates include copepod, euphausiid and salp fecal pellets and the exuvia of the crustaceans. To date the role of detritial aggregates in the pelagic waters of the Southern Ocean has received little attention. This should be a fruitful area for future research.

POM in the water column, in addition to organic carbon, contains the skeletal debris of protozoa, especially foraminiferans, diatoms, coccolithophorids (calcified skeletons), and invertebrates (especially crustacean exoskeletons which are mostly chitin). In most of the world's oceans, in addition to organic particles, there are lithogenic particles (mostly clay and rock detritus) which are transported from the land by rivers, coastal erosion, and wind. Due to the lack of river input to the Southern Ocean, lithogenic particles are much lower than in other oceans.

14.2.3 FECAL PELLETS

Fecal pellets may play an important role in the vertical transport of organic matter (Tanoue and Handa 1980) from the surface to the bottom sediments (Turner 1977; Honjo and Roman 1978). The principal producers of large fecal pellets in the Southern Ocean are the copepods, euphausiids and salps. It had been assumed that the bulk of the organic carbon and opal vertical flux with the Antarctic euphotic zone and to the deep ocean was contributed by the fecal pellets of these organisms (von Bodungen et al. 1988; Fischer et al. 1988). However, a significant proportion of the fecal pellets in the Southern Ocean have been found to be composed of small pellets (30–150 μm) (Sasaki and Hoshiai 1986; Nöthig and von Bodungen 1989). There has been much speculation as to the specific sources of these small fecal pellets, although several small metazoans (Sasaki and Hoshiai 1986) and protists (Nöthig and von Bodungen 1989) have been suggested as potential producers. Radiolarians and hydromedusae have also been reported as potential producers of small fecal pellets in temperate regions (Gowing and Silver 1985), and both of these groups are abundant in the waters of the Southern Ocean. Recent studies in the southeastern Weddell Sea indicate that dinoflagellates are capable of ingesting large particles (Nöthig and von Bodungen 1989) and producing consolidated fecal pellets. In the Scotia and Weddell Seas, Gonzales (1992a, 1992b) identified two groups of minipellet producers: phaerodarin radiolarians and unarmoured dinoflagellates. The vertical (from surface to 100 m) distribution pattern of the minipellets (5–100 μm) showed that the maximum concentration was located between the surface and 50 m. Diatom frustules were abundant in the minipellets.

Buck et al. (1990), in studies in the Weddell Sea ice edge zone during autumn 1986, found that a phagotrophic athecate dinoflagellate was common in the sea ice and the underlying water column. The single large vacuole of this dinoflagellate contained a variety of protistan prey, but the predominant item was the pennate diatom *Nitzschia cylindricus*. Membrane bound fecal pellets were produced from the vacuoles. Fifteen percent of the fecal pellet was identifiable protoplasm. Dinoflagellate concentrations in the sea ice brine ranged from 1.2×10^2 to $1.0\times10^5\ 1^{-1}$. Fecal pellet concentrations within the sea ice ranged from 3.6×10^2 to $1.8\times10^5\ 1^{-1}$, while those in the water column ranged from 6.4×10^0 to $8.9\times10^1\ 1^{-1}$. Release of the fecal pellets into the underlying water column from the sea ice upon melting may account for a significant proportion of the POC in the water column at the ice edge.

Studies of organic particle flux beneath coastal sea ice at Lutzow-Holm Bay (Fukuchi and Sasaki 1981; Sasaki and Hoshiai 1986) have identified copepod fecal pellets as a major component of the flux. Because of their large and often concentrated populations, Southern Ocean euphausiids, particularly *Euphausia superba*, are major producers of fecal pellets. In contrast to the compact fecal pellets of the copepods, pellets of *E. superba* are string-shaped, up to several 100 μm long, and about 150 μm wide

(Wefer et al. 1988). Tanoue et al. (1982) and Tanoue and Hara (1986) have examined the chemical composition and identified the remains of phytoplankton and other species present in *E. superba* fecal pellets.

The contribution of euphausiid fecal pellets to the flux of organic matter in the water column of the Southern Ocean must be considerable. They have been shown to dominate the vertical particulate flux in a number of areas (Wefer et al. 1988). *E. superba* fecal pellets have sinking rates of between 100 and 525 m per day (Ross et al. 1985). Clarke et al. (1988) measured fecal pellet production rates for this species of between 0.54 and 1.66 mg dry wt of feces h^{-1} (for a 600 mg fresh weight animal). Organic matter loss was shown to be constant and was estimated at 0.13 mg h^{-1}. On the assumption that egestion remains constant, then a 120 mg dry wt animal would produce between 4,730 and 4,542 mg dry wt of feces and 11.39 mg of organic matter per year (Clarke et al. 1988b).

Gonzales (1992b) investigated the distribution and abundance of fecal material in the Scotia and Weddell Seas. Krill fecal strings and oval fecal pellets of unknown origin were by far the most important zooplankton feces, and the highest concentrations were found in the Weddell–Scotia Confluence, often close to the ice border. Krill feces were usually more abundant in the uppermost layer, where they contributed an average of 150 μg dry wt m^{-3}. There was an exponential decrease with depth with a minimum of 0.6 μg dry wt m^{-3} in the 500–1,000 m stratum. Oval pellets were more evenly distributed in the upper 1,000 m of the water column with an average of 9 μg dry wt m^{-3}. Diatoms (in particular *Nitzschia* and *Thalassiosira* spp.) contributed the bulk of the material in the krill and oval feces.

In the Halley Bay region in January–February, Gonzales et al. (1994) found that the fecal material comprised pellets produced by krill, copepods, ostracods and appendicularians. Cyclopoid copepods were represented by two genera, *Oithona* and *Oncaea*. Higher concentrations of krill fecal material (420.9 mm^3 m^{-2}) and chl *a* were found within the upper 200 m of the water column of the polyna than in ice-covered and open-ocean areas (38.2 and 25.5 mm^2 m^{-2}, respectively). High concentrations of krill fecal material was found under the fast ice, and it contained some algal species which indicate that the krill were actively utilizing the ice algae. Sediment material collected at a depth of 50 m was dominated by krill fecal strings. Contents of small oval pellets (of probable cyclopoid copepod origin) suggested that coprophagy was involved.

14.2.4 CRUSTACEAN EXUVIA

Copepods and euphausiids undergo rhythmic moulting cycles. In *E. superba* this cycle ranges from 12 to 30 days. The cast exoskeletons result in the input of a significant quantity of organic matter to the water column. The residence time of this POM input to the water column is a function of the sinking rate and the rate of decomposition by heterotrophs.

Nicol and Stolf (1989) have studied the sinking rates of cast exoskeletons of *E. superba* and their role in the vertical flux of particulate matter from specimens collected at the ice edge south of Australia. They found that the cast exoskeletons represented 7.5% of the dry body weight. This compares with Clarke's (1976) estimate of 2.3–3.1%, and Ikeda and Dixon's (1982a) figures of 2.36–4.25%. Values for other species of euphausiids in the literature range from 5% to 12.7%. The sinking rates of the cast exoskeletons ranged from 0.06 to 1.28 cm s^{-1} (mean 0.78 cm s^{-1}, SD $>$ 0.183). This is similar to that measured for other euphausiids. Freshly molted exoskeletons had a C:N ratio of 5.6 and a mean organic content of 73.3% (Table 14.11).

Ikeda and Dixon (1982a) examined the contribution of molting by *E. superba* to organic detritus in the Southern Ocean. Calculations assuming 13 molts per year and a biomass estimate of 1.08 g dry wt m^{-2} yr^{-1} yielded values for molt production of 0.45 g dry wt m^{-2} yr^{-1}, or 0.11 g C m^{-2} yr^{-1}. Using similar calculations, Nicol and Stolp (1989) obtained a slightly higher estimate for molt production of 1.053 g dry wt m^{-2} yr^{-1}, and 0.18 g C m^{-2} yr^{-1}. These estimates are similar to those obtained for other euphausiid species (e.g., Lasker 1966).

14.2.5 MACROALGAL DEBRIS

Most parts of the world's coastal areas receive a considerable input of organic matter of terrestrial origin. However, such sources are very much reduced or lacking in Antarctica due to the paucity of ice-free land and the lack of rivers. However, dense growths of macroalgae are a conspicuous feature of shallow rocky substrates around the Antarctic coast (see Chapter 11). In the Bransfield Strait macroalgal production has been estimated at about 2,000 g C m^{-2} yr^{-1}, compared to 60 g C m^{-2} yr^{-1} for phytoplankton (Liebezeit and von Bodungen 1987). These dense algal beds are the subject of ice scour, storms, and grazing by invertebrates and fish. As a consequence, considerable quantities of algal debris—ranging from whole plants to fine fragments—collect in cracks and depressions and are sedimented to deeper waters. In their sediment trap experiments in Bransfield Strait, Liebezeit and von Bodungen (1987) found that material of macroalgal origin was a major contributor to the particle flux, increasing from 37% at 539 m to 71% at 1833 m.

Reichardt (1987) investigated the fate of macroalgal debris and its potential participation in deep-sea benthic food chains in the Weddell Sea area and the Bransfield Strait. He found that in two sediment samples at 2,280 and 1,570 m, the upper 8–10 cm contained considerable amounts of macroalgal fragments larger than 1 mm (22.9 and 20.9 g m^{-2} of ash-free dry wt, respectively) derived from red and brown algae. The thallus fragments served as a matrix for epiphytic bacteria, and thus they would form a potential food source for the polychaete-dominated infauna.

14.2.6 DISSOLVED ORGANIC MATTER (DOM)

Within oceanic waters there is a large reservoir of DOM. According to Bada and Lee (1977) oceanic waters in general contain 0.5–1.5 mg l^{-1} of DOC. The chemical composition of this DOM pool, however, is poorly known. The vast majority of the pool is composed of complex refractory materials (Bada and Lee 1977), while a small but significant proportion is composed of biologically active organic compounds. Of the biologically active dissolved compounds, amino acids, peptides, proteins, mono- and polysaccharides, fatty acids, organic acids, and nucleotides have been detected in sea water (see review by Williams 1975). The POC:DOC ratio in the ocean is on average 10:1 (Wetzel 1984).

While various sources of DOM are well known, there is only limited information available on the importance of the various sources and the mechanisms of utilizable DOM production. The most important sources are (see also Table 14.1):

1. *Phytoplankton Exudation*. Excretion of a proportion of the photoassimilated carbon from phytoplankton is now generally accepted, although the quantities and rates of excretion are still debated (Fogg et al. 1965; Fogg 1966; Hellebust 1974; Mague et al. 1979). A variety of molecular species is released. However, exudation as a percentage of the total assimilated carbon is highly variable, not only between species but for individual species depending on the specific environmental conditions. Release amounts in experimental studies range from 0% to 70% (Fogg et al. 1965; Choi 1972; Berman and Holm-Hansen 1974). Hellebust (1974) estimated that on average, approximately 10% of the photosynthate of phytoplankton is excreted as DOC, and this figure is often used in calculating carbon budgets.
2. *Sloppy Feeding*. There is evidence that there is a significant loss of algal cell contents during handling and grazing by herbivores (Copping and Lorenzen 1980; Eppley et al. 1981). The quantitative significance of such sloppy feeding in the Southern Ocean is unknown.
3. *Autolysis*. Stress may cause the death and autolysis (DEATH) of photoautotrophs, particularly in the senescent stage of a phytoplankton bloom. The *Phaeocystis* blooms, a common feature of phytoplankton dynamics in the Southern Ocean, produce large amounts of extra-cellular carbon. Unusually high concentrations of DOC have frequently been reported as a general characteristic associated with *Phaeocystis* blooms (e.g., Bolter and Dawson (1982) in the Bransfield Strait, and Eberlein et al. (1985) in the North Sea). As the bloom decays, bacteria may attach to the autolysing algae or remain in close proximity to take up the released nutrients from a high concentration.
4. *Sea Ice Microalgae*. The release of DOM by sea ice microalgae has already been discussed in Chapter 3. Any DOM that has not been utilized by the sea ice bacteria will be released into the water column upon the melting of the ice. It is also probable that DOM is released into the water column from the sea ice microalgal bottom assemblages and the sub-ice mat strand assemblages.
5. *Release of DOM by Microflagellates and Ciliates*. Andersson et al. (1985) have recently demonstrated that during the consumption of bacteria HMF released 13% of the ingested nitrogen as ammonia and 30% of the ingested phosphorus as phosphate. They also showed that the concentration of dissolved free amino acids (DFAA) increased when flagellates fed on bacteria and concluded that they played a small but significant role as a source of DFAAs in the sea. Further studies by Taylor et al. (1985) suggested that the bactivore grazing by ciliates altered the DOM pool both quantitatively and qualitatively. The presence of bactivores appeared to enhance the DOM pool by contributing organic compounds with $<5\times10^2$ to 10^4 NWW. As suggested by Fenchel and Harrison (1976), herbivorous ciliates and microzooplankton stimulate bacterial growth by reducing growth-inhibiting bacterial competition through grazing and supplying DOM through excretion and through stimulation of bacterial exudation. It is therefore likely that the abundant ciliate and microflagellate populations of the Southern Ocean play a role in carbon cycling along the lines discussed above.
6. *Benthic Microalgal Exudation*. Diatom films on rocky substrates and the benthic microalgae in the surface layers of inshore sediments are another potential source of DOM. The excretion of the sediment microalgae has proved difficult to measure because the abundant sediment bacteria would be expected to assimilate any labile organic material as fast as it is released (Pomeroy et al. 1981). It is probable that the rates of release of extracellular carbon by the benthic microalgae is comparable to that of the phytoplankton.
7. *Benthic Macroalgae*. As previously mentioned, dense growth of benthic macroalgae occur in inshore Antarctic waters, and as seen in Chapter, they grow to considerable depths. Siebruth (1969), Moebus and Johnson (1974), and Khailov and Burkalova (1976) have reported that between 23% and 40% of the photoassimilated carbon is excreted by various macroalgae. Thus, the macroalgae may contribute considerable quantities of DOM to Antarctic inshore waters.

Moran et al. (2001) investigated the production of organic matter in the Weddell and Scotia Seas during the austral summer. Percent phytoplanton extracellular release (PER = DOC/[POC + DOC]) averaged 13% (range 5–33%), a value comparable with those reported from lower latitudes. Assuming a conservative bacterial growth efficiency of

14%, as reported by recent work in Antarctic waters, their experiments indicated that phytoplanktonically produced DOC would suffice to meet bacterial demand. The results suggested a strong coupling between phytoplankton and bacterioplankton through DOC release and uptake under nonbloom conditions in the Southern Ocean.

14.3 SEDIMENTATION OF POM

Almost all nonliving POM tends to sink, and unless consumed, continues to do so until it reaches the sediment. It has been demonstrated that there is a relationship between primary production in the water column and the flux of carbon to the sediment surface (Hargraves 1975). However, the relationship is not a simple one. The greater the depth of the water column, the greater the proportion of the organic matter that is decomposed before it reaches the bottom. Furthermore, the greater the depth of the mixed layer, the greater the amount of mineralization occurring in the water column. Sedimentation of phytoplankton and larger particles such as fecal pellets are primarily responsible for the vertical flux of organic matter in the oceans. In recent years the development of automatic sediment traps which can be moored at different depths has added much to our understanding of this flux.

Recently, techniques have been developed to measure the sinking rate of particulate matter in the field (Bienfang 1981). Results from a wide range of geographic regions, including the Antarctic and Subantarctic, have revealed a dependency of sinking rate on phytoplankton cell size (Bienfang 1984; Jacques and Hoepffner, 1984), and ambient light intensity (Johnson and Smith 1986; Riebesell 1989) with increased sinking rates on overcast days. Sinking rates are also dependent on nutrient concentrations (Bienfang 1981; Bienfang and Harrison 1994), the density and viscosity of the water, and local water movements. The overall sinking rate of phytoplankton is largely a function of cell size and chain length, with the larger cells sinking more rapidly (Riebesell 1989). Increases in sinking rates can also be caused by the formation of cell aggregates, which increase in abundance during the decline of a phytoplankton bloom (von Bodungen et al. 1981). Widely different sinking rates have been reported in the literature (see Table 14.2): 0.06 m

TABLE 14.2
Sinking Rates of Different Particle Types

Particle Types	Sinking Rate (m day^{-1})	Source
Salp faecal pellets		
Two different species	450–1,210 (836) 600–2,700 (1,080)	Bruland and Silver (1981)
Three different species	320–1,987 (1,060)	Madin (1982)
Copepod faecal pellets		
Acartia tonsa	80–150	Honjo and Roman (1978)
Calanus finmarchicus	180–200	
Different species various ages	19.5–100.7	Small et al. (1979)
Adults	12–225	
Larvacean houses		
Oikopleura dioica	64.9* at 5°C 57.0* at 16°C	Silver and Aldridge (1981)
Diatom cells		
Small-celled phytoplankton (tropical waters)	0.06	Bienfang (1985)
Large-celled long chained species (temperate waters)	0.96	Bienfang and Harrison (1994)
Large-celled and pennate species		
Sub-Arctic ecosystem	0.43	Bienfang (1984)
Sub-Antarctic waters	0.1–0.52	von Bodungen et. al. (1981)
Different species	0.10–2.10*	Smayda and Buleyn (1965)
Fragilaria crotonensis	0.27*	Burns and Rosa(1980)
Natural community		
0–20 μm	0.34–0.83*	Bienfang (1980)
20–102 μm	0.95–1.65*	
Natural community	0.32–1.69 (0.64)	Brenfang (1981)
Natural community	0.21*	Smyada and Bienfang (1983)

Average sinking rates are in brackets or designated by an asterisk.
Source: From Anderson, V., Nival, P., *Mar. Ecol. Prog. Ser.*, 44, 37–50, 1988. With permission.

day^{-1} for small-celled phytoplankton in well-stratified tropical waters (Bienfang 1985); 0.96 m day^{-1} for large-celled, long-chained diatoms in temperate assemblages (Bienfang and Harrison 1994); 0.43 m day^{-1} for large centric and pennate diatoms in a subarctic ecosystem (Bienfang 1984); and 0.1 m to 0.52 m day^{-1} in subantarctic waters (von Bodungen et al. 1981).

Phytoplankton dynamics during an ice edge bloom in the Ross Sea revealed depletion of dissolved silicic acid from the water column which was closely matched by the appearance of biogenic particulate silica (Nelson and Smith 1986). The results of the study revealed low loss rate of biogenic silica (Bsi), i.e., the loss of diatomaceous material via passive sinking or grazing and subsequent downward flux of fecal material. However, diatoms made up an overwhelming proportion of the biogenic material in the sediments beneath the bloom, and sediment accumulation rates indicated that a large proportion (around 80%) of the surface siliceous production was being delivered to the sediment (Johnson and Smith 1986). Furthermore, there was a strong taxonomic correlation between the species found in the ice edge bloom (Smith and Nelson 1985a) and those in the sediments (Truesdale and Kellog 1979). To resolve questions regarding the proportion of the diatom production eventually deposited on the sea floor, recent research has been directed at determining the sinking rates of particulate material and estimating the consumption rates of phytoplankton and the fate of the unconsumed material.

Johnson and Smith (1986) have studied the sinking rates of phytoplankton assemblages in the Weddell Sea marginal ice zone in November–December 1983 (Table 14.3). Parameters measured included chlorophyll *a*, phaeophytin, Bsi, particulate carbon, particulate nitrogen and diatom cell numbers. Sinking rate varied with each measurement but exhibited the following trends: phaeophytin > biogenic silica > particulate carbon > diatom cell numbers > particulate nitrogen > chlorophyll *a*. Sinking rates as determined by chlorophyll *a* ranged from 0 to 2.73 m day^{-1} ($x = 0.89$), which were similar to those reported for temperate (Bienfang and Harrison 1994), and subarctic (Bienfang 1984) regions of the ocean. It was estimated that 8–12% of the daily production was lost from the euphotic zone, a percentage similar to Bienfang's (1984) estimate for a subarctic ecosystem.

Diatom production within the photic zone is the dominant mechanism for the uptake of dissolved silica from the water column (Heath 1974). Annual silica production on the Antarctic shelf ranges between 100 and 500 g SiO_2 m^{-2} yr^{-1}, with diatoms accounting for greater than 99% (by weight) of the total (Lisitzin 1972). This is much higher than at lower latitudes where annual silica production is only about 100 g SiO_2 m^{-2} yr^{-1}, with diatoms accounting for 35% of the total (Lisitzen 1972). Leford-Hoffman et al. (1986) have estimated that as much as one-third of the dissolved silica supplied to the oceans is ultimately deposited on the Antarctic shelf. Processes influencing the composition of the sedimentary microfossil assemblage include production in the sea ice or water column, release of microalgae from the sea ice, settling, dissolution, winnowing, resuspension, and deposition.

In McMurdo Sound, Leventer and Dunbar (1987) found that although diatom abundances in the sea ice reach 10^8–10^9 cells m^{-2} during the period October–December, diatom fluxes measured by sediment trap samples were only 10^5–10^7 individuals m^{-2} day^{-1}. However, it would be expected that this flux would increase dramatically when the sea ice melted and released the particle trapped in the ice. Fukuchi and Sasaki (1981) measured the vertical flux of POC under the sea ice in Lutzow-Holm Bay (Table 14.4). The depth of the maximum flux occurred at 100 m depth, which is comparable to that reported from other seas. Fecal material was the major contributor to the vertical flux; of this, copepod feces were the dominant component. Ice algal species were common in the fecal material. This was similar to that of the McMurdo Sound study where the sediment trap assemblage closely resembled that found in the sea ice (Leventer and Dunbar 1987) (Figure 14.2). Five species dominated the sea ice assemblage: *Amphipora* sp., *Pleurosigma* sp., *Nitzschia stellata*, *Pinnularia quadratanea*, and *Nitzschia curta*. These species were also common within the water column, along with *Thalassiosira* spp., a genus that

TABLE 14.3
Sinking Rates and Means of Particulate Matter Parameters Measured in the Marginal Ice Zone of the Weddell Sea

Parameter	Range (m day^{-1})	Average (m day^{-1})
Phaeopigment	0–5.47	1.17
Biogenic silica	0–3.44	1.11
Particulate carbon	0–4.93	1.08
Diatom cell numbers	0–2.88	0.91
Particulate nitrogen	0–3.30	0.89
Chlorophyll *a*	0–2.73	0.89

Source: Johnson, T.O., Smith, W.O., Jr., *Mar. Ecol. Prog. Ser.*, 33, 131, 1986. With permission.

TABLE 14.4
Concentration of Particulate Organic Carbon (POC) and the Vertical Flux of POC at 50 m, 100 m, and 150 m Depth Under the Ice-Covered Lutzholm Bay

Depth	Concentration of POC (mg C m^{-1})	Vertical Flux of POC (mg C m^{-2} day^{-1})
50	56	21
100	24	103
150	30	27

Source: Fukuchi, M., Saski, H., *Mem. Nat. Inst. Polar Res.*, 34, 52, 1981. With permission.

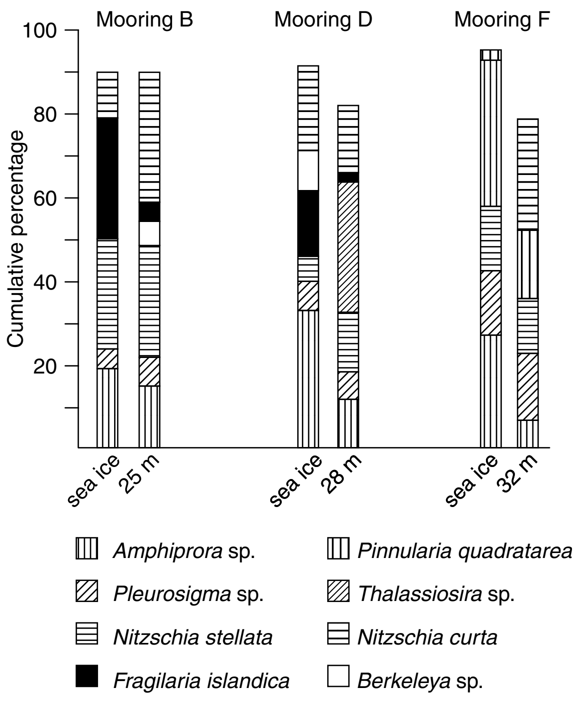


FIGURE 14.2 Cumulative percentage of dominant species of diatoms for sea ice and corresponding shallow sediment traps in McMurdo Sound; Mooring B, at the tip of Erebus Ice Tongue; Mooring D, 5 km west of McMurdo Station; Mooring F, in New Harbor. (From Leventer, A., Dunbar, R.B., *Mar. Micropaleontol.*, 12, 49, 1987. With permission.)

was quite rare in the sea ice. Within the upper 250 m of the water column, at a site in Granite Harbor, diatom flux decreased from between 47% and 79% from 34 to 20 m. Opal flux, however, decreased by only 13–40% over the same depths, indicating that the dissolution of thinly silicified diatom frustules occurred. Species common in the sea ice, especially *Fragilaria islandica* var *adeliae* and *Berkeleya* sp., appeared to be disproportionately dissolved in the water column. Lateral advection in the water column can also modify the composition of the diatom assemblage reaching the sea floor. At all sites it was found that the greatest increase in diatom flux occurred just above the sea floor. Resuspension of diatom tests and/or lateral advection, combined with the preferential dissolution of species dominating the sea ice assemblage, are responsible for the production of a sediment assemblage composed of *Thalassiosira* spp., *N. curta*, and other robust forms of *Nitzschia*.

Fecal pellet sinking rates are dependent on the size and weight of the pellets. Cadee et al. (1992), in an investigation in the Scotia and Weddell Seas, found the smallest krill fecal strings in the shallowest traps. The sinking rates of the smaller fecal strings was much lower than for the larger ones, with a total range of 50–500 m day^{-1} for fecal string volumes of 0.007–0.53 m^{3}. Smaller krill fecal strings did not leave the upper mixed layer. Smaller oval fecal pellets of unknown origin showed relatively high settling velocities (80–250 mm day^{-1} for 0.002–0.013 mm^{3}) due to higher compaction and lower form resistance to sinking.

14.4 BIOGENIC FLUXES IN THE WATER COLUMN

Liebezeit and von Bodungen (1987) determined the fluxes of organic carbon and nitrogen, total phosphorus, chlorophyll pigments, carbohydrates, amino acids and amino sugars for a depth-series sediment trap in November/December 1983 in the Bransfield Strait. Table 14.5 shows the relative contribution of the various categories to the total carbon flux. Total mass flux was relatively constant in the upper traps and increased with depth. The observed amino acid depth distribution was very uncommon. As a result of heterotrophic degradation, contribution of amino acids to both POC and POM decrease with depth both in the water column particulates (Liebezeit and Bolter 1986) and sediment trap material (Liebezeit 1985). In deeper traps sugar fluxes were significantly higher than in the upper ones. Absolute and/or relative increases of phosphorus, glucose and chlorophyll *b* fluxes and decreases of the aline flux with depth suggested a second source of organic plant material besides phytoplankton. Liebezeit and von Bodungen (1987) identified this as originating from shallow water macroalgae which are abundant in the shallow waters of the Bransfield Strait (Dieckmann et al. 1991).

Fischer et al. (1988) deployed a multi-year sediment trap in the Weddell Sea (62°26′ S, 34°45.5′ W) at 835 m depth in a total water depth of 3880 m. This station is covered by sea ice for about 70% of the year (9 on an ice-cover scale (ISC) (Zwally et al. 1983a, 1983b). Figure 14.3 depicts the total particle flux from the various sampling periods. The annual particle flux was extremely low 1.37 g m^{-2} yr^{-1}, and highly variable, very much lower than that recorded for the Bransfield Strait (107 g m^{-2} yr^{-1}). Fecal pellets played an important role in the sedimentation process, although krill pellets were extremely rare. The particle fluxes demonstrated that a large increase occurred following the spring thaw of the sea ice. Table 14.6 compares data from Fischer et al.'s (1988) study in the Weddell Sea with that from the Bransfield Strait which was very much higher (total POC g m $^{-2}$ yr^{-1} several times that of the Weddell Sea). Fluxes in the Bransfield Strait were much higher than those recorded at Arctic stations and were comparable to those measured at a station at 55°N.

Sedimentation off Vestkapp in the Weddell Sea was studied by von Bodungen et al. (1988) in the summer of 1985. The material collected in the traps was dominated by fecal material of different origin, string-shaped krill feces, copepod fecal pellets (in low numbers), and oval, or triangle-shaped, pellets of various sizes (50–300 m) of unknown origin filled with diatom frustules. Sedimentation over the study period amounted to 2–4 g C m^{-2}. It was estimated that the daily flux of POC at one station was equivalent to 43% and 65% of the daily primary production, but only between 1% and 15% for the other stations.

TABLE 14.5
Compound Fluxes in the Bransfield Strait

Compound	Depth (m)				
	18	323	539	963	1410
Total flux	558	3,170.8	3,289.7	3,462.4	4,923.4
Particulate organic carbon	8	131.9	120.3	80.3	94.3
Particulate organic nitrogen	—	14.5	13.2	7.3	9.6
Total particulate phosphate	—	0.9	1.3	2.4	4.0
Amino acid carbon	2	28.2	21.0	21.5	27.0
Amino sugar carbon	—	0.6	1.2	1.2	2.2
Monosaccharide carbon	—	5.5	10.8	9.3	17.0
Chlorophyll	—	5.5	2.9	9.3	17.0
Phytoplankton carbon	>0[a]	1.4	1.4	>0[a]	>0[a]

All values are in mg m^{-2} day^{-1}.

[a] Degraded plasma.

Source: Liebezeit, G., von Bodungen, B., *Mar. Ecol. Prog. Ser.*, 36, 23–32, 1987. With permission.

Wefer et al. (1988) deployed time-series sediment traps at 494 and 1,588 m in the Bransfield Strait from 1 December 1983 to 25 November 1984. During the austral summer (December and January) the total flux was more than 1.5 g m^{-2} day^{-1} at both depths, while during all the other months the flux was between 10 and 1,000 times lower, with the flux of the most productive months being 97% of the total (Figure 14.4). The annual total flux to the deeper trap was

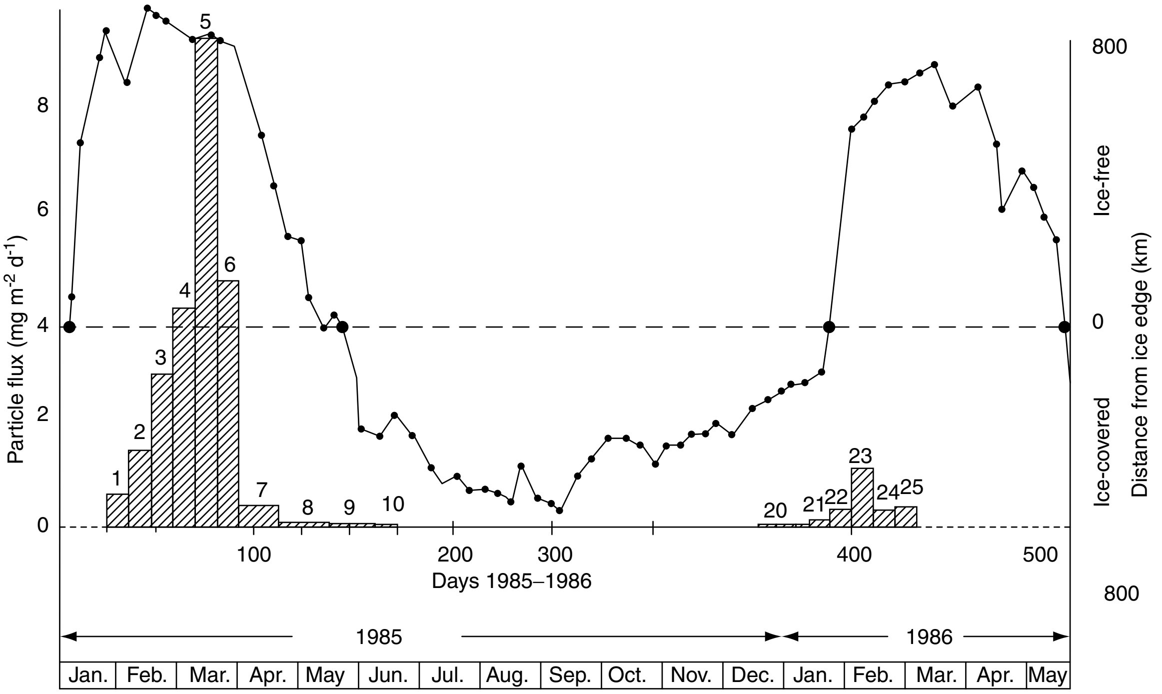


FIGURE 14.3 Total flux of particulate matter for each sediment trap sampling period for a station in the Weddell Sea (see text for details). Sample numbers are on the top of the bars. The horizontal dashed line represents the ice edge with the superimposed solid line representing the shortest distance (km) from the approximate ice edge to sediment trap site. (From Fischer, G., et al., *Nature (London)*, 335, 426, 1988. With permission.)

TABLE 14.6
Particle Flux from the Northern Weddell Sea, Compared to those from Other Studies

	Weddell Sea 62°26′S 34°45′W Jan. 1985–Dec. 1985 (g m^{-2} y^{-1})	Bransfield Strait 62°15′S 57°31′W Dec. 1985–Nov. 1984 (g m^{-2} y^{-1})	Greenland Basin 74°35′N 06°43′W Aug. 1985–Jul. 1986 (g m^{-2} y^{-1})	C. Fram Strait 78°32′N 01°22′E Aug. 1984–Aug. 1985 (g m^{-2} y^{-1})	Station P 50°00′N 144°59′W Nov. 1985–Oct. 1986 (g m^{-2} y^{-1})
Total	0.371	107.7	10.8	6.6	45
Biogenic	0.367	53.7	7.1	2.9	44.7
Carbonate	0.011	5.2	3.3	1.4	21.9
Opal	0.293	38.8	2.6	0.6	19.0
Combustible	0.063	9.7	1.2	0.9	3.8
Lithogenic	0.004	53.5	3.1	4.0	0.3
POC	0.02	3.0	0.4	0.4	3.7

The data were obtained during roughly the same time period using one year time series experiments from the Arctic, Northern Pacific, and Antarctica.
Source: Fischer, G., et. al., *Nature (London)*, 335, 426, 1988. With permission.

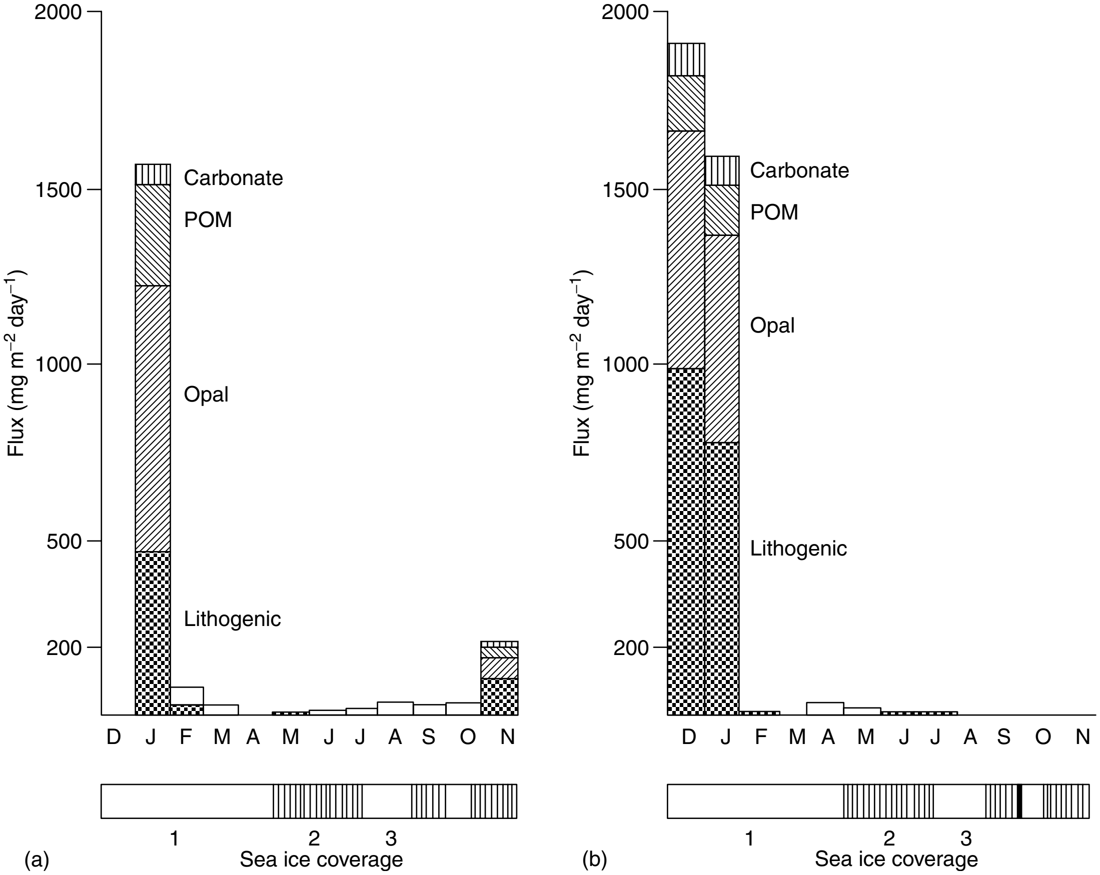


FIGURE 14.4 Flux rates at 494 m (a) and 1588 m (b) water depth in the Bransfield Strait (62°15.4′ S; 57°31.7′ W) between 1 December 1983 and 25 November 1984; total dry mass flux, partitioned into total carbonate (acid-leaching) flux, combustible flux (POM), opal (NaOH-leaching) flux, lithogenic (residue after combustion and NaOH-leaching) flux and carbonate (acid-leaching) flux. Sea ice coverage: (1), free of sea ice; (2), ice edge shifting in Bransfield Strait, (3), Bransfield Strait ice covered. (From Wefer, G., Fischer, G., Fuetterer, D., Gersonde, R., *Deep Sea Res.*, 35, 891, 1988. With permission.)

$110\ g\ m^{-2}$. Biogenic materials (carbohydrate, POM, and opaline silica) accounted for about 67% in the upper trap and 50% in the lower one. On an annual average, the fluxes were comparable to world averages (Angel 1984), although the bulk occurred in one-sixth of the year. Peak daily fluxes during this period were very high. Similar high fluxes have been reported for shortterm sediment trap deployments elsewhere in Antarctic waters during the austral summer months (Fukuchi and Sasaki 1981; Wefer et al. 1982; Dunbar 1983; Schnack 1985a; von Bodungen 1986; Gersonde and Wefer 1987). The bulk of the material in the traps consisted of krill fecal pellets resulting from krill swarms feeding on phytoplankton blooms. A number of investigations have stressed the importance of krill feeding on the sedimentation of organic carbon, e.g., Cadee et al. (1992) found that in the Scotia-Weddell Sea maximum sedimentation occurred during the grazing of the krill swarm.

Wefer et al. (1990) investigated the particle sedimentation and productivity water of the Atlantic sector of the Southern Ocean. At all sites a marked seasonality in annual flux and composition was observed with up to 97% of the annual flux occurring in a two month period. In Bransfield Strait the annual flux to 494 m was more than $60\ g\ mg^{-2}$, comparable to other near-shore, high-productivity areas. In the Northern Weddell Sea, the annual particle flux had the smallest value observed to the time of the study in the world's oceans ($0.37\ mg\ m^{-2}$).

Accornero et al. (2003a, 2003b) investigated the flux of particulate matter in the Terra Nova Bay polyna. Bsi made up the bulk of the sinking matter, reaching a maximum of 85% of the total flux for both the shallow (180 m) and deep traps (868 m). Organic carbon accounted for 2.1–23.5% of the sample mass in the shallow trap and 2.8–7.2% in the deep trap. Bsi and organic carbon peaks occurred in February–March. The export of phototrophically produced materials to depth was low in late spring-early summer, at the time when *Phaeocystis* and small flagellates were the predominant autotrophs and the microbial food web prevailed over herbivorous feeding. The highest fluxes were found in the late summer, when feces contributed up to 100% of the organic carbon. A major flux component was the pteropod *Linacina helicina*, which repeatedly sank in high amounts after the growing season.

Karl et al. (1991) carried out simultaneous measurements of the seasonal depletion of dissolved inorganic carbon (CO_2), nitrogen (NO_3+NO_2) and phosphate (HPO_4) and concentrations of C, N, and P at five representative sites in the western Bransfield Strait over a period of four months. During the spring bloom period (December–January) there was a substantial removal of dissolved inorganic carbon, nitrogen and phosphate, corresponding to a net upper water column (0–50 m) seasonal production of $8410\ mmol\ C\ m^{-2}$, $825\ mmol\ N\ m^{-2}$, and $53.1\ mmol\ P\ m^{-2}$. This study confirmed the results obtained in the investigations discussed above documenting the phenomenon of a relatively short (2–3 months) downward flux of POM. Karl et al. (1991) have tabulated the data from all previous studies of particle flux in the Southern Ocean. These show short-term fluxes of 10^2–$10^3\ mg\ C\ m^{-2}\ day^{-1}$, which are equivalent to values previously measured in upwelling conditions off central California and along the coasts of Peru (Martin et al. 1987).

Karl et al. (1991) and Leventer (1991) found that diatom resting cell formation was an important mechanism for removing intact, viable phytoplankton cells from the Antarctic coastal ecosystem. In addition to diatom resting spores and vegetative phytoplankton cells the sediment raps contained substantial concentrations of marine snow, fecal pellets (mostly from krill), unidentified eggs and mineral particles.

A number of processes appear to be important in vertical particle flux in the Southern Ocean:

1. Water mass exchange (e.g., vertical water currents, Bathmann et al. 1997).
2. Mass sedimentation of phytoplankton triggered by a reduction in light supply (Bodungen 1986).
3. Sinking of zooplankton fecal material, especially krill fecal strings following extensive grazing on phytoplankton bloom (von Bodungen 1986; von Bodungen et al. 1987; Cadee et al. 1992).
4. Sedimentation of sea ice microalgae following the melting of the sea ice (Bathmann et al. 1991).
5. Selective sedimentation of small fecal pellets probably of protozoan origin (Gowing 1989; Nöthig and von Bodungen 1989; Buck et al. 1990; Bathmann et al. 1991).
6. Sinking of aggregations of organic matter (marine snow).

14.5 BACTERIA

14.5.1 WATER COLUMN BACTERIA

In Antarctic seas, contradictory views were held on the role of bacteria in the pelagic food web. Until the late 1970s most investigators (e.g., Kriss 1973; Mitskevich and Kriss 1973) considered that the bacterioplankton of the water column in Antarctic waters was present in low concentrations and that heterotrophic activity was temperature limited. However, contrary to this hypothesis, Gillespie et al. (1976) found high microbial heterotrophic potential for the assimilation of organic substrates from Antarctic seawater at low temperatures. The data from the early investigations were critically reviewed by Sorokin and Federov (1978) who demonstrated that the early counts of bacterial numbers were too low due to the loss of bacteria in the process of concentration on membrane filters. Subsequent investigations have shown that the numbers and production of bacteria in the Southern Ocean, especially in the more productive areas, is quite considerable (Hodgson et al. 1981; Holm-Hansen 1981; Hanson et al. 1983a, 1983b; Hansen and Lowery 1985; Samyshev 1986; Mullins and Priddle 1987; Cota et al. 1990; Sullivan et al. 1990). Measurements of the activity of heterotrophic bacteria at various localities and depths in the Southern Ocean (e.g., Morita et al. 1977; Kogure et al. 1986) have indicated that they are also uniquely adapted to the prevailing low temperatures.

Microbial activities in the same order of magnitude as in temperate areas have been reported from Antarctic seas (Hodgson et al. 1981; Hanson et al. 1983a, 1983b; Billen and Fontigny 1987; Cota et al. 1990; Sullivan et al. 1990). However, others have shown that a dramatic decrease in bacterial activity occurs at below 2°C, which results in the accumulation of DOM (Pomeroy and Deibel 1986).

The basic factors controlling bacteria biomass, growth, and production in a pelagic ecosystem are substrate supply and predation. The substrate supply mainly arises from dissolved organics provided by phytoplankton excretion and by sloppy feeding. Thus, bacterial dynamics are closely coupled with primary production. In studies across the Weddell–Scotia Confluence, Kuparinen and Bjornsen (1992) found that bacterioplankton production was on average 11% of the net primary production, which clearly is a lower value than the 30% based on a review from temperate freshwater and marine ecosystems, but is comparable with values reported from the spring period in subarctic ecosystems. From the results of their survey together with data obtained from mesocosm experiments, Kuparinen and Bjornsen (1992) concluded that the flux of organic matter to eucaryote heterotrophs via bacterioplankton during the spring and early summer periods in the Southern Ocean is considerable, but not of equivalent importance as in temperate waters.

Bacterial biomass and production in the Southern Ocean have been shown to vary considerably, not only geographically but with season. Highest values are generally recorded during the austral summer, associated with the receding marginal ice zone of oceanic waters and in most neritic waters (Priddle et al. 1992). Table 14.7 lists bacterial abundance and biomass values recorded from Antarctic coastal waters. From this table it can be seen that not only do the values differ from region to region at the same time of the year, but that they show marked seasonal differences with maximum values during the spring-summer phytoplankton bloom (December–January). In Prydz Bay, East Antarctica, Leakey et al. (1996) found that bacterial biomass and production ranged from 2–8 $\times 10^8\ \mathrm{l}^{-1}$, 13–64 μg C l^{-1} and 6–14 g C day^{-1}, respectively, with maximum values recorded in mid-January.

Mordy et al. (1995) investigated the distribution of bacterial biomass and production in the marginal ice edge zone of the Weddell–Scotia Sea during the austral winter. They found that the winter distributions of bacterial biomass and production were more closely related to local hydrography than to microalgal distribution or the position of the ice edge. They found no significant difference between bacterial biomass in ice-covered and open waters. Bacterial numbers ranged from 7×10^9 to 7×10^{11} cells m^3. In winter bacterial production was reduced 85–90% relative to spring and autumn, and even though winter bacterial production in the Marginal Ice Zone ranged over 3 orders of magnitude (0.001–3.56 mg C $\mathrm{m}^3\ \mathrm{day}^{-1}$), there was no significant difference between the under-ice and open-water stations. Thus, while the influence of the pack ice coverage on bacterioplankton production in the Marginal Ice Zone was significant in the spring and summer, it was relatively small in the winter.

Satoh et al. (1986) investigated seasonal changes in the numbers of heterotrophic bacteria under the fast ice near Syowa Station (60°00′ S; 39°35′ E) from May to January. At three stations (water depths 12, 38 and 700 m), the numbers of heterotrophic bacteria began to increase in October, with the maximum number (2.4×10^2 colonyforming units mL^{-1}) being found in late December (see Figure 14.5) The changes in bacterial numbers corresponded well with those of POC, suggesting that the growth of the heterotrophic bacteria depends on the supply of POC from the sea ice microalgal assemblages which developed rapidly in the bottom layer of the sea ice in the austral spring.

It is evident that despite the low temperatures of the waters surrounding the Antarctic continent, the microbial populations maintain a high energy status indicative of active metabolism. Populations in the Drake Passage were found to have an endenylate energy charge of up to 0.8, slightly higher than populations in the South Pacific sector (0.6–0.7) (Hanson et al. 1983a). Rates of bacterial DNA synthesis (measured by tritiated thymidine uptake and incorporation) were lower in the Drake Passage (0.005–5.4 pmol $\mathrm{l}^{-1}\ \mathrm{day}^{-1}$) than in temperate coastal waters (2.4–502 pmol $\mathrm{l}^{-1}\ \mathrm{day}^{-1}$). However, the specific rates of synthesis (about 10^{-21} mol of thymidine $\mathrm{cell}^{-1}\ \mathrm{h}^{-1}$) were comparable with those of other marine areas.

Sullivan et al. (1990) and Cota et al. (1990) have investigated the bacterioplankton of the marginal ice zone in the Weddell Sea in spring and autumn, respectively. These studies have enabled comparisons to be made between processes occurring in open and ice-covered water at different times. Both studies revealed a considerable degree of coherence between the distributions of phytoplankton and bacterial biomass. In Table 14.7 microbial parameters for the ice-covered and open waters are compared. In the austral spring chlorophyll a concentrations were seven times higher in the open water than in the ice-covered water. In contrast, the bacterial biomass in the open water was less than double that of the ice-covered water. Bacterial biomass represented only about 3% of the total POC, with little variation between ice-covered and open-water regions.

Secondary production by bacterioplankton displayed a trend similar to that of primary production, with higher values in the open water. Bacterial production averaged 0.3 mg C $\mathrm{m}^{-2}\ \mathrm{day}^{-1}$ beneath the pack ice and 1.2 mg C $\mathrm{m}^{-2}\ \mathrm{day}^{-1}$ in the centre of a dense algal bloom. Previous estimates of production rates for bacterioplankton range from about 2–15 mg C $\mathrm{m}^{-2}\ \mathrm{day}^{-1}$ in coastal regions, and from 0.6 to 2 mg C m^{-2} in oligotrophic, open-ocean regions (Ducklow 1983). Rates of bacterial production during the austral spring were generally between 2% and 25% those of the primary production, and averaged 7% and 14% in ice-covered and open water respectively. Fuhrman and Azam

TABLE 14.7
Regional Means for Microbial Parameters Observed in Ice-covered versus Open Waters of the Marginal Ice Edge Zone During AMERIEZ Cruises During Austral Spring (Sullivan et al. 1990) and Autumn (Cota et al. 1990)

	Spring 1983		Autumn 1986	
Parameter	**Ice-covered waters**	**Open waters near ice edge**	**Ice-covered waters**	**Open waters near ice edge**
Chlorophyll *a*				
(mg m¯3)	0.25±0.16	2.9±2.6	0.08±0.03	0.28±0.24
(mg m¯2)	21±10	142±81	9±2	29±18
Particulate organic carbon				
(mg C m¯3)	48±30	115±100	29±20	46±47
(mg C m¯2)	4838±1302	5844±2839	2933±1178	4354±2048
Bacterial biomass				
(mg C m¯3)	1.8±2.1	3.7±1.9	2.9±1.7	3.1±2.0
(mg C m¯2)	154±119	258±89	229±59	382±172
Primary production				
(mg C m¯3 d¯1)	3.8±3.0[a]	14.8±15.8	2.1±1.8[a]	2.8±3.4
(mg C m¯2 d¯1)	269±87[a]	521±226	137±58[a]	126±81
Bacterial production				
(mg C m¯3 d¯1)	0.3±0.4	1.2±1.5	0.2±0.2	2.8±3.4
(mg C m¯2 d¯1)	20±18	70±65	19±10	126±81
Production: biomass (P:B)				
Phytoplankton[b]	0.45±0.14	0.13±0.07	0.15±0.05	0.06±0.04
Bacteria	0.17±0.09	0.35±0.27	0.07±0.03	0.40±0.19
Bacteria:phytoplankton (2°:1°)				
Biomass[b]	0.23±0.18	0.07±0.05	0.34±0.17	0.12±0.05
Production	0.07±0.07	0.14±0.09	0.14±0.13	0.76±0.45
Algal growth rate[c] doublings (d¯1)	0.08±0.06[a]	0.11±0.08	0.07±0.06[a]	0.06±0.06
Bacterial growth rate doublings (d¯1)	0.34±0.31	0.42±0.29	0.15±0.15	0.59±0.32
Amino acid turnover times[d](d)	83	13	45	18

All aereal estimates were integrated over the euphotic zone (i.e., depths less then ≤0.1% optical depth) or to a depth of 100 m if optical depths were not sampled. values are mean±SD.

[a] Values are not corrected for ambient light regime in pack ice.

[b] Assumes at C:Chl, ratio of 32 in 1983 and 100 in 1986 for all phytoplankton.

[c] Values are not corrected for non-algal components of particulate carbon.

[d] Substrates:amino acid mixture in 1983 and leucine in 1986.

Source: Cota, G.F. et.al., *Deep-Sea Res.*, 37, 1145, 1990. With permission.

(1980) suggested that a large fraction (25–29%) of the primary production may be utilized by the bacterioplankton in McMurdo Sound, and that bacterial production may often be more than 10% of the primary production. Hanson et al. (1983b) compared their estimates of bacterial production in Antarctic waters with previous literature values for primary productivity and speculated that bacterial production might be on the order of 15–45% of the primary production. Sullivan et al. (1990) reported data for the late austral winter in the Bransfield Strait which suggested that bacterial productivity ranged from less than 1% to well over 174% of primary production. In the Weddell Sea in the austral autumn, Cota et al. (1990) estimated that bacterial production in the euphotic zone of ice-covered and open waters, respectively averaged 14 and 76% of primary production. The reasons for these widely varying values will be discussed below.

In the austral autumn, bacterial production averaged 19±10 mg C m^{-2} day^{-1} in regions partially covered with ice, and in open waters mean rates were 119±69 mg C m^{-2} day^{-1}. Unlike the primary productivity values, these production rates were similar to those found in the spring,

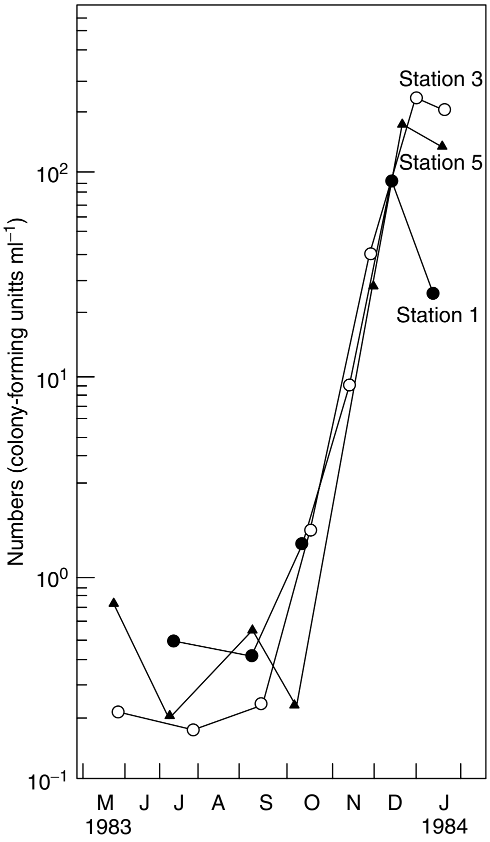


FIGURE 14.5 Seasonal variation in bacterial numbers (colony forming units mL^{-1}) at a depth of 2 m under the fast ice near Syowa Station (60°S; 39°35′ E). (From Satoh, H., Fukami, K., Watanabe, K., Takahashi, E., *Can. J. Microbiol.*, 35, 329, 1989. With permission.)

whereas the primary production was very much lower in the autumn than in the spring. Ratios of production per unit biomass (P:B ratios) provide an indication of the relative activities from different environments. Bacteria exhibited P:B ratios 2–6 times higher in open waters (Table 14.7), even though their abundance and biomass were also higher there. Comparing integrated biomass units in carbon, bacterial biomass averaged 23–34% of phytoplankton biomass under ice cover but only 7–12% in open waters.

Estimates of the turnover times for small organic molecules provided indirect indications of the role that bacteria play in remineralization. Primary bacterial parameters such as the incorporation of thymidine, uridine, mixed amino acids, and bacterial abundance were found by Sullivan et al. (1990) to be often more strongly correlated with particulate carbon (POC) or chlorophyll *a* concentrations than with the rate of primary productivity. Metabolic rates comparable to rates in temperate waters have been demonstrated for Antarctic waters during the *Eltanin* Cruise 51 in the Pacific sector (Morita et al. 1977), in McMurdo Sound (Hodgson et al. 1981), and between the Falkland Islands and the ice edge in the Weddell Sea (Bolter and Dawson 1982).

Studies of bacterial growth rates and doubling times have given conflicting results, ranging from a doubling time of 2–4 days in the Scotia Sea (Azam et al. 1998) to 18 days in Prydz Bay (Painting et al. 1985). These estimates can be compared with those of 15–33 h for northern temperate waters (Newell and Linley 1984). Production estimates likewise vary from 0.022–1.309 mg C m^{-2} day^{-1} for Prydz Bay (Painting et al. 1985), to 49–180 mg C m^{-2} day^{-1} for Sodruzhestro Sea (Samyshev 1986). As Painting et al. (1985) point out, estimates of bacterial production by H-thymidine incorporation into DNA give a wide range of values, depending on numerous factors required to convert thymidine into cellular carbon (see Fuhrman and Azam 1982; and for a critical review, Pollard and Moriarty 1984). According to Painting et al. (1985), bacterial production in the Antarctic is up to two or three orders of magnitude less than in temperate waters. This is in contrast to the conclusions of other researchers (e.g., Kogure et al. 1986) who consider the production rates to be comparable.

Table 14.8 compares estimates of bacterial abundance, biomass, production, bacterial production to biomass ratio (P:B), bacterial production as a percentage of phytoplankton production (%PP), and bacterial growth rate in Antarctic waters less than 100 m south of the Antarctic Convergence. As Cota et al. (1990) explain: "Given large spatial and seasonal differences and the wide variety of techniques employed in comparable studies of bacterioplankton in the southern ocean the degree of similarity in bacterial abundance, biomass and growth rates is striking." Most of the variation in abundance and biomass is within an order of magnitude; but the rate processes such as productivity and growth exhibit more variance (at least two orders of magnitude), ranging from values near detection limits to around 17 mg C m^{-2} day^{-1}. These differences can be attributed to the phase of the phytoplankton bloom and the time of the year during the sampling period. In their studies in the Weddell Sea, Sullivan et al. (1990) and Cota et al. (1990) found that in the autumn, bacteria were consuming about three quarters of the primary production in open water, compared with only 14% in spring when algal biomass and primary productivity were several times higher.

As emphasized by Hodgson et al. (1981), the results of investigations of bacterioplankton in the Southern Ocean have led to the following conclusions: (1) the bacterial assemblages have temperature optima for the assimilation of organic substrates that are near the ambient sea water temperatures; (2) the abundance of bacteria in the sea water is not atypically low, but is rather comparable to that of temperate oceans; and the rates of turnover times of amino acids and other DOM constituents are highly variable ranging from several days to several weeks.

14.5.2 SEDIMENT BACTERIA

To date there have been only a limited number of studies of the bacteria of sediments in Antarctic waters. Recent research efforts on the ecology of sediments have established

TABLE 14.8
Estimates of Bacterial Abundance, Biomass, Production, Bacterial Production:Biomass Ratio (P:B), Bacterial Production as a Percentage of Phytoplankton Production (%PP), and Bacterial Growth Rate in Antarctic Waters of Less Than 100 m Depth South of the Antarctic Convergence

Site	Abundance (10^{12} cells m^{-3})	Biomass (mg C m^{-3})	Production (mg C m^{-3} d^{-1})	P:B	%PP	Growth rate	Source
Ross Sea							
Nov.–Dec.	0.02–0.3	0.6–1.7	0.005–0.1	—	0.08–0.2	0.002–0.05	1
Dec.–Jan.	0.07–1.0	0.5–8.3	0.004–2.9	—	20–25	0.001–0.04	2
Drake Passage							
Sep.–Oct.	0.1–0.5	0.8–4.2	2.6–17.1	—	15–45	0.9–2.1	3
Bransfield Strait							
Sep.	—	—	0.1–0.6	—	1–174	—	4
Indian Ocean Sector							
Dec.–Jan.	0.2–1.8	<5.0–10.0	0.07–3.5	0.02–0.31	111	—	5
Dec.–Feb.	0.1–0.5	0.1–0.8	0.07–0.8	—	≤22	0.08–0.3	6
Scotia Sea							
Feb.–Mar.	0.5	—	—	—	—	0.2–0.4	7
Weddell Sea							
Nov.–Dec.							8
Open water	0.06–0.3	0.2–17.3	0.001–9.0	0.05–1.0	1–32	0.002–1.2	
Ice-covered water	0.01–0.2	0.2–5.1	0.002–2.4	0.01–0.32	2–32	0.004–0.9	
Mar.							9
Open water	0.01–0.6	03–15.2	0.05–6.7	0.18–0.88	18–151	0.04–1.8	
Ice covered water	0.03–0.4	0.5–8.6	0.002–1.0	0.01–0.16	2–14	0.007–1.1	

Values are ranges of observations for depths less than 100 m from all appropriate stations. In the Weddell Sea, studies of P:B and % PP are based upon values integrated over the euphotic zone or 100 m. 1. Kottmeier et al. (1987); 2. Fuhrman and Azam (1980); 3. Hanson et al. (1983b); 4. Kottmeier and Sullivan (1987); 5. Samyshev (1986); 6. Kogue et al. (1986); 7. Azam et al. (1981); 8. Sullivan et al (1990); 9. Cota et al (1990).

Source: Cota, G. F., et al., *Deep-Sea Res.,* 37, 1145, 1990. With permission.

that bacteria are abundant, with typical population densities of 1×10^{7} to 3×10^{9} cells g^{-1} (dry wt) of bulk sediment (Novitsky 1987; Karl and Novitsky 1988), regardless of habitat type, latitude, or water depth. Consequently, it appears that continental shelf sediments support many times as many bacteria per unit volumes than is typically found in the overlying surface seawater. The percentage of metabolically active cells have been found to range from 1% to greater than 95% of the total population (data summarized in Douglas et al. (1987)). Greater activity occurs in the top 5 cm and decreases rapidly with depth.

It has been shown that bacterial populations in Antarctic sediments can reach very high levels. White, Smith, and their coworkers (White et al. 1984, 1985; Smith et al. 1986, 1988), have studied the community structure and metabolic activity of near-shore sediments in McMurdo Sound and Arthur Harbor, Anvers Island. These investigations have shown that the bacterial populations can achieve very high biomass levels. Phospholipid analyses of the sediments off Cape Armitage, McMurdo Sound, revealed concentrations of microbial biomass equivalent to that of a subtropical Florida estuary (White et al. 1985). However, the bacterial rate of synthesis of DNA from thymidine was some 300 times slower than in the Florida estuary sediments. The Antarctic sediments contained 10 times the biomass of a deep sea area subject to abyssal storms, and 100 times that of a relatively undisturbed deep sea bottom off Venezuela. Sponge spicule mats in particular contained very rich and diverse algal and bacterial assemblages.

Smith et al. (1989) have described the benthic microbial communities of Arthur Harbor by analyses of their cell membrane phospholipid ester-linked fatty acids and metabolic rates. Biomass averaged 6 nM (phospholipid) or 3.5×10^{8} cells g^{-1} (dry wt). These biomasses were lower than those which were found in McMurdo Sound where they averaged 2.1×109 cells g^{-1} (dry wt). The difference between the two localities is probably due to the greater input of POM from the annual *Phaeocystis* bloom (Palmisano et al. 1985c), from the dense sea ice microalgal community upon the melting of the sea ice in the summer, and possibly from the rich benthic microalgal communities which have been identified in the shallow waters of McMurdo Sound (Dayton et al. 1986).

It is thus clear that Antarctic sediments, especially in shallow waters, have populations of bacteria that are comparable to those of marine sediments elsewhere in the world's oceans, but that their metabolic activity proceeds at slower rates. These sediments receive large quantities of organic detritus which is eventually brokendown with the release of nutrients. Much more research is needed to quantify the rates of mineralization and the role of the sediment microbial communities in energy cycling in Antarctic marine ecosystems.

14.6 VIRUSES

To date, relatively few studies have addressed the role of viruses in Antarctic marine ecosystems. These are reviewed by Pearse and Wilson (2003). It is now widely accepted that viruses are a dynamic and ubiquitous component of the planktonic microbial community in many aquatic environments (Wilson and Mann 1997; Fuhrman 1999; Wommack and Colwell 2000). Viroplankton abundance has been shown to correlate well with bacterioplankton abundance and is numerically the most abundant component of the plankton (Smith et al. 1992; Wommack and Colwell 2000). It has been further established that viruses play critical roles in the structure and function of aquatic food webs and nutrient cycles in the sea (Murray and Jackson 1993; Noble and Fuhrman 1997). Up to 20% of marine heterotrophic bacteria have been shown to be infected by viruses (Noble and Fuhrman 1997). Viruses are also being increasingly recognized and accepted as important contributors to element cycling within the microbial loop (Wilson and Mann 1997). It has also been suggested that another impact of virus infection on microbial communities may be its influence on the diversity and clonal composition of bacterioplankton and phytoplankton. Thus, studies of viral communities in aquatic microbial ecosystems have demonstrated that viruses can influence community structure, productivity and function, and they may also influence nutrient cycling and food web interactions. In addition, they may play an important role in the maintenance of biodiversity, the control of population size, the clonal composition of populations, and genetic exchange.

The question of whether viruses were present in the Southern Ocean was first addressed in 1991, when Smith et al. (1992) investigated viral abundance with depth and latitude, and its relationship to the distribution of bacteria. However, it was not until 1993 that Bird et al. (2001) reported the first study of viral ecology in the coastal waters of East Antarctica. They were able to determine the virus to bacteria ratios for the Southern Ocean (at between 0.7 and 6.1), when typical virus to bacteria ratios for marine systems have been quoted at between 1:1 and 50:1 (Wommack and Colwell 2000). Subsequently, Antarctic viruses were observed in the Drake Passage by Smith et al. (1992) and in the coastal waters of Paradise Harbor (Bird et al. 1993). More recently, the concentration of virus particles was determined in the surface waters of the Southern Ocean during the spring, where no significant relationship was found between the viral abundance and either cyanobacterial population density or the chl *a* concentrations (Marchant et al. 2000). The virus concentrations and virus to bacteria ratios indicate that viruses are no less important in the Southern Ocean ecosytems than elsewhere in the world's oceans (Marchant et al. 2000).

14.7 PROTOZOA

Protozoa dominate the nano- (2–20 μm) and micro-zooplankton (20–200 μm) assemblages in pelagic waters, and collectively they comprise what has been termed the protozooplankton (Siebruth 1979). Heterotrophic protozoa are now recognized as the major consumers of microbial production. They function as predators of bacteria and small phytoplankton, as prey of larger zooplankton, and as agents for remineralization and recycling of elements essential for phytoplankton and microbial growth (Sherr and Sherr 1984; Porter et al. 1985; Capriulo 1992). They can be classified according to size classes (see Table 14.9; Figure 14.5 through Figure 14.7). Figure 14.6 illustrates the composition and trophic relationships between the different size classes of the bacterioplankton, phytoplankton and protozooplankton.

Picoheterotrophs: 0.2–2.0 μm. These are small heterotrophic flagellates (Johannes 1965) and have been postulated to be important grazers of bacteria (Fuhrman and McManus 1984).

Nanoheterotrophs: 2.0–20 μm. These comprise two groups: microflagellates and naked ciliates (Figure 14.7). The HMF have been identified as major consumers of bacteria in many marine pelagic food webs (Sherr and Sherr 1984) and they may also be important grazers of autotrophic picoplankton. Heterotrophic flagellates fall taxonomically into both Phytomastigophora and Zoomastigophora. Frequently observed microflagellates include monads, bodonids, kinetplasts, nonpigmented euglenoids,

TABLE 14.9
Composition of the Microbial Community by Size Class

Size Class	Heterotrophs	Autotrophs
Picoplankton, 0.2–2.0 μm	Bacteria	Cyanobacteria
	Microflagellates	Chemolithotrophic baceria Eucaryote algae
Nanoplankton, 2–2.0 μm	Microflagellates	Phytoflagellates
	Naked ciliates	Non-flagellate algae Smaller diatoms
Microplankton, 20–200 μm	Naked ciliates	Larger diatoms
	Tintinnids	
	Larger dinoflagellates	Larger dinoflagellates
	Amoeboid protozoa	
	Rotifers	
	Other metazoa	

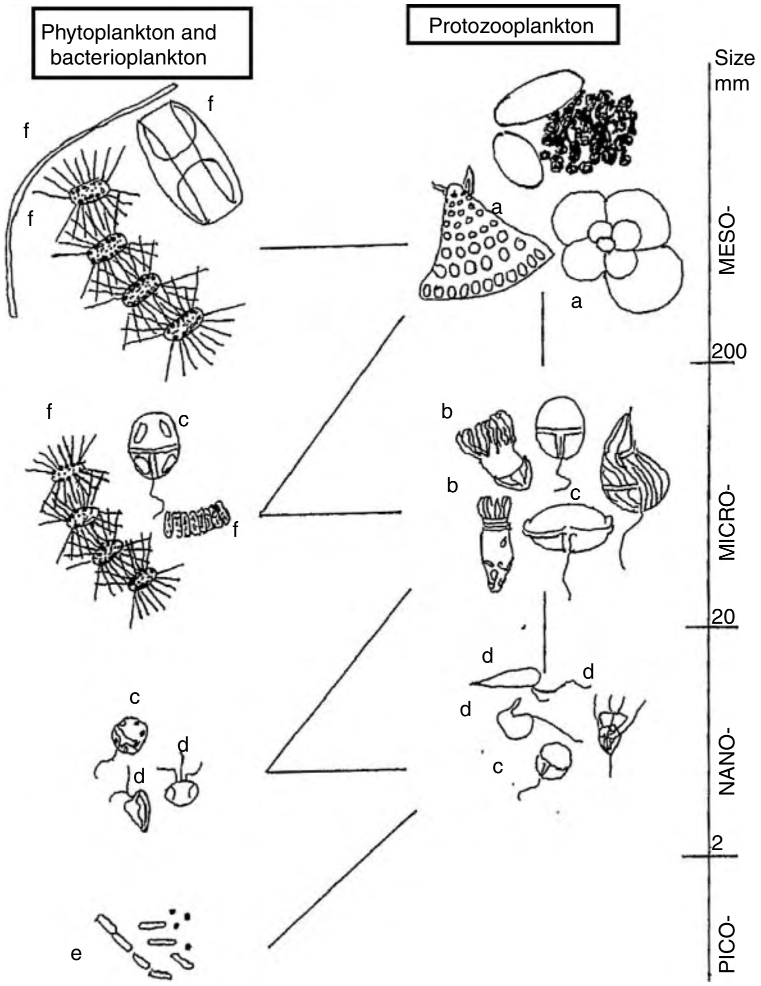


FIGURE 14.6 Illustration of the composition and trophic relationships between the different size classes of the bacterioplankton, phytoplankton and protozooplankton. Based on Fenchel (1988). (a) Large sarcodines; (b) ciliates; (c) dinoflagellates; (d) other flagellates; (e) bacteria and cyanobacteria; (f) diatoms. (From Klaas, C., *Ber. Polarforsch.*, 253, 11, 1997. With permission.)

choanoflagellates, cryptomonads, chrysomonads, dinoflagellates and biocoeids (Figure 14.8) (Siebruth et al. 1978; Fenchel 1982a). There are often pigmented and unpigmented forms that are closely related taxonomically and structurally, and there is increasing evidence that some pigmented forms may be able to utilize particulate food sources (bacteria, picoheterotrophs and picoautotrophs) (Porter et al. 1985). Thus, algal mixotrophy, the utilization of energy as particulate matter by photosynthetic forms, is another component of the food web.

Ciliates smaller than 20 μm have been observed in many parts of the world's oceans, and they may form an important component of the nanoplankton (Porter et al. 1985). Besides bacteria, such ciliates may feed on procaryote and eucaryote autotrophs in both the picoplanktonic and nanoplanktonic size ranges (Sherr et al. 1986).

Microheterotrophs: 20–200 μm. Spirotrichous ciliates are the dominant group with most species falling into the suborders Oligotrichina and Tintinnina. The most studied group is the tintinnids. Tintinnids feed mostly on small flagellated phytoplankton (Heinbokel and Beeres 1979). Naked oligotrichous ciliates are ubiquitous in marine pelagic ecosystems (Burkill 1982). Other types of ciliates, including scuticociliates, didinids, halotrichs and hypotrichs are also present, especially in the more eutrophic waters, or associated with detrital particles (Siebruth et al. 1978; Siebruth 1979; Caron et al. 1982). Photosynthetic ciliates in the genus *Mesodinium* are also common members of the microzooplankton. Up to 40% of the microplankton ciliate fauna has been found to contain chloroplasts (Stoeckner et al. 1987).

A second group of protozoa of importance in the microzooplankton are the large unpigmented dinoflagellates. About half of the dinoflagellate species lack chloroplasts and are obligate heterotrophs. Naked (nonthecate) dinoflagellates, such as species of the genera *Oxyrrhis* and *Noctiluca*, are voracious phagotrophs which consume large amounts of phytoplankton. Heterotrophic dinoflagellates with thecae, such as species of the genera *Dinopsalis*, *Protoperidinium*, and *Dinophysis*, do not ingest particles but may be

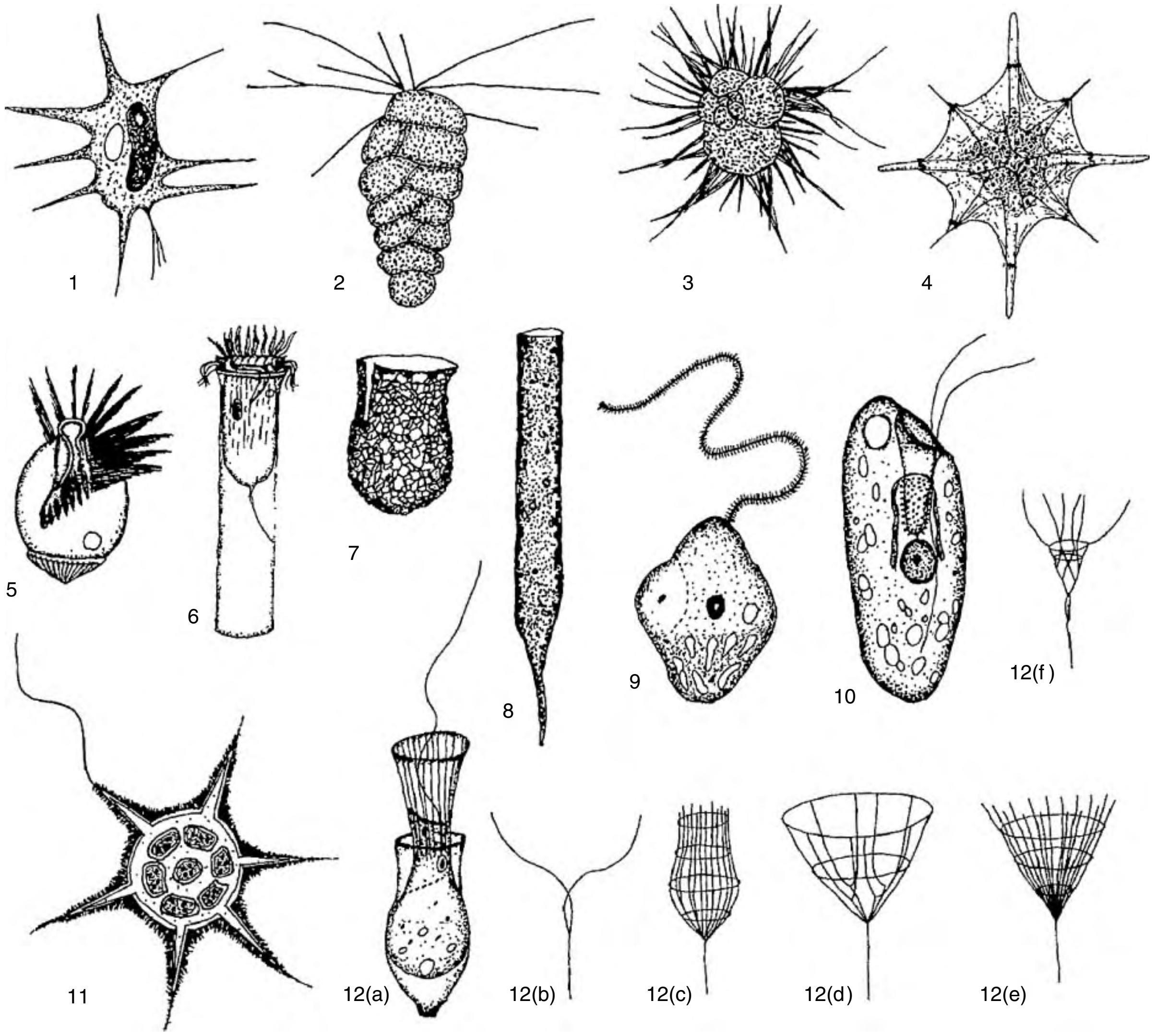


FIGURE 14.7 Some representative protozooplankton from the Southern Ocean. 1. *Chrysaoeba* sp. (Chrysamoebidae); 2. *Textularia* sp. (Forminifera); 3. *Globigerina* sp. (Foraminifera); 4. *Acanthostaurus* sp. Radiolarian); 5. *Strombidium* sp. (Oligotrich ciliate); 6. *Eutintinnus* sp. (Tintinnid with naked lorica); 7. *Tintinnopsis* sp. (Tintinnid lorica covered by sand grains); 8. *Tintinnopsis* sp. (Tintinnid with lorica covered by fine sediment); 9. *Oikomonas* sp. (Chrysophycean flagellate); 10. *Cryptomonas* sp. (Cryptomonad flagellate); 11. *Distephabus* sp. (Salicoflagellate); 12. (a–f) Choanoflagellates: (a) *Salpingoecia* sp. (showing the structure of the living animal); (b) *Bicosta spinifera* (this and the succeeding illustrations show the siliceous costal strip pattern of the lorica); (c) *Diaphanoeca multiannulata*; (d) *Paravicorbicula socialis*; (e) *Acanthooecopsis spiculifera*; (f) *Callicantha multispina*.

saprophagic. Pigmented dinoflagellates, like the pigmented ciliates, may be mixotrophic (Porter et al. 1985).

Amoeboid protozoa may be transiently abundant in pelagic ecosystems (Sorokin and Kogelschatz 1979). Common marine taxa include naked amoebae (order Amoebidae), Acantharia, heliozoans, foraminiferans and radiolarians (Siebruth 1979). Two studies of the distribution and feeding ecology of radiolarians in the Southern Ocean are those of Gowing (1989) and Nöthig and Gowing (1991). Gowing (1989) sampled phaeodarian radiolarians in autumn in the Weddel Sea and in the western Antarctic region in winter. Abundances of phaeodarians reached 3,132 m^3 and were similar to, or higher than, maximum abundance of polycystine radiolarians, foraminiferans and acantharians, and similar to or less than those of the heliozoan *Sticholonche* sp. In contrast to the more numerous flagellates and ciliates that were most abundant in the upper 100 m, phaeodinians were most abundant from 100 to 200 m and showed no distinct pattern related to the ice edge. Food vacuole contents showed that phaeodarians were omnivorous generalists, feeding on a variety of food ranging from bacteria to larger protozoa in both regions and seasons. Algal cells consumed in addition to diatoms and dinoflagellates included *Chlorella*-like cells and chrysophytes. Phaeodarians were consumed by the nonselective particle-feeding of the salp *Sapla thompsoni*. Thus, phaerodrians link the microbial food webs to macrozooplankton.

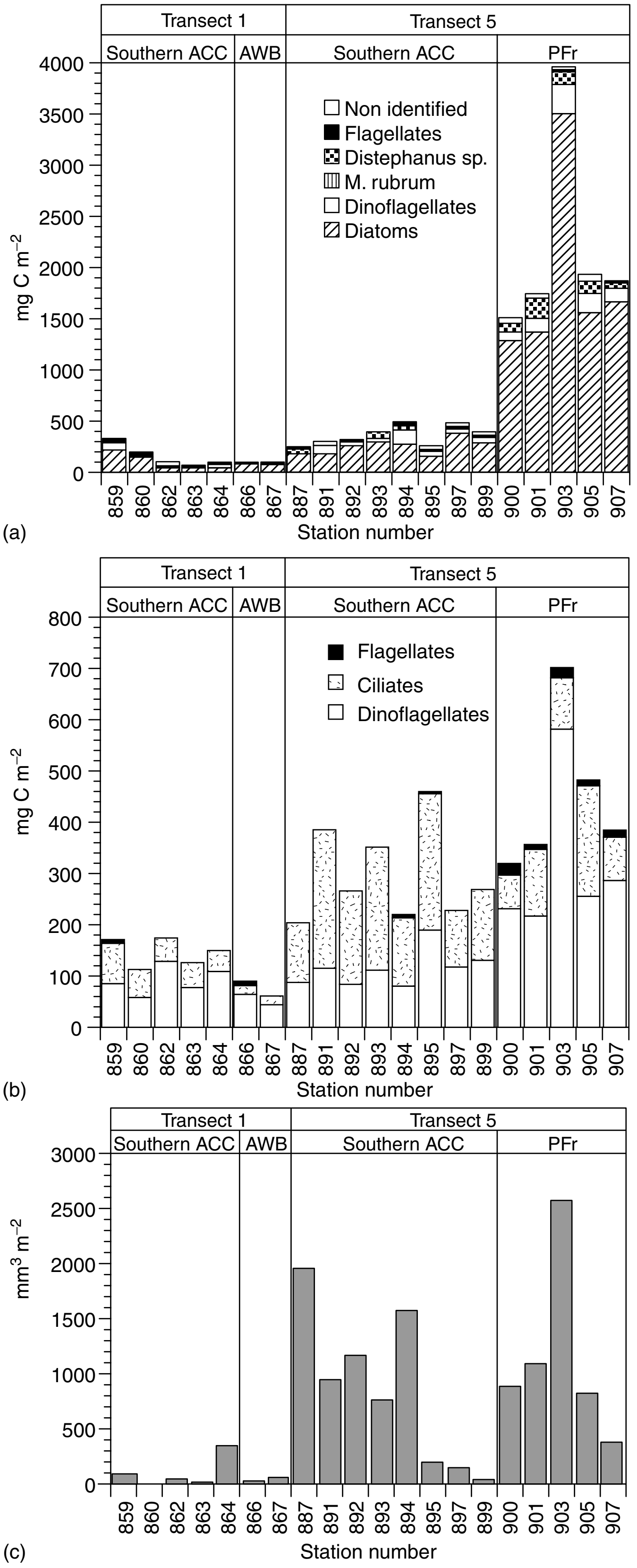


FIGURE 14.8 Distribution of protists and protozoan fecal pellets in the Weddell Sea. (a) Standing stock and composition of autotrophic protists in the meroplankton. Values integrated over the upper 100 m of the water column. (b) Protozoan fecal pellet volume integrated over the upper 100 m of the water column. (c) Standing stock of heterotrophic protists in the microplankton. Values integrated over theupper 100 m of the water column. (From Klaas, C., *Ber. Polarforsch.*, 253, 35–36, 45, 1997. With permission.)

Nöthig and Gowing (1991) investigated the late winter abundance and distribution of phaeodarians radiolarians in the Weddell Sea. They found that large (400 μm) phaeodarian radiolarians contributed more than 90% of the carbon in the large protozooplankton fraction; large protozooplankton represented approximately 38% of the total protozooplankton carbon during late winter under the close pack ice in the upper 250 m. Except for spumellarian and nassellarian radiolarians all other protozooplanktonn (foraminiferans, thecate dinoflagellates, tintinnids) were most abundant in the upper 250 m. The phaeodarians were trophic generalists and it was found that in the late winter they may have fed on organic aggregates.

Although only a small number of studies have been carried out on the protozoan communities of the Southern Ocean, the available data suggest that protozoa are as abundant as in other oceans (Silver et al. 1980; Buck and Garrison 1983; Hewes et al. 1983, 1985; Heinbokel and Coats 1985; Garrison and Buck 1989a, 1989b; Klaas 1997), and the abundance and productivity of their prey (e.g., Hasle 1969; Fay 1973; Fuhrman and Azam 1980; Hodgson et al. 1981; Azam et al. 1981, 1983) are as high in Antarctic waters as in other oceans. For fifteen stations in the Antarctic Coastal Current, the average biomass of the heterotrophic nanoflagellates was 14 μg C l^{-1} (range 7–60 μg C l^{-1}), about one half of that of the autotrophic nanoplankton (average 48 μg C l^{-1}; range 10–303 μg C l^{-1}) (Hewes et al. 1985). At five stations in the Scotia Sea, tintinnid biomass ranged from 0.24 to 3.54 μg C l^{-1} (mean 1.2 ± 1.3), and total ciliate biomass from 1.9 to 7.3 μg C l^{-1} (mean 3.6 ± 2.4). This can be compared to greater than 20 μm diatom biomass of 0.7–42.6 μg C l^{-1} (mean 13.9 ± 17.8). Tintinnid and total ciliate biomass was found to be proportional to that of the flagellates, consistent with the view that nanoflagellates are food for ciliates (Hewes et al. 1985). In two geographically distinct areas (deep Weddell Sea and shallow Scotia Ridge), it was found that ciliates could effectively control population growth of the dominant phytoplankton species, and that the less fed-upon phytoplankton species had much higher measured growth rates.

The relative proportions of autotrophic and heterotrophic biomass reported by Hewes et al. (1985) are consistent with other data from the Southern Ocean. von Brockel (1981) found that the protozooplankton biomass ranged from 8–110 mg C m^{-2} in the northern part of the Weddell Sea, to 325 mg C m^{-2} near South Georgia, and averaged 16% of the total "phytoplankton" biomass. Choanoflagellates are an especially abundant and conspicuous component of the Southern Ocean pelagic ecosystem. They have been reported from the waters of Terre Adelie (Deflandre 1960), the Weddell Sea (Silver et al. 1980; Buck 1981; Buck and Garrison 1983; Marchant 1985), Lutzow-Holm Bay (Takahashi 1981), Prydz Bay (Marchant 1985), from King George Island (Bo Chen 1994), and from the pack ice (65°50′ S; 155°16′ E) (Tanoue and Handa 1986). In the Weddell Sea choanoflagellates have been reported to average 3.6×10^5 cells l^{-1} (approximately 5 μg C m^{-2}) (Silver et al. 1980; Buck 1981; Buck and Garrison 1983; Marchant 1985), which compare with a total phytoplankton biomass of 1.9–3.3 μg C m^{-2} (Hewes et al. 1985). Hara et al. (1986) in their study of heterotrophic protists along 75°E in the Indian Ocean sector in the summer of 1983–1984 found that naked amoebae and choanoflagellates were dominant and that most groups were represented. In the Prydz Bay region Marchant (1985) found that choanoflagellates comprised 10–40% of the total nanoplankton. The recorded genera in open ocean samples were *Acanthecopsis*, *Bicosta*, *Calliacantha*, *Crinolina*, *Diaphanoeca*, *Parvicorbicula* and *Pleurasigma*. The overall mean abundance averaged $2.7 \pm 1.7 \times 10^4$ cells l^{-1} for the oceanic sites, but at the inshore stations in the summer, 10-fold higher cell concentrations were recorded. Marchant found that in addition to bacteria, the food of the choanoflagellates included nanoplanktonic autotrophs, particulate extracellular products, and cellular debris from larger phytoplankton. Tanoue and Hara (1986), in a study of the fecal pellets of *E. superba*, found that they contained abundant remains of choanoflagellates and estimated that they occupied 10% of the total plasma volume of the pellets.

Buck and Garrison (1988) investigated the distribution and abundance of choanoflagellates across the ice edge zone of the Weddell Sea in March. Choanoflagellate abundance varied over two orders of magnitude in the upper 100 m. The lowest abundances were recorded at the bottom of the water column under ice cover and the highest abundances occurred in the upper 30 m of open water. Abundances of total choanoflagellates and some individual species were correlated with primary and secondary biomass and production, indicating a response to gradients in potential food resources. This suggested that they are an important link between bacteria-sized particles and metazoan grazers.

Klaas (1997) investigated the distribution of protozooplankton in the Weddell Sea as part of the Southern Ocean-Joint Global ocean Flux Study (SO-JGOGS). The area surveyed extended from the ice edge in the southern Antarctic Circumpolar Current (ACC) at 38°51′ W to the ice-covered Weddell Gyre at 6°W, and between the ice edge in the southern ACC and the Polar Frontal region (PFr) along the 6° Meridian. Transect 1 started 57°S 38°51′ W and proceeded eastwards along the ice edge of the southern ACC and into the ice-covered ACC/Weddell Gyre Boundary (AWB) until the 6° W Meridian. Transect 5 was carried out along the 6° W Meridian, from the ice edge at 56° S across the open water of the southern ACC into the Pfr.

Figure 14.8a graphs the standing stock and composition of the autotrophic protists; Figure 14.8b graphs that of the heterotrophic protists in the microzooplankton; Figure 14.8c graphs the protozoan fecal pellet volume over the upper 100 m of the water column along the two transects. Along transect 1, chlorophyll *a* concentration increased eastward, ranging from 0.5 μg l^{-1} at 38°51′ W to less than 0.2 μg l^{-1} in the AWB. Along transect 5, chlorophyll *a* concentrations were low (~0.2 μg l^{-1}) at the southern ACC and increased in the PFr with a peak of 1.6 μg l^{-1} at 49°S. Carbon stocks of microphytoplankton were dominated by diatoms. During both transects, microphytoplankton standing stocks,

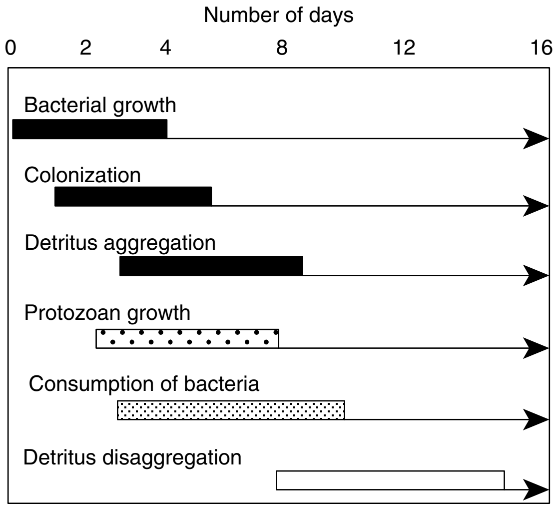


FIGURE 14.9 Schematic diagram of microbial succession during phytoplankton decomposition in sea water. (From Biddanda, B.A., Pomeroy, L.R., *Mar. Ecol. Prog. Ser.*, 42, 79, 1988. With permission.)

integrated over the upper 100 m of the water column, followed changes in chlorophyll *a* and ranged between 77 and 3964 mg C m^{-2} in the AWB and Pfr, respectively. Microzooplankton stocks ranged between 60 and 665 mg C m^{-2}.

The most comprehensive investigation to date of pelagic protozoa in the Southern Ocean is that of Garrison and Buck (1989a, 1989b) who sampled the protozooplankton from the open water across the ice edge zone into the pack ice in the Weddell Sea during the austral spring of 1983 and the austral autumn of 1986. The biomass and production of the organisms they found are summarized in Table 14.10. Protozooplankton biomass in the upper 100 m of the water column ranged from 55 to greater than 650 mg C m^{-2}. Heterotrophic flagellates were the dominant component of the protozooplankton, comprising 24–75% of the protozoan biomass during the austral spring and 62–79% of the biomass during the austral autumn. Naked (nonloricate) flagellates were usually dominant, followed by dinoflagellates and choanoflagellates. Although a variety of ciliates were present, nonsheathed oligotrichs (i.e., *Strombidium* spp.) dominated the ciliate biomass on both occasions. Tintinnids were rare during the spring cruise, but they made up a significant fraction of the ciliate biomass during the autumn cruise. Other protozoa (e.g., radiolarians and foraminiferans) were rare.

During the spring cruise (Garrison and Buck 1989b) integrated protozoan biomass in the upper 100 m ranged from 7% to 12% of the autotrophic biomass, while during the autumn it was slightly higher relative to the phytoplankton biomass, ranging from 15% to 23% of the autotrophic biomass at ice-covered stations and 9–24% in the open water (see Table 14.10). Bacterial biomass predominated over that of the protozoa at ice covered stations in both cruises, but the protozooplankton biomass reached up to twice that of the bacteria at some open water stations during the 1976 autumn cruise.

The biomass of the different protozoan groups was positively correlated with primary production, chlorophyll *a* concentrations and bacterial biomass and production. It appears that it was largely controlled by prey availability and production. Garrison and Buck (1989b) estimated the potential importance of the protozoa as consumers using

TABLE 14.10
Summary of Phytoplankton and Bacterial Production and Biomass and Protozooplankton and Macrozooplankton in the Weddell Sea During the Austral Spring 1983 and Austral Autumn 1986

	Production (mg C m^{-2} day^{-1})		Biomass (mg C m^{-2})			
Cruise	Phytoplankton	Bacteria	phytoplankton	Bacteria	Protozoo-plankton	Zooplankton
Austral spring 83						
Ice covered	225.6–345.6	11.8–42.6	566–1320	60.4–247.2	55.3–130.5	—
	(284.8)	(24.9)	(944.5)	(172.1)	(88.3)	
Ice edge to open water	242–758.4	105.7–154.3	1508–6449	351.2–512.6	199.5–494.9	—
	(516.8)	(138.0)	(4372.3)	(384.1)	(426.8)	
Austral autumn 86						
Ice covered	99.6–201.6	2.8–16.6	656–1076	197.4–272.7	101.7–252.6	45.8
	(161.1)	(11.5)	(819.7)	(228.9)	(165.8)	
Open water	80.8–2274.6	83.2–126.6	4121–7149	249.4–582.0	485.5–651.6	175.2–304.80
	(207.3)	(111.2)	(4989.5)	(394.9)	(551.9)	

Values integrated over 100 m. Means are given in brackets.

Source: Modified from Garrison, D. L., Buck, K. R., *Polar Biol.,* 10, 211–219, 1989a. With permission.

clearance rates in the literature. They used the lower range of clearance rates measured by Davis and Siebruth (1984) for flagellates feeding on bacteria (0.04–0.61 h^{-}1 individual^{-}1), and the lower rates measured by Lessard et al. (1987) for heterotrophic dinoflagellates (0.4–6.0), naked ciliates (0.8–2.0) and tintinnids (0.4–1.0 l h^{-1} individual^{-1}) feeding on H-thymidine-labelled cells in McMurdo Sound. They calculated that daily population clearance rates within the upper 50 m of the water column ranged from 11% of the water column (or prey biomass) at ice covered stations up to 55% at open water stations. Thymidine uptake measurements (Krempin 1985) indicated bacterial generation times of 5 to more than 10 days at ice-covered stations and 2.5 days in open-water stations, and Garrison and Buck (1989a, 1989b) concluded that it was not unreasonable to consider the protozoa as capable of utilizing most of the daily production.

In studies in McMurdo Sound, Lessard et al. (1987) concluded that the protozoa were primarily consuming bacteria. However, other studies (Heinbokel and Beeres 1979; Smetacek 1981a, 1981b; Jacobsen and Anderson 1986; Buck et al. 1987) have shown that ciliates, especially tintinnids, are capable of preying on larger diatoms. Lessard and Swift (1985) measured clearance rates of microalgae by protozoa in low latitudes of 1.0–200 l h^{-1} individual^{-1}. Using the lower ranges of clearance (1–2 l h^{-1} individual^{-1}), Garrison and Buck (1989b) estimated protozoan clearance rates in the Weddell Sea of 14% and 20% of the water column day^{-1} at ice covered stations and open water stations, respectively. They concluded that if the phytoplankton stock doubling times were 3 to >8 days, then the protozoan grazing rates could be sufficient to maintain the phytoplankton stocks at the low levels that they observed.

Bjørnsen and Kuparinen (1991) studied the growth and herbivory of heterotrophic dinoflagellates (*Gymnodinium* sp.) from the Weddell Sea and the Weddell/Scotia Confluence in 100 l microcosms. In microcosms exposed to 'dim' light PP was almost balanced by dinoflagellate grazing. They concluded that heterotrophic dinoflagellates may contribute significantly to the maintenance of the low phytoplankton biomass found in oceanic waters of the Southern Ocean.

Davidson and Marchant (1992) investigated concentration of protozoa during a *Phaeocystis*-dominated bloom in Prydz Bay. They found that microheterotroph abundance peaked during or immediately after the *Phaeocystis* bloom. Their peak coincided with very high concentrations of organic carbon, particularly DOC, which exceeded 100 mg l^{-1}, and low bacterial abundance. The principal ciliates were tintinnids and *Strombidium* spp. The tintinnid population was dominated by *Eutintinnus* spp., while *Codonellopsis* was occasionally observed. The coincidence of *Phaeocystis* and tintinnids has also been observed by Admiral and Venekamp (1986), who reported blooms of tintinnids immediately following *Phaeocystis* blooms. The choanophyte population was dominated by *Bicosta spinifera*, *Crinolina aperta*, *Calliacantha* spp. and *Parvicorbicula socialis*, the latter commonly in aggregates. The peak in choanoflagellates that coincided with the *Phaeocystis* bloom attained concentrations approximately of an order of magnitude higher than those reported for the Weddel Sea by Garrison and Buck (1991). The concentration of these species increased during the *Phaeocystis* bloom. Garrison and Buck (1989b) observed inoculation of the water column with protists from the ice biota. Such a release could have contributed significantly to the sudden increase in concentration of *Phaeocystis*, organic carbon and protozoa that was observed during the ice breakup. After the *Phaeocstis* peak, the concentration of microzooplankton, namely ciliates, heterotrophic dinoflagellates, and choanoflagellates, declined sharply.

Becquevort et al. (1992) investigated the dynamics of the protozoa in the Indian Sector of the Southern Ocean in early spring and late summer. Protozoan biomass, although low in absolute terms, contributed 30% and 20% to the total microbial biomass (bacteria, phytoplankton and protozoa) in early spring and late summer, respectively. Nanoprotozoa dominated the total protozoan biomass. Phototrophic flagellates dominated the Sea Ice Zone, whereas bacteria were predominant at the end of summer in the PFr and Coastal and Continental Shelf Zones. Phagotrophic flagellates were ingested by both nano- and microzooplankton. In contrast, bacteria were only ingested by nanoprotozoa. Protozoa controlled up to 90% of the daily bacterial production over the period of the study. The spring daily protozoan ingestion controlled more than 100% of the daily phototrophic flagellate production. This control was less strong at the end of the summer when protozoan grazing controlled 42% of the daily phototrophic flagellate production. Bacterioplankton production was always controlled by protozoa. Therefore the microbial loop (DOM–bacteria–protozoa) could not have been a significant carbon pathway to metazooplankton due to intermediate trophic levels. Assuming a protozoan growth yield of 0.38 and two trophic steps before being available for metazooplankton, only 3% of the primary production became available to metazooplankton when channeled via the microbial loop.

14.8 BACTERIA–PROTOZOA–POM INTERACTIONS

In oceanic water, POM is generally five times that of the phytoplankton biomass and ten times that of the DOM on a carbon basis (Cauwet 1981). The mineralizaton of this enormous quantity of organic matter is achieved by the activity of the heterotrophic bacteria (e.g., Williams 1975; Joint and Morris 1982). Because the bacterial biomass is kept at relatively low and constant levels (Anderson and Fenchel 1985), the importance of microprotozoan predator control of bacterial biomass has been emphasized (Sorokin 1981; Fenchel 1982c; Siebruth and Davis 1982; Garrison and Gowing 1992). In the following sections we will examine the microbial processes associated with the degradation of various categories of detritus such as phytoplankton derived detritus, amorphous aggregates, and copepod, euphausiid and salp fecal pellets.

14.8.1 PHYTOPLANKTON-DERIVED DETRITUS

Fukami et al. (1985a, 1985b) and Biddanda and Pomeroy (1988) have examined the pattern of microbial succession in the decomposition of detritus derived from phytoplankton. Biddanda (1985) and Biddanda and Pomeroy (1988) observed that during the early stages of decomposition of particulate detritus derived from phytoplankton (the 1- to 8-day period, when bacterial numbers colonizing the detritus increased rapidly), aggregation and formation of macroaggregates occurred (here termed *detrital–microbial complexes*), identical to those described by Hobbie et al. (1972), Wiebe and Pomeroy (1972), and Pomeroy and Diebel (1980) and others. During the first few days of the incubation of the detrital material in seawater, there appeared an increasing proportion of rod-shaped bacteria. These were then replaced by a mixed assemblage of cocci, spirilla, rods and filamentous forms (Biddanda 1985). Biddanda (1986) has shown that the aggregate formation that occurs is microbially mediated through the production of sticky extracellular mucopolysaccharides by the bacteria. These are sometimes referred to as microbial exopolymer secretions (Decho 1990) (see Section 14.8.4). Subsequently, mixed assemblages of bactivorous protozoa such as flagellates, ciliates, choanoflagellates and amoeboid forms colonize the aggregate and keep the bacterial numbers in check. The bacteria rapidly convert the POM in the detritus into DOM by means of exoenzymes and assimilate and respire it (Hoppe 1984). The combined activities of the bacteria and protozoa disrupt the structure of the aggregate and result in disaggregation. Figure 14.9 is a schematic diagram of this process of microbial succession.

14.8.2 AMORPHOUS AGGREGATES

In a study of amorphous aggregates (marine snow), Herndl and Peduzzi (1988) found dense assemblages of both autotrophic and heterotrophic microorganisms associated with the aggregates. The autotrophic component was enriched on the aggregates by a factor of up to 1,000. Both diatoms (mostly living) and dinoflagellates (mainly empty frustules) were found. Coccolithophorids were enriched on the aggregations with a mean enrichment factor of about 500. Heterotrophic bacterial density ranged from 1.94 to 64.95×10^8 cells g^{-1} (marine snow dry weight). HMF reached densities only one order of magnitude lower than those of the bacteria. In terms of biomass, expressed in carbon equivalents, bacteria reached 3–95% of the HMF biomass. In terms of cell concentration, HMF comprised between 32% and 71% of the total microflagellate (autotrophic and heterotrophic) community. On occasions large cyanobacteria populations (2.72×10^8 cells g^{-1} marine snow dry weight) were found. The settling of these amorphous aggregates accounts for much of the vertical transport of surface material to the deep oceans and the sea floor. There have been a limited number of investigations of marine snow in Antarctic waters. Marchant et al. (1996) investigate marine snow aggregates at Syowa Station. The abundance of these aggregates that were less than 1 mm differed widely, from less than $1.1\,l^{-1}$ to greater than $10\,l^{-1}$. Marine snow collected in mid-January consisted principally of diatoms and mucilage derived from the sea ice community while collections made at the end of that month contained much colonial *Phaeocystis*. The Enrichment Factor was around 10 for bacteria and varied from around 200 to over 600 for eukaryote protists.

14.8.3 FECAL PELLETS

Fecal pellets generally constitute the bulk of the material collected in sediment traps in the oceans. Although they may often account for only a small percentage of the suspended organic particles, they often constitute the bulk (over 90% in many instances) of the total vertical mass flux. Adult copepods can defecate from 25 to 200 pellets individual^{-1} day^{-1} (Marshall and Orr 1955; Smetacek 1980). The contents of such fecal pellets comprise three general categories: fragments of living organisms, pigments, and miscellaneous compounds. Fragments include diatoms, radiolarians, coccoliths, silicoflagellates, foraminiferans, whole cells and cell organelles and parts of prey such as copepods (Silver and Alldredge 1981). Pigments are generally degradation products of photosynthetic pigments.

Jacobsen and Azam (1984) found that freshly egested fecal pellets from the copepod *Calanus pacificus* were rapidly colonized by free-living bacteria. In 24 h, the bacteria covered 27% of the available area of the pellets. Bacterial concentrations reached 1×10^5 cells fecal pellet^{-1} (average volume of pellets 3×10^6 m^{-3}) after 14 h incubation. The number of bacteria associated with the fecal pellets then steadily declined to 1×10^4 cells fecal pellet^{-1} in 4 days. The sinking of the fecal pellets through a column of sea water increased the rate of initial colonization.

Euphausiid fecal pellets, especially those of *E. superba*, form a significant proportion of the POM in the waters of the Southern Ocean. However, their quantitative occurrence and microbial colonization have not been studied. Tanoue et al. (1982) and Tanoue and Hara (1986) have examined the species composition of the food particles in *E. superba* fecal pellets and have compared their chemical composition with that of their prey species (Table 14.11). In a transect from the Scotia Sea to the Weddell Sea, Cadee et al. (1992) found that free-floating sediment traps collected larger, more degraded krill fecal strings in the deeper (150 m) than in the 50 or 75 m traps. The smallest fecal strings were only present in the shallower traps. Sinking velocity of the smaller fecal strings was, as expected, much lower than for the larger ones, with a total range of 50–500 m day^{-1} for fecal strings volumes of 0.007–0.53 mm^{-3}. Krill feeding on diatoms produced larger strings with higher settling velocities than those feeding on nondiatom phytoplankton. Small fecal strings did not settle out of the upper mixed layer. In the uppermost layer (0–50 m) krill feces contributed an

TABLE 14.11
Comparison of the Characteristics of *Euphausia superba* Faecal Pellets and Cast Exoskeletons

	Cast Exoskeletons		Faecal Pellets[a]	
	Minimum	Maximum	Minimum	Maximum
Daily production (mg dry wt day^{-1})[b]	0.25[c]	0.63[d]	13.0	39.8
Sinking rates (m day^{-1})	52	1019	100	525
Organic matter (% of dry wt)	64.9	81.3	−8	−27
Carbon (% of dry wt)	12.3	22.9	5.0	13.7
Nitrogen (% of dry wt)	1.9	4.2	0.4	1.9
C:N ratio	5.1	8.0	8.4	14.6

[a] Data from Ross et al. (1985) and Clarke et al. (1988b).
[b] Based on 120 mg dry wt animal.
[c] 12 moults per year.
[d] 30 moults per year.

Source: Nicol, S., Stolf, M., *Deep-Sea Res.,* 36, 1753, 1989. With permission.

average of 130 µg dry wt m^{-3} (Gonzales 1992). There was an exponential decrease with depth, with a minimum of 0.6 µg dry wt m^{-3} in the 500–1,000 m stratum. Thus, it appears that krill fecal strings are largely retained and recycled in the upper 150 m of the water column. A factor in their breakdown could be their consumption by macrozooplankton (coprohexy, Lampitt et al. 1990; or coprochaly, Noji et al. 1991), leading to their disintegration. The roles of the macrozooplankton and that of bacterial and protozoan activity in the breakdown process needs to be elucidated.

Studies of salp fecal pellets have shown a similar pattern of utilization by bacteria and protozoa to that of copepod fecal pellets and amorphous aggregations. Salps which frequently occur in the waters of the Southern Ocean in dense swarms have high filtration and defecation rates (Madin 1982; Pomeroy et al. 1984; Andersen 1985). They filter water at very high rates (relative to other planktonic organisms) and remove minute particles (less than 5 µm) with high efficiency by means of a mucous feeding net (Alldredge and Madin 1982). The daily defecation rate of these pelagic organisms constitutes a large proportion of their body weight, and they produce large (greater than 1 mm) fecal pellets that sink rapidly (Madin 1982). Because of these characteristics, grazing by salps can be an important mechanism for the rapid vertical flux of particulate matter in the oceans (Madin 1982; Pomeroy et al. 1984; Andersen 1985).

The sinking rate of salp fecal pellets depends on the amount and kind of particulates collected and ingested. When food is abundant, salps produce compact feces which sink rapidly (Madin 1982; Pomeroy et al. 1984). Small salps produce a fecal ribbon which breaks into segments and smaller fragments after release (Pomeroy and Deibel 1980). Caron et al. (1989) found that in large pellets, little microbial degradation occurred due to their cohesive nature and rapid sinking rate.

14.8.4 MICROBIAL EXOPOLYMER SECRETIONS

Microbial expolymers are high molecular weight mucous secretions of bacteria and microalgae (Geesey 1982; Decho 1990). They range from tight capsules which closely surround cells to the loose-slime matrix associated with aggregates, sediment, detritus and other surfaces. They are largely polysaccharide in composition and can exist in dissolved and particulate form. Due to their physical properties, expolymers are highly absorptive and rapidly sequester DOM. The ingestion of this exopolymer-bound DOM could represent a means whereby DOM could directly reach higher trophic levels (HTL) (Figure 14.10).

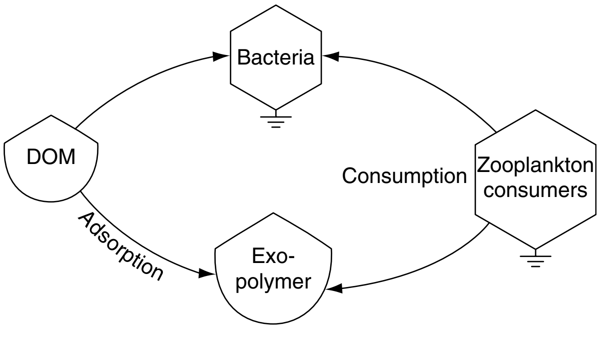


FIGURE 14.10 Diagram showing the conceptual role of microbial expolymers in pelagic food webs. DOM is absorbed and concentrated on the expolymers and can then be directly transferred to consumer animals via ingestion of the expolymers by the passing microbial metabolism of DOM. (Modified from Decho, A.W., *Oceanogr. Mar. Biol. Annu. Rev.*, 28, 73, 1990. With permission.)

14.9 INTERACTIONS OF BACTIVOROUS GAZERS AND HETEROTROPHIC BACTERIA

As discussed above, biodegradable organic material in the sea is supplied from a variety of sources, with the bulk being mostly supplied by excretion and lysis of phytoplankton in the form of macromolecular polymers (Billen 1984). These cannot be directly taken up by bacteria and have first to be hydrolyzed through the action of coenzymes and converted to monomeric substances. Exoenzymatic hydrolysis therefore constitutes the limiting step in the whole process of organic matter utilization (Sommerville and Billen 1983). On the other hand, the uptake of direct monomeric substrates is very rapid, so that their concentration is maintained at a steady low value (Billen et al. 1980; Billen 1984; Linley and Newell 1984). Once taken up by the bacteria, direct substrates can either be catabolized and respired or used for biosynthesis. The bacterial biomass that is formed is subject to mortality, caused either by grazing or virus-induced lysis (Servais et al. 1985).

Figure 14.11 illustrates the close coupling that occurs between phytoplankton production during a *Phaeocystis* bloom and bacterial activity and production (Billen and Fontigny 1987). Three measures of bacterial activity—exoprotolytic activity (Figure 14.12b), direct substrate utilization (Figure 14.12c) and bacterial production (Figure 14.12d)—show a distinct two-peak pattern which corresponds to the two peaks of the phytoplankton biomass (Figure 14.12a). The data demonstrate a rapid response of the bacterioplankton to the production of organic matter by the phytoplankton. Fuhrman (1987) confirmed this in a study of the release and uptake of DFAAs. He found that the release and uptake of DFAAs were tightly coupled, as evidenced by direct measurements, as well as by rapid turnover.

Williams (1981), on the basis of the rather limited data available at that time, suggested that bacterial production averaged about 20% of primary production. Cole et al. (1988) have reviewed the available data since then. For all plankton systems analyzed, bacterial production ranged from 0.4 to 150 μg C l^{-1} day^{-1} and averaged 20% (median 16%) of planktonic primary production. On an aerial basis for the entire water column, bacterial production ranged from 118 to 2439 mg C m^{-2} day^{-1} and averaged 30% (median 27%) of the water column primary production. Cole et al. (1988) concluded that: (1) bacterial production both in the water column and in the sediments is broadly predictable; and (2) bacterial production is a large component of total secondary

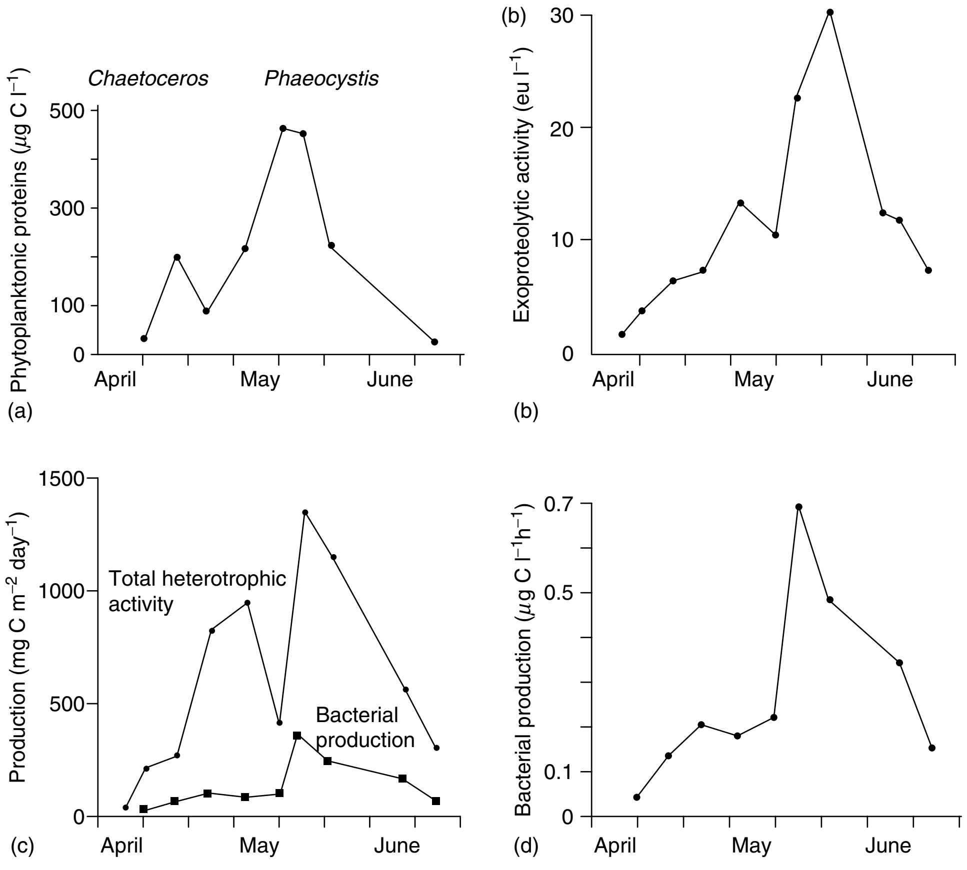


FIGURE 14.11 Seasonal variation in (a) proteolytic phytoplankton biomass; (b) exproteolytic activity; (c) direct substrate utilization (monosaccharides + amino acids + glycolate utilization); and (d) bacterial production, showing the close coupling between phytoplankton production during a *Phaeocystis* bloom. (From Billen, G., Fontigny, A., *Mar. Ecol. Prog. Ser.*, 37, 249, 1987. With permission.)

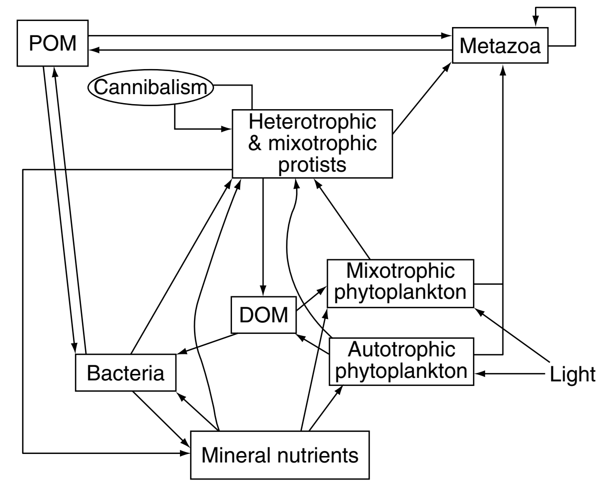


FIGURE 14.12 Representation of the major pathways particulate organic matter; DOM: dissolved organic matter. (From Davidson, K., *Mar. Ecol. Prog. Ser.*, 145, 280, 1996. With permission.)

production in planktonic ecosystems, and is roughly twice that of the macrozooplankton.

Recent information, reviewed in Azam et al. (1983), Ducklow (1983), Siebruth (1984), and Taylor et al. (1985), suggests that bactivory (ingestion of bacteria) by microzooplankton (20–200 μm in diameter, primarily ciliated protozoa and micrometazoa) and nanozooplankton (2–20 μm in diameter, primarily heterotrophic mastigophora and ciliated protozoa), may regulate standing stocks, species composition, and metabolic activity of bacterioplankton. As we have seen, planktonic protozoa represent a diverse and ubiquitous component of the water column biota, contributing a biomass of 1–16,000 μg C l^{-1} (Taylor 1982). A number of investigators (e.g., Sorokin 1981; Fenchel 1982c; Siebruth 1982; Azam et al. 1983) have shown that HMF in the size range of 3–10 μm are effective bactivores, capable of filtering 12– 67% of the water column per day. These are principally choanoflagellates and colorless chrysomonads. However, while these microflagellates are conspicuous grazers on bacteria, most are omnivorous, grazing also on wide assortment of phytoplankton, especially the smaller pico- and nanophytoplankton (Goldman and Caron 1985). The densities of HMF on microscopic detrital aggregates can exceed their densities in the surrounding water by as much as four orders of magnitude (Caron et al. 1982, 1986). Thus protists, with and without chloroplasts, can occupy overlapping roles; therefore, the two groups need to be studied together to give true estimates of predation on bacteria (Estep et al. 1986).

The grazing of greater than 20 μm ciliates, particularly tinitinnids, on nanoplankton (2–20 μm) phytoplankton has been established as a significant pathway in the marine planktonic food web (Verity 1986). Recent studies also suggest that pelagic ciliates can consume and grow on picoplankton (less than 2 μm) cells, i.e., tiny eucaryote algae, cyanobacteria and bacteria (Sherr and Sherr 1984; Rassoulzadegan et al. 1988; Sherr et al. 1989). Sherr et al. (1989) estimated that it would be possible for a choreotrich (less than 15 μm in size) to grow at a rate of about 0.5 day^{-1} on an exclusive diet of bacteria at a concentration of 10^6 bacteria mL^{-1}, but that larger ciliates would obtain less than 15% of their food rations as bacteria.

14.10 THE MICROBIAL LOOP

The classical paradigm concerning marine planktonic food webs that persisted until the mid 1970s has been summarized by Steele (1974) in his book *The Structure of Marine Ecosystems*: "The phytoplankton of the open sea is eaten nearly as fast as it is produced so that effectively all plant production goes through herbivores." Coincidentally, at the same time Pomeroy (1974) proposed a new paradigm that included an alternative energy-flow pathway known as the microbial loop. This paradigm integrated emerging evidence that much of the organic matter synthesized by the primary producers entered an extracellular pool as algal exudates and losses during feeding and excretion by metzoans and was utilized by heterotrophic microorganisms, principally bacteria. As discussed above, other organisms such as microflagellates and ciliates also contribute to this extracellular organic pool (see Table 14.1).

14.10.1 THE ELABORATION OF THE MICROBIAL LOOP CONCEPT

In a landmark review, Williams (1981) attempted to reconcile the classical view of a herbivore dominated food chain with the observations of high growth yields (50–80%) for bacteria based on glucose and amino acid substrates (Crawford et al. 1974; Williams et al. 1976), and concluded that at least 50–60% of the primary production should pass through the planktonic heterotrophs before it is mineralized. However, Williams (1981) stressed that calculations on the proportion of the primary production entering the bacterioplankton are very sensitive to estimates of the proportion of primary production exuded as DOC, as it has been shown that while the net growth yield on labile soluble substrates may be high (up to 85%), the net growth yields on particulate matter is much lower (15–19%) (Linley and Newell 1984).

Azam et al. (1983) further elaborated the concept of the microbial loop. Their hypothesis envisaged primarily phytoplankton derived DOM supporting bacterioplankton production, a part of which may be transferred to the traditional grazing food chain via bacterioplankton, nanoflagellate and ciliate links. Bacteria (0.3–1 μm) utilize the DOM. When sufficient DOM is available for bacterial growth, their populations generally do not exceed about 3×10^{-3} cells mL^{-1} as they are preyed upon primarily by heterotrophic nanoflagellates and small ciliates (Wright and Coffin 1984; Rassolzadegan and Sheldon 1986). The HMF may reach densities of 5×10^6 cells mL^{-1}. Figure 14.12 diagrams the major pathways in the microbial loop. Bacteria and phytoplankton compete for mineral nutrients and are preyed upon by a variety of protozoa which are themselves ingested by mesozooplankton predators. Bacteria utilize (DOM; a large fraction of which is released by phytoplankton) and compete with the phytoplankton for mineral nutrients. The marine consumers of the bacteria are small (less than 5 μm) nonpigmented flagellates (Capriulo et al. 1991). Other protists also prey on bacteria.

Figure 14.13 presents a schematic model that illustrates the roles of bacteria and other microbes in the water column. Azam et al.'s (1983) model was based on the Sheldon et al. (1972) particle size model, the main feature of which is that organisms tend to utilize particles one order of magnitude smaller than themselves. However, this may not be strictly true. Goldman and Caron (1985) found that the phagotrophic

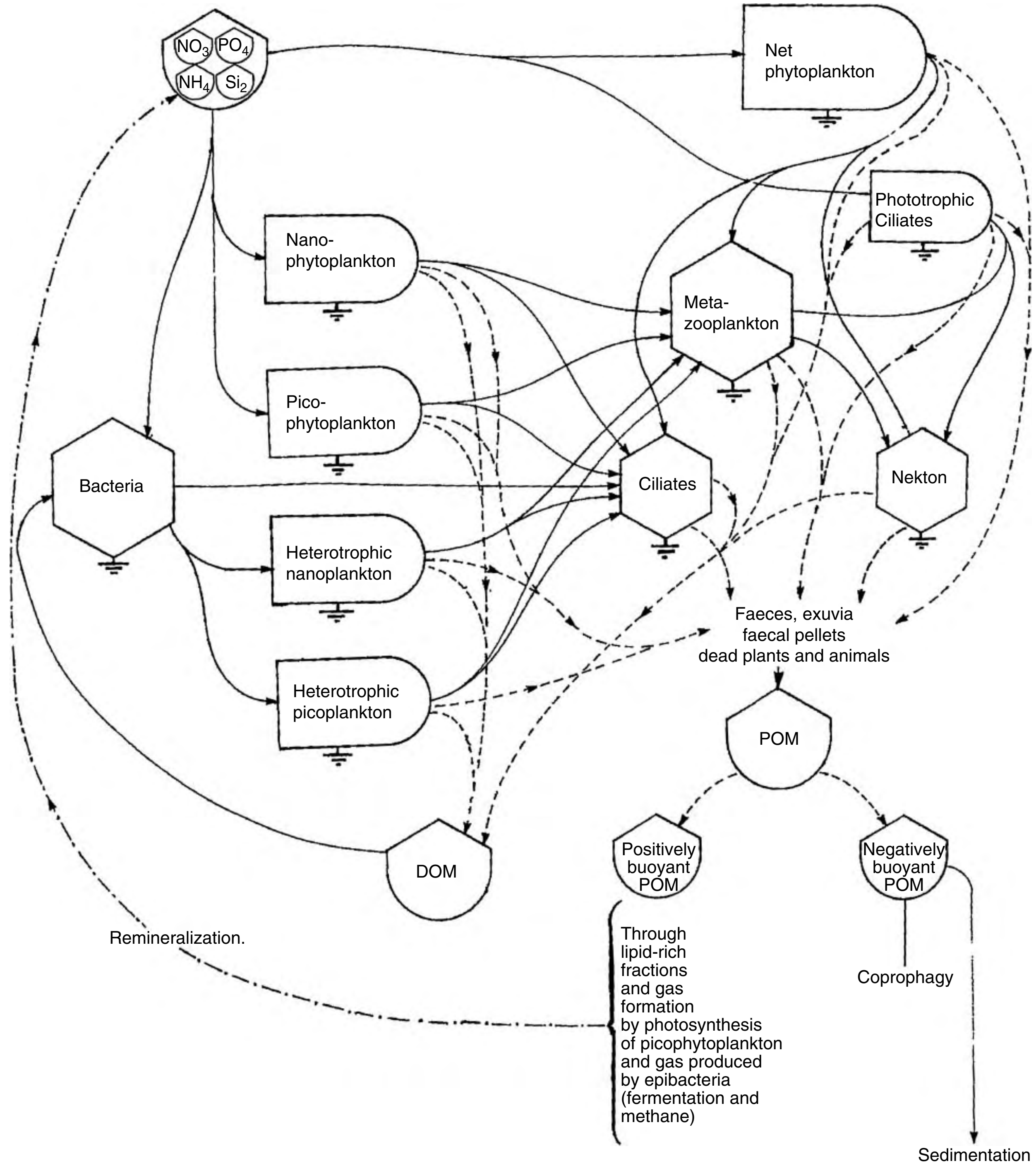


FIGURE 14.13 Conceptual model illustrating the pathways of energy flow from photoautotrophs and bacteria to consumers in the pelagic food web.

marine microflagellate *Paraphysomonas imperfecta* grazed on a wide assortment of phytoplankton species as well as on bacteria, and that it also resorted to cannibalism when food was in short supply. Cell ratios of acceptable prey varied 400-fold from 0.5 μm^{-3} bacterial cells to 200 μm^{-3} cells of the chlorophyte *Dunaliella*. Goldman and Caron (1985) concluded that omnivorous behavior may be a common feeding strategy amongst heterotrophic protozoa and that the size ratios between predator and prey at the microbial level may not be rigid, and may in fact approach 1.

The situation is further complicated by the fact that chloroplast-containing nanoflagellates and ciliates have been observed to prey on bacteria. Estrep et al. (1986) found that nanoflagellate chrysophytes could be maintained for extended periods on bacteria. Current in situ estimates of nanoflagellate predation on bacteria assume that only flagellates without chloroplasts are predatory (Fenchel 1982c; Sherr and Sherr 1983; Davis and Siebruth 1984). However, it is clear that protists with and without chloroplasts can occupy overlapping roles. Thus, if chloroplast containing nanoflagellates consume bacteria, then the transfer of material from bacteria to protists may be greater than currently estimated.

Karl (1993) has presented a diagrammatic model of the role of bacteria in the microbial loop (Figure 14.14). The bacteria rely on the availability of utilizable low- and high-molecular-weight dissolved organic matter (LMW DOM and HWM DOM) for their carbon and energy demands. The molecular composition of these available carbon pools determines the production rate and growth yield of the bacteria. HMW DOM, which cannot be used directly, is made available by the action of attached (periplasmic) cell-freeenzymatic activities or by chemical hydrolysis. Dissolved nutrients including N, P, and S, and a variety of trace elements, are also required for balanced growth. Depending on the molecular composition of the substrates utilized, N may be regenerated. Bacterial biomass is removed by the combined effects of protozooplankton grazing (PROTO) and HTL, DEATH, and viral infection (VIRUS), all of which return carbon and energy to both the LMW and HMW DOM POOLS.

Clarke and Leakey (1996) have given an account of the composition and seasonal cycle of the microbial community at a near-shore, shallow-water station at Signy Island. Figure 14.15 illustrates the biomass of diatoms, bacteria, dinoflagellates and all other flagellates. It can be seen that they all peak in the spring-summer period (November–March). The magnitude of the increase in the summer over the winter maximum is shown in Table 14.12. The summer peak of primary production was dominated by large diatoms. Peak concentrations of nanoplankton, predominantly from flagellates, were much lower, but the bloom lasted longer and the winter biomass of the nanoplankton was higher than that of the microplankton. Populations of all taxa (Table 14.12) were low under the winter sea ice; naked flagellate and dinoflagellates averaged 10^3–10^4 cells L^{-1} and populations of ciliates were even lower (10^2 cells L^{-1}). In summer, numbers increased dramatically, and peak numbers of all taxa except aloricate choreotrichs exceeded 1500 cells L^{-1}. These populations are similar to those reported elsewhere in the Southern Ocean (Buck et al. 1992). Broadly similar bacterial abundance have been reported in Antarctic near-shore waters from McMurdo Sound (Gustafson et al. 1990; Rivkin et al. 1989), Prydz Bay (Gibson et al. 1990; Davidson and Marchant 1992), and offshore from Adelie Land (Delille 1993) and King George Island (Vosjan and Olanczul-Neyman 1991).

14.10.2 THE ROLE OF DETRITAL AGGREGATES

As discussed in Section 14.2.2, the important role of aggregates of various sizes in marine planktonic

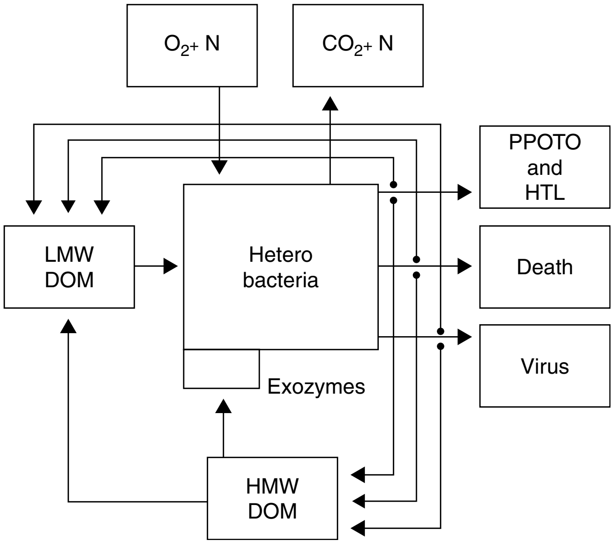


FIGURE 14.14 Schematic diagram of the role of heterotrophic bacteria (HETERO BACTERIA) in the Antarctic marine microbial loop. In the ecosystem model, bacteria rely upon the availability of "utilizable" low- and high-molecular-weight dissolved organic matter (LMW DOM and HMW DOM) for their carbon and energy demands. The molecular composition of these available carbon pools determines the production rate, growth yield, and end-product formation. In the absence of available substrate, bacteria exhibit a characteristic starvation-survival response. HMW DOM, which cannot be used directly, is made available by the action of attached (periplasmic) or cell-free exoenzymatic activities or by chemical hydrolysis (e.g., polysaccharides$+H_2O$ monosaccharides). During metabolism, heterotrophic bacteria consume oxygen (O_2) and produce carbon dioxide (CO_2). The stoichiometry of O_2/CO_2 dynamics is again determined by the DOM pool composition. Dissolved nutrients (N), including N, P, S, and a variety of trace elements, are also required for balanced growth. Depending upon the molecular composition of the substrate utilized, N may also be regenerated. Bacteria biomass is removed by the combined effects of grazing by protozoan (PROTO) and higher trophic levels (HTL), death and autolysis (DEATH), and viral infection (VIRUS), all of which return energy to both the LMW and HMW DOM pools. (From Kark, D.M., *Antarctic Microbiology*, Friedman, E.L., Ed., Wiley-Liss, New York, 16, 1993. With permission.)

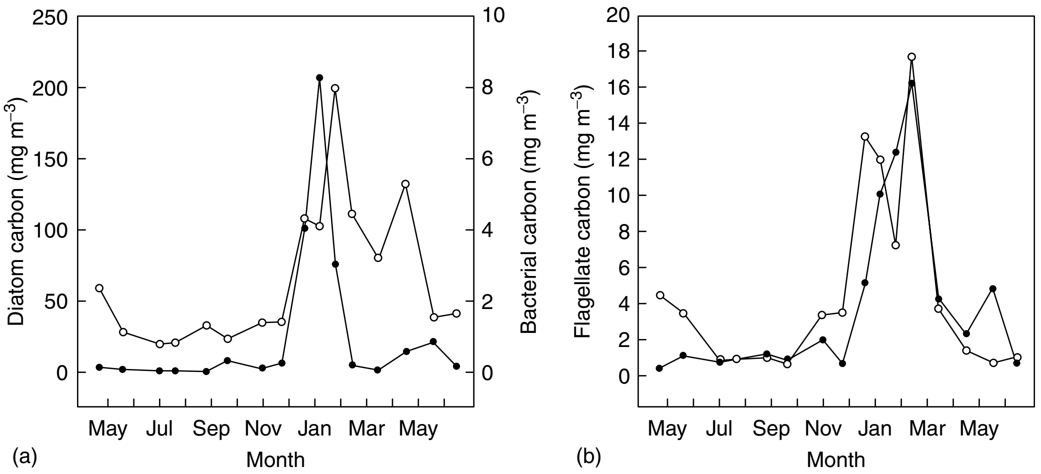


FIGURE 14.15 Biomass of selected microbial taxa in the vicinity of Signy Island. All data for the period April 1990–August 1991. All data expressed as carbon (mg m^{-3}). A. Diatoms (●) and bacteria (○). B. Dinoflagellates (●) and all other flagellates (○). Note displacement of vertical axis for clarity and differing vertical scales for diatoms and bacteria. (From Clarke, A., Leakey, R.J., *Limnol. Oceanogr.*, 41, 1287, 1996. With permission.)

ecosystems is increasingly being recognized (Newell et al. 1981; Goldman 1984a, 1984b; Biddanda 1985, 1986; Biddanda and Pomeroy 1988). The rapid turnover of microbial populations in oligotrophic waters has inspired several authors to consider whether microbial populations occur in some sort of structured nutrient environment, or in macroaggregates (Goldman 1984b). It has also been hypothesized that bacteria and microzooplankton may even establish a zone of enriched nutrients around the aggregates (Hoppe 1981), and that the microorganisms maximize their position within such nutrient fields, leading to the formation of microbial clusters in the vicinity of such aggregates (Azam and Ammerman 1984). Biddanda and Pomeroy (1988) have called this microenvironment the detritosphere, which is similar to the phycosphere concept used by Bell and Mitchell (1972) to describe the environment of bacteria associated with live phytoplankton cells exuding soluble organic materials.

Biddanda and Pomeroy (1988) have demonstrated that regardless of its source, organic detritus suspended in sea water develops a remarkably similar and well defined sequence of microbial succession. They proposed that there is a regular process of aggregation of organic matter, microbial colonization and utilization, followed by a process of aggregate disaggregation (Figure 14.16). Depending on their density and the vertical density structure of the water column, the aggregates sink at varying rates. Some will be lost from the photic zone and some will sediment to the bottom. Turbidity currents and upwelling, and in shallow water, wave action, will result in resuspension of the aggregates. This model is driven by inputs from primary and secondary production. The loss of detritus and biomass by respiration and sinking is compensated through new primary and secondary production inputs as well by resuspension. Thus, the fate of detritus in the water column is seen as aggregation–disaggregation sequences in time and space.

In his experiments on phytoplankton (diatoms)-derived detritus, Biddanda (1986) found that about 30–35% of the carbon in the detritus is mineralized (34–39% is utilized) by the microbial community in 4 days, whereas 63% is mineralized within 16 days. The period of rapid detritus utilization coincides with the period of detritus aggradation (Biddanda and Pomeroy 1988). The rate of utilization decreases steadily

TABLE 14.12
Composition of the Water Column Microbial Community in Winter and Summer, Borge Bay

	Winter		Summer	
Taxon	Biomass	%	Biomass	%
Bacteria	0.74	19.6	5.53	4.1
Diatoms	0.74	19.6	95.71	71.1
Dinoflagellates	0.71	18.8	12.94	9.6
Other flagellates	0.79	21.0	12.35	9.2
Tintinnid ciliates	0.0	0.0	5.35	4.0
Aloricate ciliates	0.79	2.0	2.73	2.0
Total	3.77		134.61	

Winter data are for sample taken on 30 June 1990; summer data are mean of samples taken on 5 January, 23 January, and 10 February 1991. All data given as carbon biomass (mg m^{-3}).

Source: From Clarke, A., Leakey, R.J., *Limnol. Oceanogr.*, 41, 1281–1294, 1996. With permission.

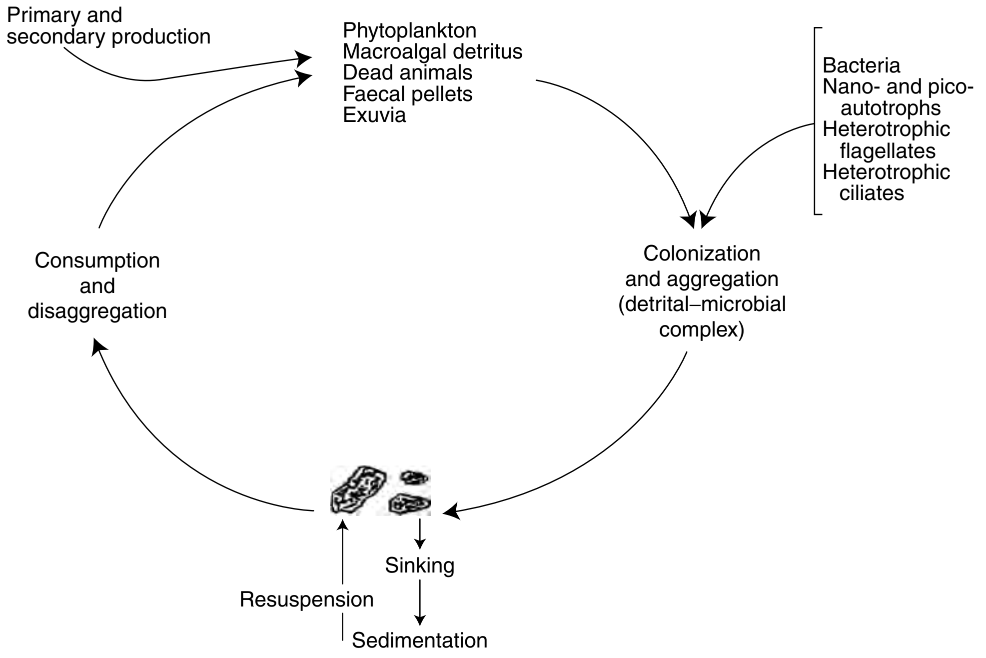


FIGURE 14.16 Schematic diagram of microbial succession during phytoplankton decomposition in sea water. (From Biddanda, B.A., Pomeroy, L.R., *Mar. Ecol. Prog. Ser.*, 79–88, 1988. With permission.)

as the more refractive compounds in the particulate and dissolved pools are gradually mineralized or incorporated by the microbial community. Heterotrophic bacteria can actually only utilize dissolved compounds, and therefore must colonize particles and convert them into dissolved substances. It is thus difficult to distinguish between particle-attached and free-living bacteria.

In the Southern Ocean pelagic ecosystem, episodic events such as the collapse of phytoplankton blooms, the production of large quantities of feces by feeding swarms of krill, and the release of the sea ice microalgae and detritus upon the melting of the ice, present sudden and large available detrital resources to the heterotrophic microbial communities. In their study of the factors influencing the fate of sea ice microalgae released from melting sea ice in the northern Weddell Sea, Riebesell et al. (1991) found that there was a high propensity to form aggregates, the sinking rates of which were three orders of magnitude higher than those of dispersed sea ice microalgae. They suggested that the sea ice microalgae released from the melting ice were subject to rapid sedimentation. If an average residence time in the mixed layer of 30 days is assumed, the results of Biddanda's (1986) studies indicate that because 25%, 32%, and 63% of the organic matter in the detritus is mineralized by 2, 4, and 16 days, respectively, there is ample opportunity for a rapid recycling of detritus-bound carbon.

As we have seen, aggregates become rapidly colonized by bacteria, microalgae and heterotrophic flagellates and ciliates. Small flagellates have high swimming speeds relative to their size (Throndsen 1973; Fenchel 1982a), and hence have the potential to migrate among the aggregates even though the density of such aggregates may be low. Motility in marine bacteria is common and swimming speeds of up to 20–40 $\mu m\ s^{-1}$ have been observed (Azam and Ammerman 1984). In addition, chemotaxis may be a characteristic of the bacteria. Thus, although the percentage of microbe-bound microbes has been used in the past as an indicator of the degree to which aggregates contribute to microbial interactions in the pelagic environment, Azam and Hodgson (1981) suggest that this may give a false picture of particle-microbe dynamics.

14.10.3 CONSUMPTION OF BACTERIA, DETRITUS, AND PROTOZOA BY MARINE ZOOPLANKTON

As we have seen, detritus dominates the suspended organic particulate matter in the sea. This greater abundance of detritus compared with estimates of phytoplankton standing stocks has promoted speculation on the importance of detritus and its associated microbial community as a food source for pelagic zooplankton (Marshall and Orr 1955; Heinle and Flemer 1975). The importance of bacterioplankton (comprising 10–40% of the phytoplankton carbon biomass) also has been the subject of much controversy. Marine larvaceans (Williams 1981; Ducklow 1983), salps (Mullin 1983), calanoid copepods (*Eurytemora* sp.; Boak and Golder 1983) and *Euclanus* and *Eucalanus*; Sorokin 1981) have been found to ingest free living bacteria, but with less efficiency than larger ($>3.0\ \mu m$) particles.

In a study of the carbon budget of the copepod *Eurytemora affinis* (Heinle and Flemer 1975; Heinle et al. 1977), it was concluded that detritus must be a food supply for the copepods. The hypothesis was tested by rearing copepods on standardized diets of detritus, with and without microorganisms, using copepods grown on algal diets as controls. The conclusion was that copepods could grow and produce eggs on a diet of detritus when microorganisms were present, or on a mixed diet of microalgae and detritus, but that they did not thrive on a diet of detritus that had been autoclaved to control the microorganisms. The results further suggested that they could also do very well on a diet of ciliates. When fed on a protozoan infusion, egg production was as high, if not higher, than for copepods fed on algal cultures. Sorokin's work on the consumption of bacteria by zooplankton supports the above conclusions. He found that the appendicularian *Oikpleura* could take up to 100% of its body weight a day from bacteria, and that the cladoceran *Penilla* could take about 50% at an assimilation efficiency of about 35%. He also found a small but significant uptake of bacterial biomass by the copepods *Euclalnus* and *Paracalanus*, and suggested that they were able to filter from the water 20–30% of the bacteria present in aggregates.

One of the problems in determining the extent to which protozoa provide energy for zooplankton is that they are predominantly soft-bodied and readily digestible, so that they do not leave recognizable remains in the stomach contents and fecal pellets. Tanoue and Hara (1986) found many costal strips of the choanoflagellate *P. socialis* in *E. superba* fecal pellets. Because of their high abundance in the pelagic waters of the Southern Ocean, their known feeding habits (bacteria, picoplankton such as cyanobacteria), Tanoue and Hara (1986) postulated a food chain nonliving particulate matter and dissolved organics bacteria → choanoflagellates → krill → vertebrate krill consumers.

The possible pathways which may be involved in the utilization of bacterioplankton and detritus with its associated microorganisms (the detritalmicrobial complex) are shown in Figure 14.17. The consumption by zooplankton of bacterial aggregates may be of greater importance than single bacterial cells because coarse filterers such as copepods are not efficient at ingesting very small particles. The relative importance of the various possible routes is unknown at this time for the Southern Ocean. However, the combination of alternative pathways may have an important stabilizing effect on the pelagic food webs.

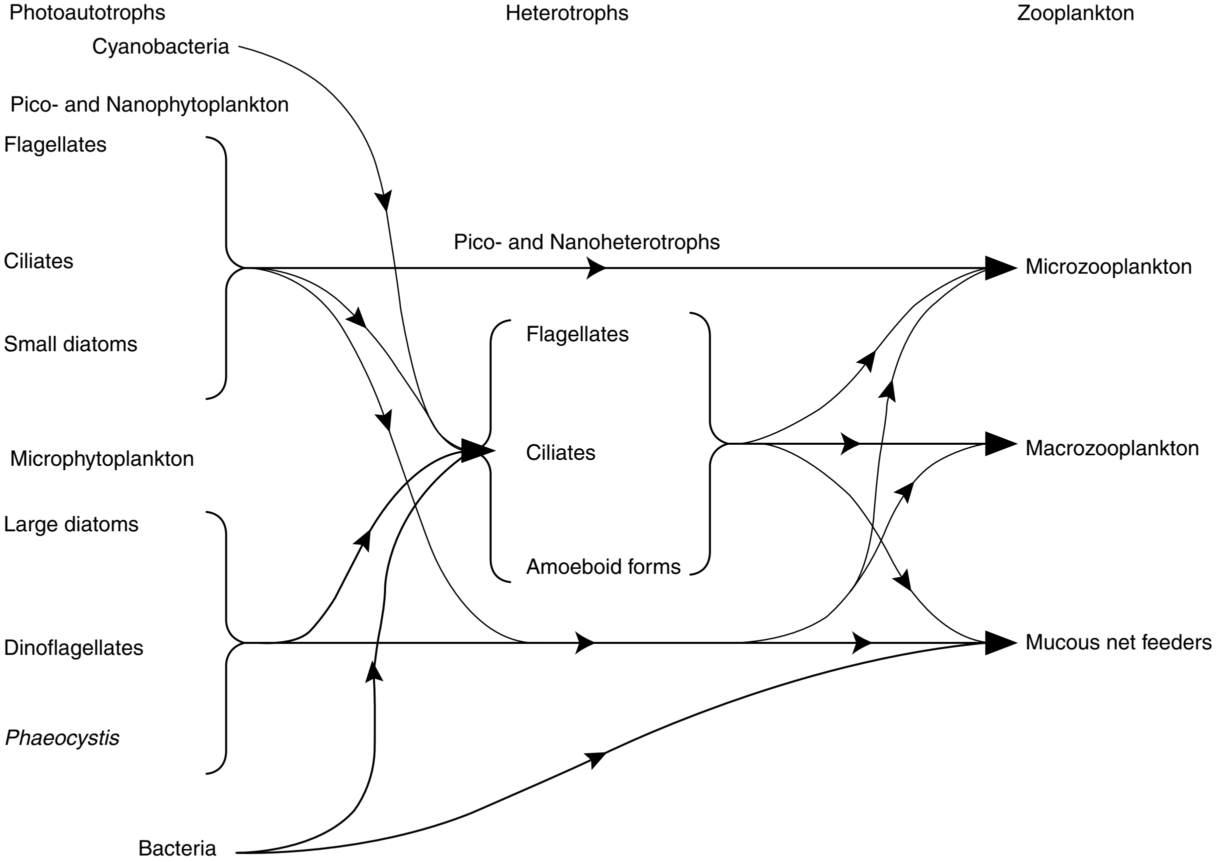


FIGURE 14.17 Conceptual model illustrating the consumption of photoautotrophs and bacteria by consumers in the pelagic food web. Possible food chains involving bacteria, protozoa, and zooplankton are: Cyanobacteria → Flagellates → Zooplankton; Cyanobacteria → Flagellates → Ciliates → Zooplankton; Bacteria → Flagellates → Zooplankton; Bacteria → Ciliates → Zooplankton; Bacteria → Flagellates → Ciliates → Zooplankton; Bacteria → Amoeboid forms → Zooplankton.

14.11 NUTRIENT CYCLING

14.11.1 INTRODUCTION

In aquatic systems, nutrients are a major limiting factor for microbial production. Among the most important nutrients are the autotrophic nutrients which serve as raw materials for primary production. The nutrients required for plant production are numerous, including C, N, P, Si, S, K, Mg, Na, Ca, Fe, Mn, Zn, B, Cu, and V and the vitamins thiamin, cyanobalamin, and biotin. Of these the first four are the ones most heavily used for plant growth, although silicon is only required by diatoms. Over the past few decades a considerable amount of research has been carried out on nutrient cycling in the Southern Ocean (e.g., Holm-Hansen et al. 1977; Biggs 1982; Ronner et al. 1983; Holm-Hansen 1985; Koike et al. 1986; Karl 1993).

14.11.2 "NEW" AND "REGENERATED" NITROGEN

In the oceans generally a spring bloom of phytoplankton is initiated by both increasing isolation and a decreased mixing depth. This then declines after the major source of nitrogen—nitrate injected into the mixed layer from below in winter—is utilized. The paradigm of "new" (nitrogen derived from upwelling) and "regenerated" (nitrogen in the form of ammonia produced by bacterial transformation and excretion by protozooplankton and zooplankton) production (Dugdale and Goering 1967) has dominated thinking concerning the cycling of nitrogen in the ocean. Features of the microbial community follow this annual cycle (Cullen 1991): diatoms dominate the spring bloom and are consumed by large herbivores, while the regenerative phase of the community comprises smaller primary producers grazed by microheterotrophs in the microbial loop.

Figure 14.18 is a schematic representation of the open water and ice-associated *N* cycles in the region west of the Antarctic Peninsula. The dissolved pools include N_2O (nitrous oxide), NO_3^- (nitrate), NH_4^+ (ammonium), and dissolved organic nitrogen (DON). The dotted lines and arrows represent the process of bacterial nitrification. Not shown in this diagram are atmospheric deposition of organic and inorganic and inorganic compounds or the flux of dissolved nitrogen gas into marine plankton via the process of N_2 fixation. Neither of these processes is considered to be a major flux of *N* in marine ecosystems of the Antarctic Peninsula region.

Parts of the ocean, sometimes characterized as "high nutrient, low chlorophyll" (HNLC, see Chisholm and Morel (1991)) do not conform to the paradigm introduced by Dugdale and Goering (1967). In such regions nutrient concentrations are not reduced to limiting levels by the spring bloom. Much of the Southern Ocean falls into this category. There, nitrogen is not depleted, and summer nitrate concentrations are commonly of the order of 10–30 mmol m^{-3} in surface waters. These values are comparable to, or higher than, winter surface nitrate concentrations in the North Atlantic (Garside and Garside 1993).

Organic matter resulting from the excretion, defecation, and death of the pelagic biota is subject to decomposition by microorganisms with the eventual release of nutrients. While this process occurs as the organic particles sink down the water column, much of it is deposited in the sediments where the bulk of the decomposition takes place. Marine bacteria are both a source and sink for ammonium. Recent studies by Tupas and Kioke (1991) and Tupas et al. (1994) in Gerlache Strait during the 1989 spring bloom demonstrated that mixed bacterial assemblages simultaneously assimilate and regenerate ammonium. While the ammonium supplied up to 80% of the new nitrogen, more than half of the DON taken up by the bacteria was remineralized to free ammonium. In the Gerlache Strait during the 1989 spring bloom, Tupas et al. (1994) found that bacteria accounted for 8–25% of total ammonium assimilation, while at the same time bacteria regenerated ammonium at 2–4 times the rate at which they assimilated it. Ammonium supplied 35–60% of the bacterial nitrogen demand, with the rest probably supplied by ON nitrate. These data imply that bacteria both compete with phytoplankton for available ammonium and help to replenish that ammonium, and also rely on phytoplankton and zooplankton for DON. It is clear that the rapid recycling of nitrogen by bacteria is crucial in maintaining the high rates of primary production seen in the coastal embayments of the Antarctic Peninsula.

In Chapter 2, the relative roles of new (nitrate-N derived primarily from upwelling) and regenerated nitrogen (principally ammonium, derived from microbial remineralization within the euphotic zone) were discussed in detail. Spring phytoplankton blooms are composed mainly of *Phaeocystis* and diatoms, which assimilate both nitrate and ammonium. Much of the production is fueled by new nitrogen in the form of nitrate from upwelling at the Antarctic Divergence and this dominates the particulate nitrogen pool. This forms the basis of the classic food web in which a large proportion of the organic matter produced by the microplankton is exported from the eutrophic zone to deeper water and the sediments through the rapid sinking of large diatoms and fecal pellets. As the spring advances, localized nitrogen depletion occurs, but the levels do not fall to those which can severely limit phytoplankton growth as is often the case in temperate waters. Stabilization of the water column limits the supply of new nitrogen from deeper waters and the particulate nitrogen pool becomes more and more based on ammonium (regenerated nitrogen) derived via microbial decomposition and grazing. This microbial loop cycle proceeds principally in the euphotic layer with rapid recycling through the excretion of microheterotrophs and bacterial remineralization. This system is a weak exporter of organic matter to the deeper layers as it is dominated by highly buoyant microorganism (Jacques 1989). If local ammonium production simultaneously becomes greater than ammonium consumption by phytoplankton, which will be the case in the declining phase of a bloom, accumulation of ammonium will occur in the water column. Thus,

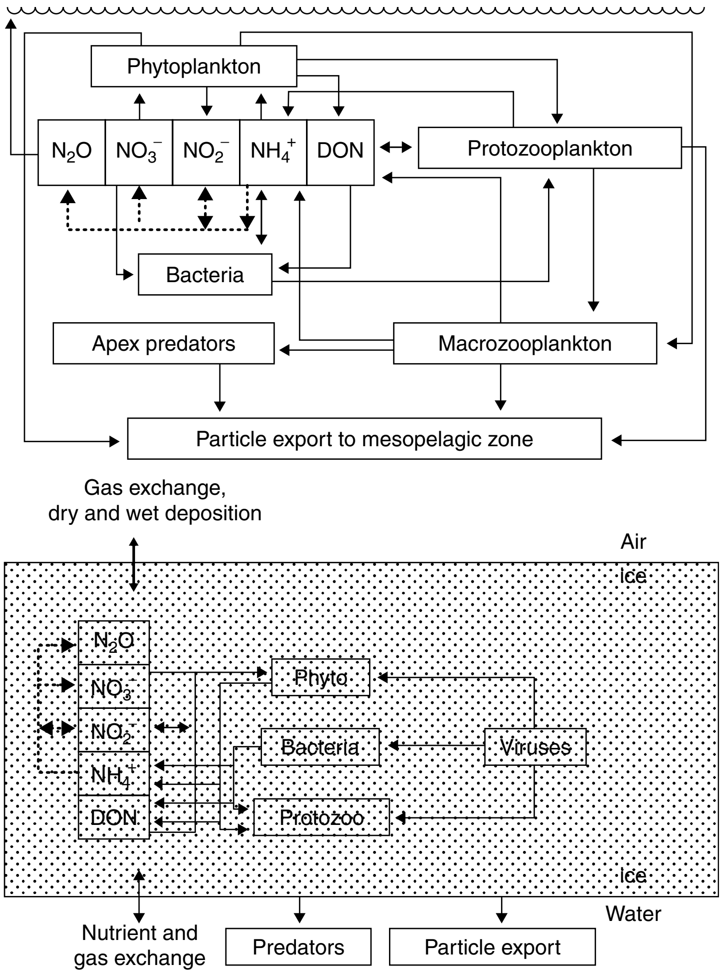


FIGURE 14.18 Schematic representation of the "open water" and "ice-associated" *N* cycles in the region west of the Antarctic Peninsula. The dissolved *N* pools include: N_2O = nitrous oxide; NO_3^- = nitrate; NH_4^+ammonium and DON = dissolved organic nitrogen. The dotted lines and arrows represent the process of bacterial nitrification. Not shown in this diagram are atmospheric deposition of organic and inorganic compounds or the flux of dissolved nitrogen gas into the marine plankton via the process of N_2 fixation. Neither of these processes is considered to be a major flux of *N* in marine ecosystems of the Antarctic Peninsula region. (From Karl, D.M., Christian, J.R., Dore, J.E., *Ant. Res. Ser.*, 70, 317, 1996. With permission.)

a shift in nitrogen consumption toward ammonium occurs, and by the summer, about 80% of primary production is supported by ammonium; the composition of the phytoplankton community shifts from one that is diatom-dominated to one dominated by nano- and picophytoplankton. Over the autumn and winter the ammonium in the water column is gradually dissipated, either by advective or oxidative processes. In the following spring the cycle of ammonium production and utilization begins anew.

Preferential uptake of ammonium over oxidized forms of inorganic nitrogen by phytoplankton has been reported in many marine environments, including the Southern Ocean (Dugdale and Goering 1967; Olson 1980; Ronner et al. 1983; Probyn and Painting 1985; Koike et al. 1986) Even in the early spring, when the ammonium concentration in the surface waters was low (0.1–0.4 μM), phytoplankton in the Scotia Sea assimilated approximately half of their nitrogen as nitrate and half as ammonium (Olsen 1980). In the late summer, when ammonium concentrations in the same area had increased to approximately 1.0 M, the phytoplankton obtained more than 60% of their nitrogen as ammonium (Gilbert et al. 1982). Other studies by Ronner et al. (1983) and Koike et al. (1986) showed that ammonium uptake averaged 78% in oceanic areas of the Scotia Sea in the early austral summer, and from 65% to 93% in an area of the Scotia Arc in the late summer. The observed shift in nitrogen source from nitrate to ammonium generally parallels a shift in the size of the microbial community from larger to smaller cells, as described for the Bransfield Strait area by Dore et al. (1992).

Koike et al. (1986) have estimated that standing stocks of nitrogen in the euphotic zone of Antarctic waters near Elephant Island in the summer (see Table 15.3). The partitioning of the nitrogen stocks in Antarctic waters has several interesting features compared to other oceanic regions. According to Koike et al. (1986) the total nitrogen in the water was about 5.5 times higher than the global average for surface waters. About 73% of this total was in the form of nitrate. Particulate organic nitrogen, of which about 84% occurs in living organisms, represented less than 4% of the total nitrogen. Bacterial biomass represented about 27% of the total microbial biomass, which falls into the upper range of estimates for coastal waters (3–25%; Ferguson and Rublee 1976). Microzooplankton-N was ∼6% of the total microbial biomass-N (9% of the phytoplankton-N). This is somewhat lower than previous estimates by von Brockel (1981). The large amounts of inorganic nitrogen, including ammonia, were sufficient to support over four generations of exponential phytoplankton growth.

In most oceans nitrate exhaustion by a preceding phytoplankton bloom is assumed to be the triggering factor leading to the establishment of a regenerating system in which autotrophs are dependant on the release of reduced nitrogen by the heterotrophs. In open Antarctic waters, however, the regenerating community establishes itself in the presence of abundant nitrate. While ammonium provides the bulk of the microbial nitrogen requirements (Olsen 1980; Kioke et al. 1986), nitrate can also be utilized (between 20% and 50%, according to Holm-Hansen 1985). Thus, nitrate exhaustion by a spring bloom is not necessary for the establishment of a regenerating community in Antarctic waters.

In the Weddell Sea in the winter the plankton consisted of an active regenerating community functioning at very great dilution (Smetacek et al. 1990). Such communities are flagellate dominated. However, the autotrophs in these communities utilize both ammonium and nitrate and they cannot be categorized exclusively as either "new" or "regenerating" systems as they combine characteristics of both. Smetacek et al. (1990) have suggested that the term "regenerating" system is more appropriate. The "regenerating" system is then the characteristic system of the Southern Ocean pelagic zone with blooms representing transitory events superimposed on the basal state (see Figure 15.5).

Krill and other large zooplankton also play a role in cycling nitrogen. Atkinson and Whitehouse (2000) investigated ammonium excretion by *E. superba* in the South Georgia region. Freshly caught krill excreted 1.6–2.8 mmol ammonium mg^{-1} dry mass h^{-1}. Maximum rates of ammonium excretion were determined by placing acclimated krill in large containers. During the period, saturated food concentrations of the mean daily ration was ∼32% of body carbon day^{-1} of the values for freshly caught krill. This equates to a maximum loss of ∼2% of body nitrogen day^{-1}. Excretion rates decreased during the one-day periods without food, and rates during feeding periods were ∼30% higher than those without food. However the bulk of the ammonium production by zooplankton was by small copepods. Copepod and small euphausiids were estimated to excrete at least one third of the ammonium potentially required by the phytoplankton. Heterotrophic flagellates and ciliates are also major contributors to the ammonium stocks. Karl et al. (1998) estimated that at least half of the recycling of ammonium in the area west of the Antarctic Peninsula is carried out by nano- and microzooplankton.

14.11.3 SEDIMENT–WATER FLUX OF NUTRIENTS

Bottom sediments are important sites of degradation and remineralization of organic matter (Newell 1978), particularly where the water column is shallow and deposition of organic matter from the water column onto the bottom sediments occurs relatively rapidly (Jorgensen 1983). Under such circumstances a considerable proportion of the organic matter derived from water column primary production may be degraded by microbial activity in the bottom sediments to ammonium, silicate and phosphate. The sediments therefore play a role in maintaining water column primary production by acting as a source of nutrients. This source will be greatest where the water depth is small.

Bioturbation can have a significant effect on the rates of exchange between sediments and the water column, increasing the vertical transport rates of solutes across the sediment–water interface. Depending upon the bioturbating species, the reported stimulatory effects upon O_2 uptake generally range from 40% to 80% (Binnerup et al. 1992). In Antarctic shallow-water sediments, the bioturbating species are primarily polychaetes, bivalves, holothurians, and crustaceans. The surface layers of inshore Antarctic sediments are characterized by the presence of dense populations of amphipods, predominantly *Cherimedn femorata*, *Pontogenea rotundifrons* and *Trophosa kerguelensis*.

Nedwell and Walker (1995) measured the rates of exchange of nitrate and ammonium across the sediment-water interface in an inshore environment at Signy Island. The sediment was a source of ammonium to the water column but a sink of nitrate, although nitrate exchange rates were very variable. Bioturbation by a largely amphipod benthic infauna which was confined to the top 2 cm of sediment was investigated experimentally. Removal of bioturbation depressed sedimentary O_2 uptake by 33% and sedimentary release of NH_4^+ by 50%. In contrast, in the absence of bioturbation, the removal of NO_3^2 increased in rate. However, in the presence of amphipods, the release of NH_4^+ increased. It was not clear whether the enhancement of NH_4^+ exchange rates by the presence of amphipods was the direct result of their excretion of NH_4^+, or of the stimulation of vertical transport processes.

14.11.4 THE SILICON CYCLE

The major role of the Southern Ocean in the global production of Bsi has been emphasized by many studies (reviewed in Tréguer and van Bennekom 1991). Recently Tréguer and van Bennekom (1991) gave an estimate of 50 T mol Si yr^{-1} for the total annual production of BSi in the Southern Ocean. However, particulate Si data show considerable regional differences with enhanced (greater than 1 μmol l^{-1}) in the Polar Front region (Treguer et al. 1990), the continental shelf areas (Nelson and Smith 1989), and the ice edge (Nelson et al. 1989). For surface water of the Circumpolar Current and the Polar Front in the Indian sector, observed total particulate Si concentrations fluctuated between 0.6 and 3 μmol l^{-1} (Dehairs et al. 1995). By assuming interannual differences in winter nutrient distribution to be minimal, Jennings et al. (1984) estimated the average net production rate to be about 12 mmol Si m^{-2} day^{-1} for a 60- to 90-day period, from the depletion of silicic acid in the surface layer of the eastern Weddell Sea from winter to spring. Tréguer and van Bennekom (1991) estimated the mean silica production rate in summer (November–April) to be about 7 mmol Si m^{-2} day^{-1} in the South Scotia area and at the Weddell Sea Confluence, based on ^{14}C production rates and Bsi/POC ratios.

Along a transect through the Weddell Sea from Joinville Island to Cap Norvegia in November–December, Leynaert et al. (1993) estimated the annual production of Bsi in the northern Weddell Sea to be 810–870 mmol m^{-2} yr^{-1}. On the basis of these results, they gave a revised.estimate of the total annual Bsi production in the Southern Ocean of between 11 and 32 Tmol Si yr^{-1}. This is lower than previous estimates. However, large uncertainties remain, primarily as a result of uncertainties for the ACC, for which silica production cannot yet be estimated from direct measurements. They also estimated that no more than 1% of the silica produced annually by phytoplankton in the upper water column reaches a depth of 800 m.

15 Ecosystem Dynamics

CONTENTS

15.1 INTRODUCTION

This chapter attempts to undertake an holistic approach to the Southern Ocean ecosystem. Table 15.1 lists the principal environmental features of this system. Whether the Southern Ocean is considered a single ecosystem or a series of interconnected ecosystems is purely a matter of choice. The sea ice, the pelagic waters, and the benthic sediments can be viewed as separate ecosystems, and these can be further subdivided on geographic and depth criteria. However, it must be borne in mind that they are all interconnected. Previous chapters have discussed submodels of component populations or trophic levels. Models of whole systems, or ecosystems, focus on the ways that the individual components of the ecosystem are linked to each other, and the ways that the state variables (components, or compartments within the system, e.g., trophic levels) are linked together, and how the variables interact with the ecosystem, forcing functions (inputs, e.g., energy) that drive the system. A systems model provides a conceptual hypothesis within which to explore different sets of data. It can identify which critical observations have not been made, and it suggests laboratory and environmental experiments that might be performed (Knox 1986).

Early models assumed linear food chains of the Lindeman (1942) type, consisting of phytoplankton, zooplankton, benthos, and fish (Clarke 1946 Riley 1963). The compartments of such models were equated with trophic levels, and ecological transfer efficiencies were applied to evaluate energy flux. Ryther (1969) attempted to show that fish production was limited by the number of energy transfers. Steele (1974) developed a bifurcated compartmental model with one pathway involving phytoplankton, zooplankton herbivores, zooplankton carnivores, and pelagic fish, and the other pathway involving fecal pellets, bacteria, benthic meiofauna, benthic macrofauna, epibenthos, and demersal fish. In a landmark paper Pomeroy (1979) presented a compartmental model of energy flow through a continental shelf ecosystem, examining the potential for substantial energy flow through dissolved organic matter (DOM), detritus (POM), and microorganisms to terminal consumers. This model was further developed by Pace et al. (1984). These models involved the abandonment of the classic idea of trophic levels and instead regarded food webs as anastomosing structure that defy classification into trophic levels. Pomeroy demonstrated that it was possible for energy to flow either through the grazer, or alternatively pathways, to support all major trophic groups at a reasonable level, and to maintain fish production at commonly occurring levels.

As discussed in previous chapters, the Southern Ocean sustains large populations of krill, seabirds, and seals, and in the past times it was the world's most productive whaling ground (Laws 1985). It is also the site of 75–85% of biogenic siliceous sedimentation in the world's oceans (DeMaster 1981; Leford-Hoffman et al. 1986). Although these indirect lines of evidence indicate high primary production, estimates

TABLE 15.1
Environmental Features of the Southern Ocean

A. Epipelagic Zone

An oceanic ring surrounding a central land mass.
Free connection with the world's major oceans, the Atlantic, Pacific and Indian Oceans.
Zonal transport by circumpolar currents (Antarctic Circumpolar Current and Antarctic Coastal Current dominates over[4] meridional transport.
Temperature between 3–4 °C (summer) 2 °C (winter) at the Antarctic Convergence and approaching ∼2 °C at the ice shelves.
No dilution of inshore waters by freshwater inflow but surface dilution in summer due to sea ice melting.
No pronounced stratification or vertical stability except at the ice edge during the retreat of the sea ice. Considerable sinking of high salinity water (greater than 34.5%) and low temperature (less than 0.5 °C) near the continent, and up welling of high salinity (34.7%) and high temperature (1–2 °C) in the region of the Antarctic Divergence.
Continuous high nutrient levels in the euphotic zone.
Variable sea ice cover.
Light intensity providing ample Photosynthetically Available Radiation (PAR) in the summer but very low in the winter and under ice cover.
High degree of stability of the marine climate over the past 3 million years.

B. Benthic Shelf Habitats

Continental shelf narrow in most places, partly under ice shelves. Shelf mostly deeper than in other world oceans, 300–800 m deep.
Mozaic of glacial marine sediments, including muds, fine and coarse sands and large and small boulders. Sediments generally poorly sorted. No river-borne sediments.
Depths down to 300–400 m subject to iceberg scour.
Intertidal and near-shore zone abraded by sea ice and anchor-ice.
Meridional transport by Antarctic Bottom Water, zonal transport by circumpolar currents.
Temperature low and stable, ranging from c. 2–3 °C near the Antarctic Convergence to −2 °C at the continent.
Water well-mixed and oxygen levels high.
Rich supply of phytoplankton and detritus (POM) during the short summer production period.
Light intensity low in most places due to water depth and ice over.

using ^{14}C incorporation rate measurements in the Southern Ocean indicate production rates typical of oligotrophic oceans elsewhere (Holm-Hansen et al. 1977; El-Sayed 1978, 1984; Jacques and Treguer 1986; Priddle et al. 1986a). However, recent work on ice edge phytoplankton blooms (Smith and Nelson 1985a, 1985b; Smith et al. 1987; Fryxell and Kendrick 1988; Sullivan et al. 1988) have provided some answers to this paradox. The succeeding sections of this chapter show the degree to which our understanding of productive processes and their magnitude in the Southern Ocean has undergone dramatic changes in the last decade.

15.2 PELAGIC ZONATION

The productivity of the Southern Ocean is to a large extent determined by its unique environmental features. These are listed in Table 15.1. The circulation system, coupled with the seasonal changes in the light regime and sea ice cover, have imposed a north–south pattern in bioproductivity, species composition, distribution of biological resources, the pattern of food webs, and the trophic relationships of marine organisms (Hart 1942; Lubimova 1983) for phytoplankton (Voronina 1968; Lubimova et al. 1980; Lubimova 1982) and for the zooplankton distinguish similar latitudinal zones (Figure 15.1). Descriptions of these zones are given by Lubimova (1982) and Hempel (1985a, 1985b).

The pelagic zonation is determined by the Southern Ocean circulation pattern and the positions of the various fronts separating water masses (Bracher 1999). The northern boundary of the Southern Ocean is marked by the Subantarctic Front (SAF) (Smith and Nelson 1986; Priddle et al. 1990). To the south lies the Antarctic Polar Front (APF) with the transition region between the SAF and the APF constituting the Polar Frontal Zone. The Marginal Ice Zone (MIZ) varies in accordance with the season. The region between the APF and the MIZ is usually referred to as the *Permanently Open Ocean Zone* (POOZ). South of the MIZ is the area of fast ice and the ice-free parts of the shelf referred to as the *Continental Shelf Zone* (CCSZ).

15.2.1 ICE-FREE ZONE OR ZONE OF OPEN ANTARCTIC WATER

This zone covering an area of some 27 million km^{-2} is ice-free all year round and occupies the area of the Antarctic Circumpolar Current (ACC). It is rich in nutrients, but relatively poor in primary production. Two peaks of phytoplankton production occur each year. Nanoplankton dominates the phytoplankton biomass while herbivorous copepods, salps, and small euphausiids dominate the zooplankton, with high biomasses being recorded to a depth of 700–1000 m for most of the year (Hart 1942; Foxton 1956; Vorinina 1960, 1971; Vorinina et al. 1980a, 1980b). According to Voronina et al. (1980b) secondary production of the copepods in the productive mesopelagic layer equals $70\ g\ m^{-2}\ yr^{-1}$. Krill are not a significant feature of this zone (Figure 15.1).

The highly productive mesopelagic layer is inhabited by mesopelagic fish which belong to the family Myctophidae (Lubimova et al. 1980). Both the meso- and bathypelagic waters of this zone are inhabited by a number of species of notal and Antarctic cephalopods that eat mainly mesopelagic, plankton eating fish. They include species such as *Monoteuthis ingens, M. knipovitchi, Gonatus antarcticus, Glaiteuthis aspersa, Batoteuthis scopolis, Mesonychaeteuthis hamiltoni*, and some other species known primarily from the analysis of the stomach contents of sperm whales (Filipova 1972).

15.2.2 SEASONAL PACK ICE ZONE

Encompassing an area of some 19 million km^{-2}, the Seasonal Pack-Ice Zone is covered by ice in the winter and spring, but is mainly ice-free in the summer and autumn. It occupies most of the Antarctic Coastal Current and its large eddies along the Antarctic Divergence, and includes the northern branch of the Weddell Gyre and the waters off the Antarctic Peninsula. Stabilization of the euphotic zone at the ice edge, following the melting of the sea ice and the seeding of the water column by the release of the sea ice microalgae, make this zone the most productive on a yearly basis. With the breakup and retreat of the pack ice in the spring and summer, a series of phytoplankton blooms proceed from north to south. In contrast to the Ice-Free Zone, there is a single peak of phytoplankton production (Figure 15.1).

The food web is a complex one with copepods, salps, euphausiids, fish larvae, and chaetognaths (Hopkins 1985b) Krill, because of its large biomass and swarming behaviour, provides the food base for large populations of baleen whales, crabeater and fur seals, and penguins.

Krill are largely restricted to the south of approximately 60°S, which corresponds to the mean northern boundary of the drifting ice (Maslennikov 1980; Lubimova et al. 1980). Krill is the most available food for baleen whales and seals, which are widely distributed in the epipelagic zone of the drifting ice during the summer. Krill and other euphausiid species are most available to the permanent inhabitants of the zone, such as the minke whale and the crabeater, leopard, and foss seals, or those bird species that spend the summer on breeding colonies around the continent such a Adélie and chinstrap penguins and the Antarctic and snow petrels (Figure 15.2), but is less available to some of the migratory species of baleen whales, e.g., the sei whale, which does not penetrate into the Seasonal Pack-Ice Zone.

15.2.3 PERMANENT PACK-ICE OR FAST-ICE ZONE

The Permanent Pack Ice Zone, including the Fast Ice Zone, is the near-shore zone that is covered by ice for most of the year. The fast ice comprises the sheets of sea ice that are attached to the shore and which only break out in the late summer (February–March). In some areas the ice does not

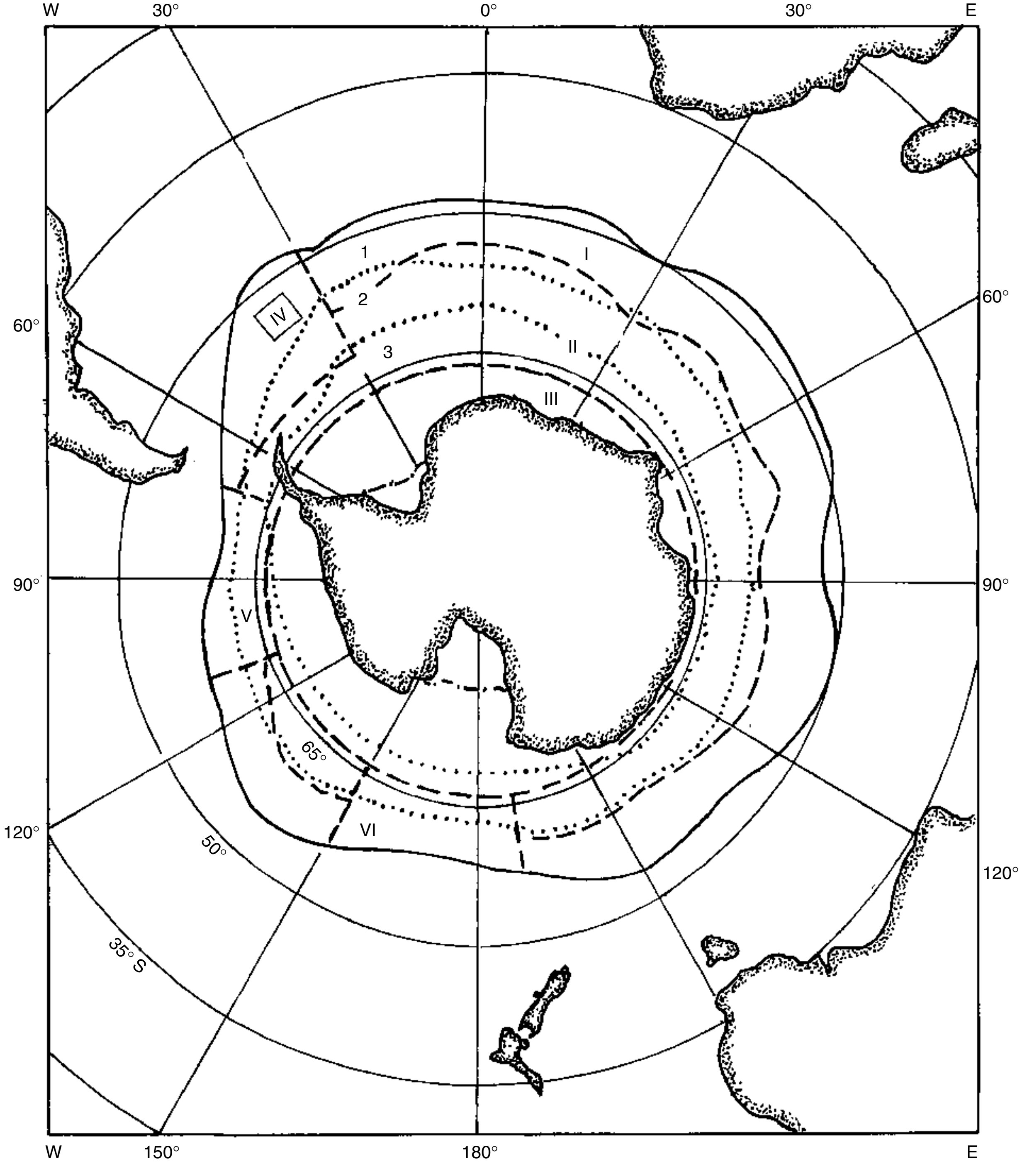


FIGURE 15.1 Zonation of phytoplankton (Roman numerals and dashed lines; after Hart 1942) and zooplankton (Arabic numerals and dotted lines; after Voronina 1971) in the Southern Ocean. I Ice Free Zone or Zone of Open Waters; II Seasonal Pack Ice Zone; III Permanent Pack Ice or Fast Ice Zone. (From Hempel, G., *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer-Verlag, Berlin Heidelberg, 3, 1985. With permission.)

break out each year, and if not, multi-year ice results. This Permanent Pack-Ice Zone roughly coincides with the area covered by the pack ice at the time of the maximum retreat towards the Antarctic Continent. Within this area polynyas of various sizes and duration are conspicuous features. Pack ice extends over the area of very cold, near-shore water masses (ice-shelf water) that are partly separated from the Antarctic coastal current by the continental divergence. Such water masses are particularly well developed in the shallow parts of the inner Weddell Sea and the Ross Sea. A characteristic feature of parts of this zone is the extensive development of platelet ice that often forms a band of loosely aggregated platelets up to several meters thick on the lower surface of the sea ice (Figure 15.1).

Phytoplankton production is restricted to a brief, intense summer period. Zooplankton diversity and biomass are not as high as in the Seasonal Pack-Ice Zone. Krill is largely replaced by the smaller *Euphausia crystallorophias*, and krill-eating mammals are less abundant than in waters to the north. Pelagic fish, especially *Pleurogramma antarcticum*, are particularly abundant. The bulk of the primary production is not consumed, but sediments to the bottom where it is incorporated in the sediments or consumed by the extremely rich epibenthic fauna of suspension feeders.

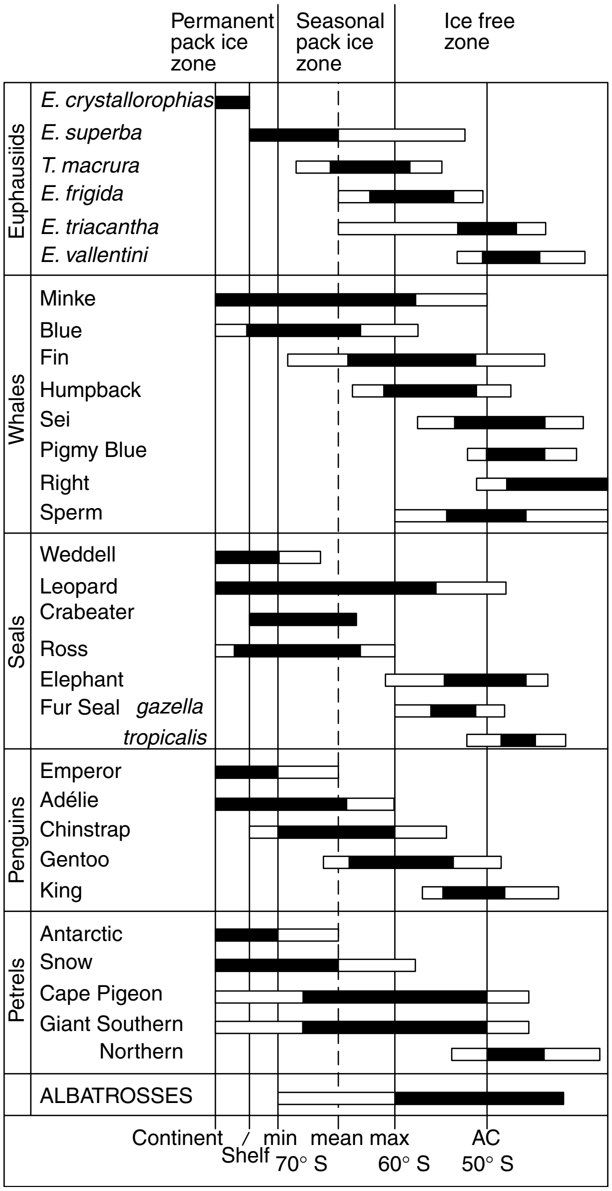


FIGURE 15.2 Comparison of the zones occupied by selected species of euphausiids, marine mammals and birds from the Antarctic Continent northwards. The relative area of the shelf, the minimum, mean and maximum area of pack ice; and the area south of the Antarctic Convergence (AC) are indicated, as is the pelagic zonation (Ice-Free, Seasonal Pack-Ice, and Fast-Ice Zones). Each species has a circumpolar distribution, and the range indicated is the approximate average latitudinal range, with the grey indicating higher densities. (From Laws, R.M., *Adaptations Within Antarctic Ecosystems*, Llano, G., Ed., Smithsonian Institution, Washington, DC, 411, 1977. With permission.)

15.3 PHYTOPLANKTON AND PRIMARY PRODUCTION

15.3.1 INTRODUCTION

Early studies using net plankton hauls gave the impression that large diatoms dominated the Antarctic phytoplankton community. However, although they often dominate the cell numbers south of the Antarctic Convergence, many are small, 10 μm in size (of nanoplankton dimensions; Weber and El-Sayed 1986a). The diatom species *Nitzschia cylindricus* and *N. pseudonana*, which are only 3–6 μm in length, often constitute the bulk of the diatom species present. It is now well established that the size distribution of the primary producers plays an important role in the overall community structure and trophic organization of marine pelagic ecosystems (Pomeroy 1974; Siebruth et al. 1978; Williams 1981; Siebruth and Davis 1982; Stockner and Anita 1986; Stockner 1988). As discussed in Chapter 2, it is now recognized that phototrophic nanoplankton (generally considered to be phytoplankton 2–20 μm in size) account for a high proportion of the biomass and production of most marine phytoplankton communities (see Pomeroy 1974; Hannah and Boney 1983; and Reid 1983 for examples and reviews of the literature). More recently, phytoplankton investigators have become aware of a sub-population of even smaller cells (1–2 μm), the picophytoplankton (Glover et al. 1985; Probyn and Painting 1985; Harrison 1986; Stockner and Anita 1986; Stockner 1988). The waters of the Southern Ocean resemble those of other oceans with respect to the roles played by pico- and nanophytoplankton.

15.3.2 PHYTOPLANKTON COMMUNITIES

Blooms that are typically observed in the vicinity of the fronts and in the MIZ tend to be dominated by net-phytoplankton (>20 μm), as opposed to the areas between the fronts where mainly nanophytoplankton (>20 μm) form the community (Holm-Hansen and Mitchell 1991; Laubscher et al. 1993; Bracher et al. 1999) (Figure 2.3). Laubscher et al. 1993 found that only in the early summer were net-phytoplankton consistently the major component of the frontal blooms, while in the late summer (March) the phytoplankton community at the APF was mainly formed from nanophytoplankton, and major net-phytoplankton blooms were only encountered south of the APF where silicate levels exceeded 20 μM.

The net-phytoplankton, of which the Southern Ocean blooms mainly consist, are large-celled and colonial diatoms (e.g., El-Sayed and Taguchi 1981; von Brockel 1985; El-Sayed and Weber 1986; Jacques 1989; Crawford 1995; Bracher et al. 1999). Blooms formed by *Phaeocyctis* colonies are often observed in the Coastal and Continental Shelf Zone (CCSZ), especially in the western Ross Sea (Palmisano et al. 1986) and the Weddell Sea (Garrison et al. 1987; Jacques and Panouse 1991; Bracher et al. 1999). Figure 2.3 from Bracher's 1999 study in the Atlantic Sector shows that diatoms dominated in the frontal zones, while in the regions of the ACC all four groups of phytoplankton were represented.

15.3.3 IMPORTANCE OF PICO- AND NANOPHYTOPLANKTON

It is only comparatively recently, starting with the paper by von Brockel (1981), that the relative importance of pico- (<2 μm) and nano- (2–30 μm) phytoplankton has been recognized (Hewes et al. 1985; Weber and El-Sayed 1986a). Kosahi et al. (1985) concluded that picophytoplankton were negligible in Antarctic waters, but that nanophytoplankton constituted as much as 55% of the chlorophyll biomass. On the other hand, Hewes et al. (1985) found that >50% of the total chlorophyll found in Antarctic waters was contained in the pico- and nanophytoplankton size fractions, although they did not determine their relative proportions. In a like manner, many investigators have not separated their relative contributions to biomass and production, and have included the pico- and nanophytoplankton together.

The most recent review of the contributions of net nano- and picophytoplankton to the phytoplankton standing of crop and primary production in the Southern Ocean is that of Weber and El-Sayed (1986a). They reported that the relative contributions of nano- and picoplankton are highly variable both in space and time. In the vicinity of Elephant Island, Drake Passage, and the Bransfield Strait (western Atlantic sector) the contribution of nanoplankton to integrated water column chlorophyll was 39–98% (mean = 40% for 26 stations). In the western Indian sector of the Southern Ocean 31–92% (mean = 64% for 69 stations) of the chlorophyll was in the nanoplankton size fraction. Picoplankton accounted for 5–74% (mean = 40% for 6 stations) and 7–42% (mean = 15% for 14 stations) in the Drake Passage/Bransfield Strait region and the Indian sector, respectively. Size-fractionated measurements of carbon uptake in the Indian Ocean sector revealed nanoplankton account for 16–92% (mean = 53% for 26 stations), and picoplankton for 0–32% (mean = 53% for stations), of the primary production. It seems that a considerable proportion of the primary productivity is dominated by cells in the nano- and picoplankton size ranges. For 166 Stations occupied south of the Antarctic Convergence, nanoplankton contributed a mean (and median) of 66% to the total integrated water column chlorophyll *a*. In contrast to conclusions drawn from studies in temperature to tropical waters, the relative contribution of nanoplankton to total chlorophyll *a* does not appear to be a function of the total phytoplankton standing stock (the correlation coefficient between percentage contribution of the nanoplankton was only −0.21). Many studies have revealed that the concentration of chlorophyll *a* in the net size fraction is subject to large fluctuations (e.g., Malone 1980; Kosahi et al. 1985).

The limited data on Antarctic picoplankton suggested that cells which pass through a 2.0 μm filter often constitute only a small percentage of the Antarctic phytoplankton community (Reid 1983; Kosahi et al. 1985; Probyn and Painting 1985; Hosaka and Nemoto 1986), ranging from 2 to 22% (mean = 7–18%). However, in the studies carried out by Weber and El-Sayed (1988a, 1988b) in the Bransfield Strait and the waters of the Indian Ocean picophytoplankton accounted for up to 74 and 42% of the integrated chlorophyll *a*, respectively. It is probable that picophytoplankton is of greater importance than hitherto considered. Apart from the blooms dominated by net phytoplankton, most of the standing stock and primary production of Southern Ocean phytoplankton can be attributed to cells that pass through a 20 μm (and in some cases a 2.0 μm) filter. This has important implications for the overall community structure and trophic organization of Antarctic marine pelagic ecosystems.

15.3.4 PHYTOPLANKTON SUCCESSION

In those regions where ice edge or coastal phytoplankton blooms occur there is a well-defined pattern of phytoplankton succession. This was first described by Bunt (1964a, 1964b) for McMurdo Sound. Early November to mid-December a limited range of diatoms was found with *Nitzschia serrata* as the dominant species. Mid-December to early January was characterized by a *Phaeocystis antarctica* bloom, which in late January was replaced by a diverse assemblage of diatoms more typical of northern Antarctic waters, such as *Thalassiosira antarctica* and *Synedra pelagica*. On December 13 diatom cell concentrations were only $0.01\times10^6\,l^{-1}$, while at the height of the *Phaeocystis* bloom they reached $3\times10^6\,l^{-1}$. During the latter stages of the succession in late January diatom concentrations were $0.36\times10^6\,l^{-1}$, and during the latter stages of the succession in late January diatom concentrations were $0.36\times10^6\,l^{-1}$. Marchant et al. (1987) reported a similar process of succession in Prydz Bay, with *Phaeocystis* being the most abundance alga at the time of the fast ice breakout in late December to early January. Following *Phaeocystis* the diatom *Nitzschia lanceolata* became numerically dominant in the water column, reaching a concentration of 5.8×10^7 cells l^{-1} in February and dominating until just after sea ice formed in early March. The contribution of the nanoplankton chlorophyll was at a minimum during the phytoplankton blooms of late November to early January (<20%). In May the proportion was 80%, decreasing to 50% in October and 30% in early November.

As discussed in the previous chapter, the Marginal Ice-Edge Zone is characterized by both *Phaeocystis* and diatom blooms. In the early spring the melting of the sea ice at the retreating ice edge introduces sea ice microalgae into the water column. This results in chlorophyll *a* concentrations up to 0.4 $\mu g\, l^{-1}$ and phytoplankton blooms in which chlorophyll reaches as high as 10 $\mu g\, l^{-1}$ grow in the stabilized less saline surface layer (von Bennekon et al. 1989). It is during these blooms that the vertical flux of phytoplankton-derived detritus is high, resulting in the sedimentation of large quantities of organic matter towards deeper water and the sediments. However, bloom senescence and zooplankton grazing, especially by krill, can rapidly reduce the volume of the blooms. Heterotrophic protozoa increase rapidly in abundance and the phytoplankton community shifts towards one dominated by nano- and picophytoplankton. Table 15.2 lists the main trends in this succession process and the concomitant changes in other indices of pelagic ecosystem structures.

Recent studies in widely spread geographic locations have shown that the “macro” pathway (net phytoplankton) is preponderant wherever the total primary production is high (blooms), and the “micro” pathway (pico- and nanophytoplankton) is dominant in situations where phytoplankton biomass is low (Jacques and Panouse 1991). The latter is the usual situation in the Ice Free Zone south of the Antarctic Convergence, and post-bloom conditions in the Seasonal Pack Ice Zone. As Platt and Harrison (1985) predicted, one would expect that each province of the Southern Ocean can occupy, at a given time, in a given place, and at a given depth, any position in the total spectrum from extreme oligotrophy to extreme eutrophy. Jacques and Panouse (1991) stress that this is a more realistic view than the one that definitively classifies a given oceanic region as either oligotrophic or eutrophic.

TABLE 15.2
Phytoplankton Succession and Associated Indices of Ecosystem Structure

	Winter	Spring	Summer
Phytoplankton biomass	Low	Increasing rapidly	Decreasing
Diatoms	Low	High	Decreasing
Nano-and picophytoplankton	Moderate	Low	Increasing rapidly
Nitrate	High	Reduced	Increasing
Ammonia	Low	Increasing	High
Silicate	High	Decreasing	Increasing
Bacteria	Low	Increasing	High
Heterotrophic protozoans	Low	Increasing	High
Sedimentation	Low	High	Decreasing

15.3.5 SEA-ICE MICROALGAL PRODUCTION

As outlined in Chapter 3, the sea ice microalgal production is a significant component of the overall productivity of the Southern Ocean. The sea ice microalgal contribution to Southern Ocean food webs can be summarized as follows:

1. There is now evidence that significant microalgal production and increase in biomass occurs after the formation of the sea ice in late March before the onset of winter, thus providing the conditions for the growth of sea ice bacterial and heterotrophic protozoa. The algal biomass thus produced is available to consumer during the austral winter.
2. Release of DOM by the sea ice microalgae provides the organic material for an increase in the numbers of the water column bacteria in the early spring before the melting of the ice occurs (Gibson et al. 1990).
3. It is now clear that the development of the various kinds of bottom microalgal assemblages provides a significant food resource for larval and adult copepods (Hoshiai et al. 1987), larval and adult krill (Smetacek et al. 1990), larval fish, and other members of the cryopelagic community (Knox 1990), especially in the winter and early spring when phytoplankton stocks in the water column are low.
4. Copepod larval stages, especially in the Fast Ice Zone, live and grow in the bottom sea ice microbial assemblages where there is an abundant food supply throughout the austral winter and early spring (Hoshiai et al. 1987).
5. The release of DOM by the sea ice microalgae provides the organic substrate for the growth of the sea ice bacteria, which in turn provides a food resource for the sea ice heterotrophic protozoa.
6. When the sea ice melts in the late spring and early summer the sea ice microalgae are released into the water column. A proportion of this may sediment to deeper water where it becomes available to the zooplankton, especially the copepods which are characteristic of such waters. It also provides a food resource for the zooplankton in the surface waters before the onset of the spring phytoplankton blooms.
7. Most of the species of the sea ice microalgal assemblages are identical to those found in the water column. When they are shed into the water column on the melting of the ice, they probably “seed” the water and some species grow rapidly, forming ice edge blooms in the favourable conditions of ample light and nutrients, and water column stability which result from the release of freshwater by the melting ice.
8. When the sea ice melts, the sea ice bacteria and heterotrophic protozoa are also released to “seed” the water column.

15.3.6 THE IMPORTANCE OF ICE EDGE BLOOMS

As discussed in Chapter 13, ice edge (or marginal ice) phytoplankton blooms (defined as greater than those present in the absence of ice) have clearly been shown to be consistent features of the MIZ (Hart 1942; Marshall 1957; El-Sayed 1971a, 1971b; El-Sayed and Taguchi 1981; Smith and Nelson 1985a, 1985b; Smith et al. 1990; Garrison et al. 1986a, 1986b; Fryxell and Kendrick 1988; Sullivan et al. 1988). Oceanographic processes operating within ice edge region stimulate primary production, and this increased production through assimilation by herbivorous zooplankton supports elevated standing stocks of higher trophic levels. The extent of the sea ice, and its production and meltback, influence the productivity and release of the sea ice microalgae into the water column. According to Sullivan et al. (1988) if it is assumed that there is a relatively uniform content of photosynthetic pigments of $10\,\mathrm{mg\,m^{-2}}$ (Kottmeier and Sullivan 1987) contained in the melted ice of the Southern Ocean between 30 and 45°W in the Weddell Sea, then 5.5×10^5 tonnes of pigment would be released with the meltwater. This would seed the actively growing algal cells at 0.2 mg chlorophyll *a* $\mathrm{m^{-3}}$, which is equal or greater than the pigment concentrations derived from the sparse phytoplankton found in the water column under the ice. These algal cells would provide an inoculum for the observed ice edge blooms. If the model that Sullivan et al. (1988) have proposed is correct, then it would be expected that enhanced biological productivity would occur along the entire circumpolar ice edge.

Sullivan et al. (1988) point out that the interannual variability in the ice extent potentially induces large variations in predicted primary productivity at the ice edge. The magnitude of such variations can be as much as 50% from one year to the next and is highly dependent on the seasonal ice dynamics. Thus, it would be expected that there would be considerable mesoscale spatial and temporal variability in the aerial extent and intensity of the ice edge blooms, as well as biological variability related to local ice dynamics in a particular region. The dynamics of the ice edge blooms could also be highly variable from one location to another depending on weather conditions, water column stability, local hydrology, and the intensity of grazing by herbivorous zooplankton, especially krill. For a receding ice edge in the Ross Sea, Smith and Nelson (1986) estimated that the bloom could persist on the order of two months (rate of ice retreat approximately $5.2\,\mathrm{km\,day^{-1}}$; Nelson et al. 1987). Fryxell and Kendrick (1988) estimated that during summer in the Weddell Sea, the spatial extent of the blooms at the ice edge and northwards was in the order of 250 km.

15.3.7 ROLE OF *PHAEOCYSTIS*

Phaeocystis antarctica, a prymnesiophyte, is one of the few phytoplankton species that exhibit a life-cycle alternation between free-living flagellated zoospore and a gelatinous colonial aggregation of non-motile cells. It occurs most prominently in the plankton in this later stage, and enormous blooms of colonial *Phaeocystis* have been documented over the past hundred years in many oceans, including the Southern Ocean (see Chapter 2). It is also common as a member of the sea ice microalgal communities in many parts of the Seasonal Pack-Ice Zone and the Fast-Ice Zone, and is released into the water column on the melting of the ice. Colonies can be formed by two mechanisms: the formation of colonies from solitary cells; and the cleavage of large colonies into daughter colonies. As discussed in Chapter 14 the production of DOC and mucilage is an integral part of the physiology of *Phaeocystis* (Chang 1984), and this requires substantial fractions of the photosynthate (Lancelot and Mathot 1985). Studies of the C metabolism have suggested that *Phaeocystis* produces exopolymeric substances in light that are stored in the gelatinous matrix and used in the dark to meet the energetic need of the cells (Lancelot and Mathot 1985; Veldhuis and Admirall 1985). Physiologically *Phaeocystis* is a remarkably complex species, evidenced by the degree to which it adapted to low light levels following advection under the fast ice in McMurdo Sound (Palmisano et al. 1985c).

Bunt (1964a) was the first to draw attention to the occurrence of *Phaeocystis* blooms in Antarctic coastal waters. During the seasons of 1961–1962 and 1962–1963 phytoplankton rich in *Phaeocystis* appeared quite suddenly, coinciding with widespread deterioration of the sea ice to the north of McMurdo Sound. Since then, *Phaeocystis* blooms have been shown to be a regular annual occurrence (Knox 1990). The development of a *Phaeocystis* bloom is a complex process that is, as yet, poorly understood. *Phaeocystis antarctica* is widely distributed in Antarctic waters (as mapped by Fryxell and Kendrick 1988). Blooms have been reported from the Weddell Sea (El-Sayed 1971b; Buck and Garrison 1983; Garrison and Buck 1985b; Fryxell and Kendrick 1988) and from McMurdo Sound (Bunt 1964a; Palmisano et al. 1988; Knox 1990). El-Sayed (1971a, 1971b, 1971c) found *Phaeocystis* in large numbers (1.7×10^6 cells $\mathrm{l^{-1}}$) in the Weddell Sea, while Garrison and Buck's (1985b) Weddell Sea studies found that *Phaeocystis* made up greater than 35% of the cells in net samples and 53% of the cells in just-forming ice samples, but only 1% in melted ice samples. *Phaeocystis* is also common in other inshore areas around Antarctica, and it was reported in extensive blooms, extending deep into the water column, along the barrier edge of the Ross Ice Shelf in the austral summer of 1978 (El-Sayed et al. 1983).

Phaeocystis blooms and their contribution to the planktonic food webs and energy flow are of great interest. It has been suggested that the colonial forms are not consumed by herbivores, due to their production of biochemical substances that prevent their consumption. Schnack et al. (1985) found no evidence of predation by copepods on *Phaeocystis*. On the other hand, culture experiments have shown that *Phaeocystis* can be excellent prey for various copepod species (Huntley et al. 1987; Tande and Bamstedt 1987). In studies in the Arctic, Estep et al. (1990) found that predation on *Phaeocystis* colonies was a function of the physiological state of the colonies. Healthy colonies were not consumed, possibly as a result of the production of anti-predator compounds. They speculated that without this anti-predator ability, *Phaeocystis* would have great difficulty in maintaining itself for prolonged periods as a bloom species since the colonies would represent easily captured parcels of food for copepod species. They discovered that unhealthy colonies found during the latter stages of a bloom were consumed by zooplankton at higher rates than those for co-occurring diatom species. The ability of *Phaeocystis* to avoid predation pressure has important implications for differential predation pressure and the species composition of Antarctic food chains.

The slimy colonies of *Phaeocystis* have not been thought to contribute significantly to the vertical flux of phytoplankton-derived detritus, due to their buoyancy. However, Wassman et al. (1990) reported that sedimentation rates of POC, PON, and especially pigments from a *Phaeocystis* bloom in the Barents Sea were among the highest rates recorded from northern cold temperate waters. They concluded that *Phaeocystis* is a significant contributor to marine snow (Alldredge and Silver 1988) in polar and boreal oceans, enhancing the removal of particulate and dissolved matter from the surface waters. The extra-cellular polymeric material of aged *Phaeocystis* colonies gives rise to adhesive and sticky capsular secretions that are readily colonized by bacteria, pennate diatoms, and heterotrophic protozoans (Estep et al. 1990). These aggregates sink and also remove other particles (e.g., algae, fecal pellets, and detritus) from the upper layers. It is highly probable that a similar process takes place in the Southern Ocean. Autolysis, production of exudates, bacterial colonization of sinking colonies and amorphous material during *Phaeocystis* blooms (Davidson and Marchant 1987; Vaque et al. 1989), and ingestion of bacteria-rich aggregates by copepods (Estep et al. 1990) suggest that the particulate and DOM derived from *Phaeocystis* blooms are effectively recycled in the upper layers of the aphotic zone (Figure 15.3).

It would appear that *Phaeocystis* plays a dual role in ice edge and coastal phytoplankton dynamics. The release of living cells from melting ice may provide "seed" for the bloom that follows. In addition, large amounts of extracellular DOM and mucilage provide a ready substrate for bacterial growth and subsequent development of heterotrophic protozoa. The activities of both the bacteria and the heterotrophic protozoa result in the remineralization of organic matter, producing large amounts of ammonia which is the preferred form of nitrogen for subsequent diatom blooms. One aspect of phytoplankton succession, which has had little attention in the Southern Ocean, is the question of "conditioning" the water by the bloom of one microalgal species, leading to a milieu that favours the development of another species.

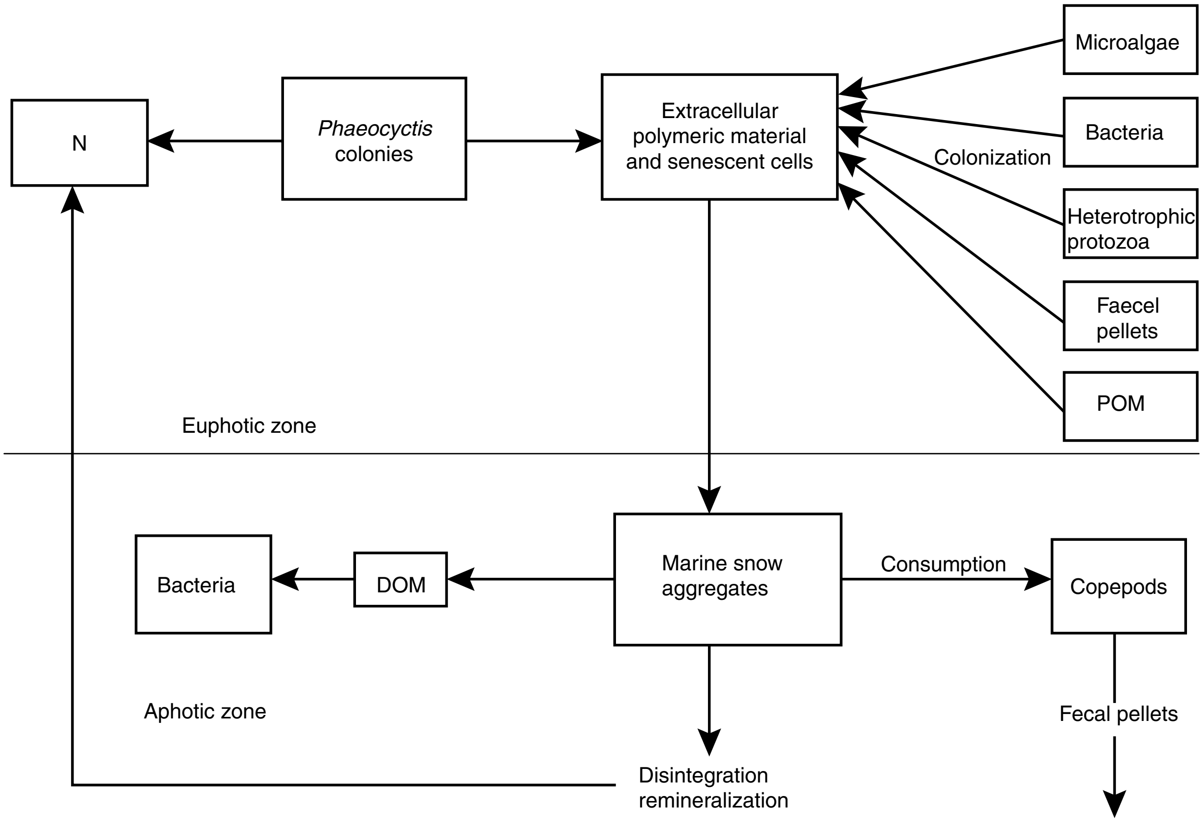


FIGURE 15.3 Fate of organic matter produced during a *Phaeocystis* bloom.

15.4 FOOD WEBS

15.4.1 INTRODUCTION

The transfer of food energy from its source in phytoplankton through a series of organisms with repeated eating and being eaten is referred to as a food chain. At each transfer a large proportion, 80–90% of the potential energy, is lost as heat. Therefore, the number of "links" in the chain is limited. Food chains have been considered to be of two basic types: the *grazing food chain*, which starts with phytoplankton that are eaten by grazing herbivores (primary consumers), and that in turn are eaten by carnivores (secondary consumers); and the *detritus food chain*, which starts with particulate organic matter that is consumed by bacteria and heterotrophic protozoa, thus forming the detrital–microbial complex that is consumed by detritus feeding organisms which are, in turn, consumed by predators. However, in the marine pelagic ecosystem these food chains are often not clearly separated. As detailed in the previous chapter, primary consumers such as the euphausiids and copepods may consume bacteria, heterotrophic protozoa, phytoplankton, small metazoans, and detrital aggregates with their associated microbial community. Thus, food chains are not isolated sequences but are interconnected to form an interlocking pattern, the *food web*.

Our view of the functioning of pelagic ecosystems has changed dramatically in the last fifteen years (Williams 1981; Fenchel 1988) (Figure 15.4). It is now recognized that phototrophic and heterotrophic protozoa play a substantial and sometimes dominating role in the cycling of matter in the sea; that plankton food chains include a higher number of

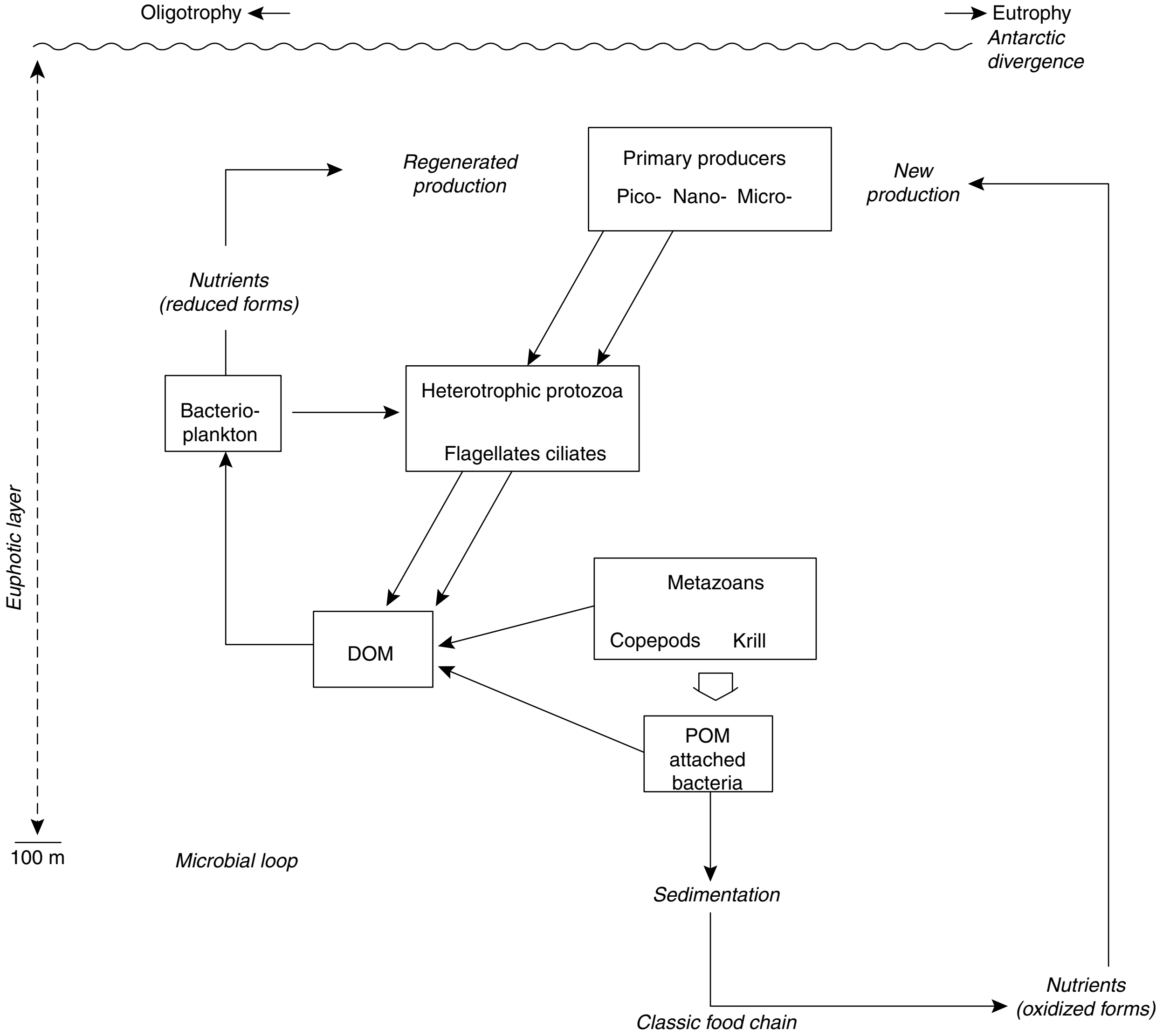


FIGURE 15.4 Diagram illustrating the relationship between the "classical food web" and the "microbial loop" and nutrient supply in the euphotic zone. Abbreviations: DOM, dissolved organic matter; POM, particulate organic matter. (Modified from Jacques, G., *Vie et Milieu*, 1, 1989. With permission.)

trophic levels than previously believed; and that a large proportion of the primary production is not consumed directly by primary consumers, but is channelled through a pool of dead organic matter before it becomes available—via bacterial degradation—to phagotrophic organisms (Fenchel 1988). It has frequently been stated that the Southern Ocean pelagic ecosystem is characterized by short food chains—the classic phytoplankton-krill-baleen whale food chain. However, it appears that only a maximum of 3% of phytoplankton primary production is consumed by krill, and that something in excess of 90% is not consumed directly by herbivores. It is now clear that food webs in the Southern Ocean are not radically different from those of other oceans.

Figure 15.5 is a compartmental model based on the elaboration of Pomeroy's (1979) model by Pace et al. (1984), in which some of the complexity of the Southern Ocean pelagic food web is depicted. Implicit in this model is the recognition of: (1) the complementary roles of pico-, nano- and net phytoplankton, (2) the central role of DOM produced from a great variety of sources, (3) the utilization of this pool of DOM by bacteria and their consumption by heterotrophic protozoa (the *microbial loop*), (4) the diversity of food items consumed by the herbivores or primary consumers, and (5) the role of sedimentation of POM (primarily phytoplankton and fecal pellets). In the following sections we will explore the roles of selected groups of organisms in the Southern Ocean pelagic food web.

Legendre (1996) and Legendre and Michaud (1998) have discussed the ways in which biogenic carbon is produced and its eventual fate in the marine pelagic ecosystem. They define three pools of biogenic carbon by reference to the time elapsed between the photosynthetic uptake of carbon and its return as carbon dioxide to surface waters or the atmosphere (i.e., turnover time) (Legendre and Le Fevre 1989, 1992). These three polls are short-lived organic carbon ($<10^{-2}$ years), long-lived organic carbon (10^{-2}–10^{2} years), and sequestered biogenic carbon ($>10^{2}$ years).

Short-lived biogenic carbon consists of organisms with high turnover rates and labile dissolved organic compounds. This type of carbon mainly passes through the microbial food web, which comprises small phytoplankton, heterotrophic bacteria and protozoa (flagellates and ciliates as described in Chapter 14, Section 10). Long-lived biogenic carbon includes renewable marine resources. It flows into long-lived animals, and also includes microbial heterotrophs involved in the breakdown of organic matter derived from large heterotrophs. Sequestered biogenic carbon comprises organic remains buried in the sediments, inorganic deposits of biological origin (e.g., calcareous ooze), refractory DOM and dissolved CO_2 in deep waters resulting from the oxidation of organic compounds (respiration). Figure 15.5 shows how the major trophic pathways channel the three size classes of phytoplankton production (i.e., large and small cells, and DOC) into the three pools of biogenic carbon. Short-lived organic carbon mainly results from the oxidation of DOC by heterotrophic bacteria and from respiration within the microbial web. The flux of organic carbon into the long-lived pool is mediated by mesozooplankton (mainly crustaceans) grazing on large cells, organic aggregates (e.g., marine snow), and on microzoolankton; and by microphagous macrozooplankton feeding on small particles and aggregates. Part of this flux reaches large metazoans such as fish, marine mammals, and birds. Finally, sedimentation to deep waters of rapidly sinking aggregated algal cells and fecal pellets (mainly from microphagous macrozooplankton) is a condition for the sequestration of biogenic carbon at depth.

Figure 15.6 shows the two major grazing pathways through which primary production is channelled, essentially herbivorous and microbial. A third trophic pathway through which primary production is channelled is microphagy, which is. direct feeding by large zooplankton on small particles (e.g., <2–5 μm). Salps, pteropods doliolids, and appenducularians feed on very small particles. Fortier et al. (1994) hypothesized that pelagic organisms which package small particles into larger ones (i.e., microphagous macrozooplankton) generally contribute to lengthening biogenic carbon turnover times and even transforming carbon from a given pool to a longer-lived one. In the Southern Ocean pteropods, doliolids, and appendicularians are found under the sea ice, and salps at the ice edge (e.g., Harrison 1988). In addition, krill and large copepods can feed on small particles less than 5 μm, at least when larger food items are absent. Thus small particles can escape the short-lived carbon pool through microphagous grazing, not only by pteropods, doliolids, and appendicularians but also by some large plank tonic crustaceans.

15.4.2 ROLE OF BACTERIA

It is now generally accepted that the biomass of bacteria in the Southern Ocean is similar to that of other oceans (Fuhrman and Azam 1980; Hanson et al. 1983a, 1983b; Painting et al. 1985). Bacterial production has averaged 5–20% of the net primary production in many coastal locations and the open oceans, implying that 10–50% of the primary production is cycled through the bacteria, if one assumes their growth efficiency is 50% (Ducklow 1983). Studies by Cota et al. (1990) and Sullivan et al. (1990) have suggested that the bacterioplankton contribute about 11% of the net primary productivity in the MIZ in the austral spring, with lower values in ice-covered waters and slightly higher ones in open waters. In their studies of the MIZ of the Weddell Sea, Cota et al. (1990) and Sullivan et al. (1990) discovered that while the spring phytoplankton biomass (as measured by chlorophyll *a*) was ten times more abundant in the open water of the ice edge than within the pack ice, the difference in the autumn was only threefold. In contrast, there was usually less than a 2-fold difference, regionally or seasonally, in the bacterial biomass.

Ratios of production per unit biomass (P:B ratios) provide an indication of the relative activities of populations in different environments. In contrast to phytoplankton, where P:B ratios were several times higher under the pack ice than in the open waters as a result of the low biomass

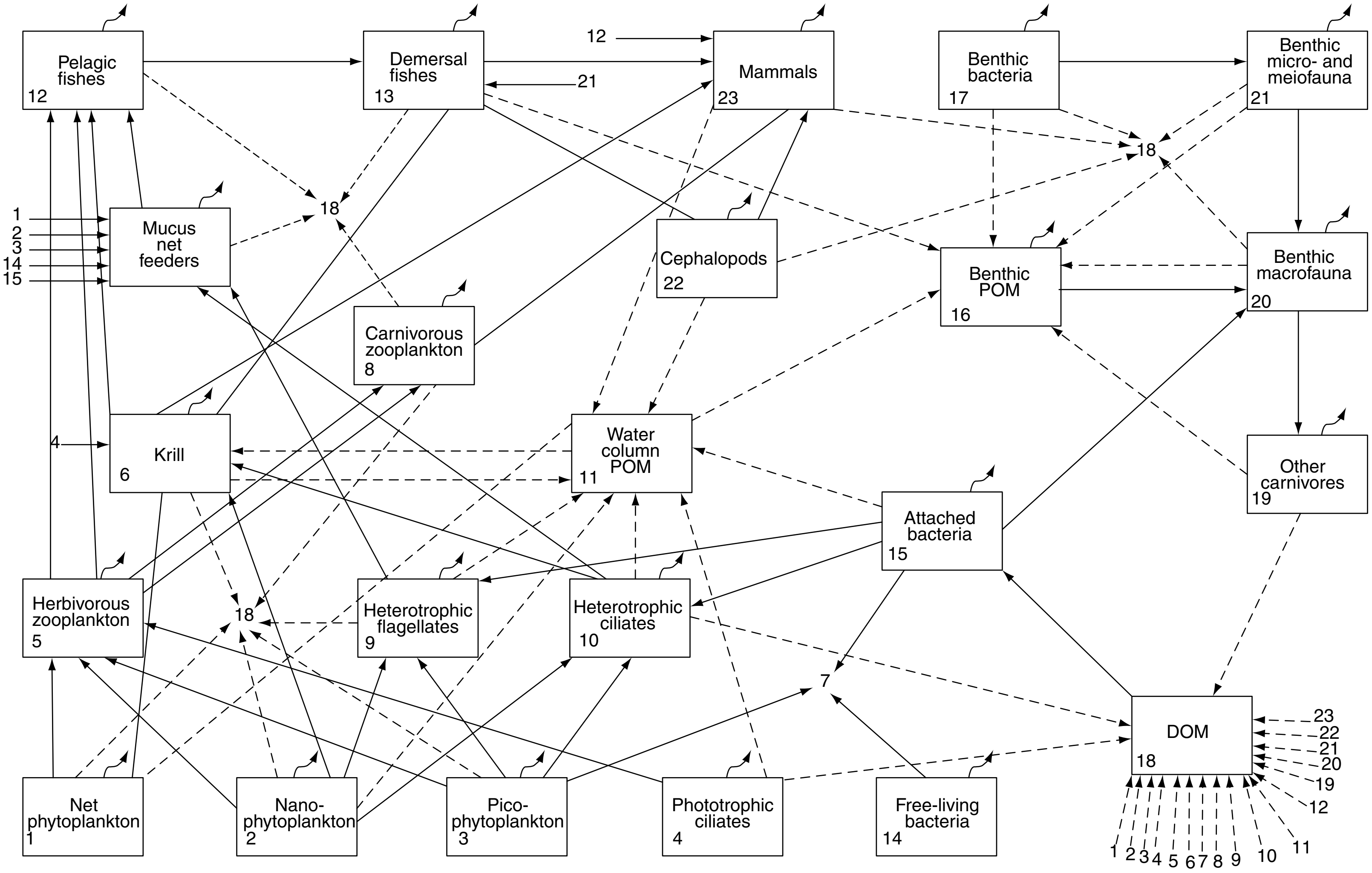


FIGURE 15.5 A compartmental model of the Southern Ocean euphotic zone food web. Each compartment is numbered and the numbered inputs to some of the compartments refer to the input from the corresponding numbered compartment.

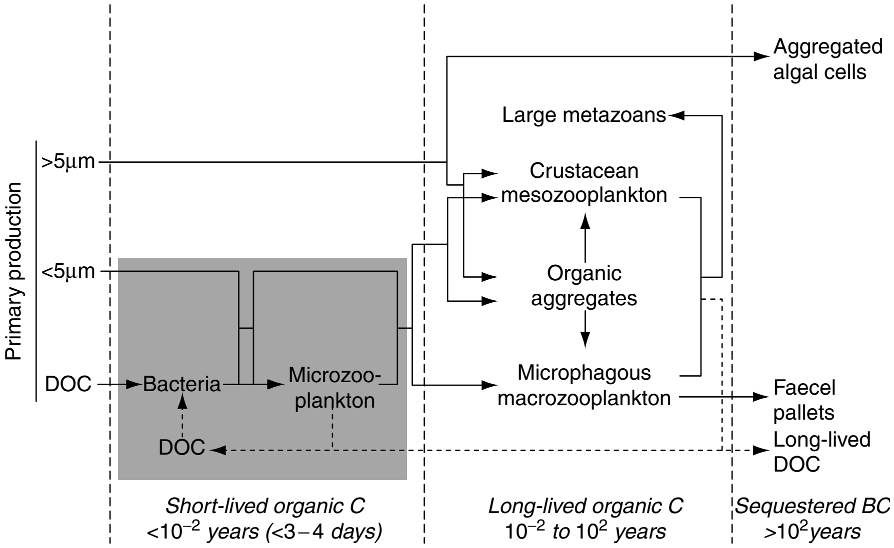


FIGURE 15.6 Conceptual model of the pelagic food web mediated C flux modified from Legendre (1996) and Legendre and Rassoulzadegan (1996). Solid arrows major flows of biogenic carbon in the euphotic zone of the oceans, for three size classes of net (vs. gross) primary production (cells >5 μm, cells <5 μm, and DOC) to three carbon pools (short-lived, long-lived and sequestered, Legendre and Le Fevre 1992). Dashed arrows: food-web recycling of DOC, from consumers to heterotrophic bacteria (as a consequence of viral lysis, sloppy feeding, excretion by herbivores, and degradation of fecal material and other detritus, and carbon sequestration as long-lived DOC. The shaded rectangle delineates the microbial food web. (From Legendre, L. and Michaud, J., *Mar. Ecol. Prog. Ser.*, 1, 164, 1998. With permission.)

levels under the ice, bacteria exhibited P:B ratios 2–6 times higher in open waters, even though their abundance and biomass were also higher there. Bacterial carbon biomass averaged 23–24% of phytoplankton biomass under ice cover but only 7–12% in open waters. The portion of the primary production that is consumed by bacteria depends upon numerous physiological and environmental factors, but the most important appears to be the growth phase of the phytoplankton bloom (Cota et al. 1990). In the autumn bacteria were consuming about three-quarters of the primary production in the open water, compared with only 14% in the spring when algal biomass and productivity were several times higher. The sequence of events appears to be as follows. In spring bloom conditions, the bacteria do not increase rapidly enough to consume the available DOM released by the microalgae. As the bloom progresses and decays in the late summer, bacterial biomass has built up to higher levels, and with algal senescence and autolysis greater amounts of POM and labile DOM become available to the bacteria. However, the build up of the heterotrophic protozoan populations results in higher levels of grazing on the bacteria, and this results in the decline of their populations to winter levels (Figure 15.7). Thus the bacteria play a dual role in the Marginal Ice-Edge Zone, one as mineralizers making "regenerated" nitrogen available to primary producers, and another as secondary producers that are eaten by other organisms in the pelagic food webs, especially the heterotrophic flagellates.

Bacteria have been shown to be abundant in the sea ice of the Fast Ice Zone (Sullivan and Palmisano 1981, 1984; McConville and Wetherbee 1983; Grossi et al. 1984; Kottmeier et al. 1987). The sea ice bacteria are more abundant and of five to ten times greater volume than the bacterioplankton, and are frequently found in long chains typical of bacteria from organic-rich environments. Similarly, bacteria in the pack ice are more abundant and larger than the bacterioplankton, and are associated with a high concentration of microalgae (Marra 1980; Miller et al. 1985; Sullivan 1985; Garrison et al. 1986a, 1986b). Kottmeier et al. (1987) estimated that bacterial production in the fast ice is as high as 9% of primary production, with growth rates of up to 0.2 day^{-1} during the austral spring microalgal bloom.

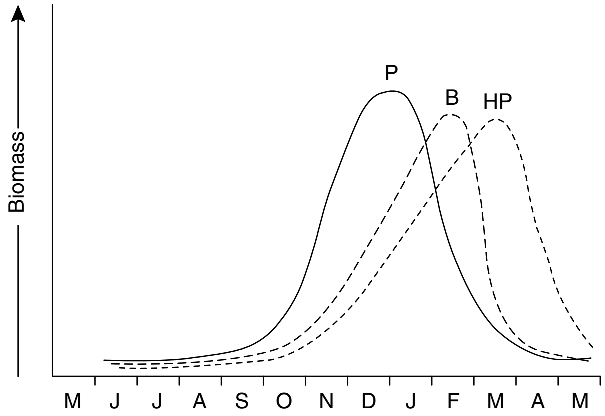


FIGURE 15.7 The inter-relationship between a phytoplankton bloom (P) in the marginal ice edge zone and the growth of bacteria (B) and heterotrophic protozoa (HP).

Kottmeier and Sullivan (1990) have studied bacterial biomass and production in the pack ice during the spring, autumn, and late winter. They hypothesize that bacteria accumulate in the pack ice as a result of both physical and biological processes. During the formation and growth of the ice, physical processes act to concentrate and accumulate bacteria within the ice matrix. This is followed by growth along the physicochemical gradients that are found in several sea ice microhabitats. Bacterial biomass and production were much greater than in the underlying seawater (Table 15.3) and equal to that in several meters of water. Among microhabitats, highest bacterial production and most rapid growth rates (>1 day^{-1}) were found in saline ponds on the surface of the floes and in the pore water in the interior on the floes (Table 15.4). Bacterial carbon production ranged from 2% of primary production in surface brash to 45–221% of primary production in surface ponds and pore water. Table 15.4 demonstrates the close relationship between microalgal and bacterial biomass. It is also evident that the bacterial production supports subsequent populations of microheterotrophs of the “microbial loop”, which in turn may support organisms at higher trophic levels. The sea ice bacteria may provide remineralized, inorganic nutrients for the continued microalgal growth in localized microhabitats within the ice, or they may compete with the algae for nutrients. Upon the melting of the ice, the actively growing bacteria are released into the water column where they contribute to the microbial biomass in the seawater.

15.4.3 THE MICROBIAL FOOD WEB

The microbial food web has been discussed in detail in Chapter 14, Section 9. Davidson (1996) has discussed the modelling of microbial food webs with reference to some thirteen systems models that have incorporated aspects of the microbial food web. These models have confirmed the general importance of microbial food webs, and that the specific inclusion of protozoan predators in models is necessary to simulate the observed dynamics. Simulations have indicated that the effect of the microbial food web on the food chain may vary greatly, depending on the imposed physical or biological conditions. The manner in which nutrient regeneration from protozoan predators and its subsequent reutilization by bacteria is simulated is of importance in microbial food web models. These models have increased our understanding of the interaction between grazing and nutrient cycling, and the behaviour of food chains and webs.

Marchant and Murphy (1996) have reviewed the interactions at the base of the Antarctic food web with particular reference to the microbial food web (see Section 15.6.3.1 for further details). Garrison and Mathot (1996) have discussed the importance of pelagic and sea ice microbial communities with particular reference to research carried out west of the Antarctic Peninsula. Figure 15.8 is a conceptual model of the pelagic food web depicting the importance of the microbial communities. In Antarctic waters the importance of many of the microbial components has been underestimated because of the idea that this region is characterised by a short, simple, largely diatom-krill dominated, grazing food chain. While this may be the case in areas of diatom blooms, in the bulk of the Antarctic seas and in post-bloom areas algal assemblages are dominated by autotrophic nano- or picophytoplankton (Stockner and Anita 1986).

The organisms comprising the microbial food web are autotrophic nano- and picophytoplankton, heterotrophic flagellates, and ciliates and bacteria. von Brockel (1981) was the first to address the importance of autotrophic nano- and picophytoplankton in Antarctic waters. Hewes et al. (1983, 1985) collected data of autotrophic and heterotrophic nanoflagellates in surface water during a cruise that circumnavigated the Antarctic Continent. Based on fractionated chlorophyll *a*, they reported that $>50\%$ of the biomass was in the nano- and picophytoplankton fraction. Their observations indicated that about 30% of the nanoplankton flagellates were heterotrophs. They reported that

TABLE 15.3
The Inter-Relationship Between a Phytoplankton Bloom (P) in the Marginal Ice Edge Zone and the Growth of Bacteria (B) and Heterotrophic Protozoa (HP)

	Core J	Core K
Microalgal biomass[a] (diatoms, autotrophic dinoglagellates and other flagellates)	24.1	200
Bacterial biomass	25.6	217
Heterotrophic biomass (flagellates, ciliates, amoebae and micrometazoans)	3.09	17.2
Total biomass	52.8	434.2
Bacterial: microalgal biomass (%)	106	108
Microheterotrophic: microalgal biomass	12.80	8.60
Microheterotrophic: bacterial biomass	12.10	7.93
Microheterotrophic: microalgal + bacterial biomass	6.22	4.12

[a] Chlorophyll $a \times 38$ (Sullivan et al. 1985).

Source: From Kottmeier, S.T., Sullivan, C.W., *Deep-sea Res*. 37, 1311, 1990. With permission.

TABLE 15.4
Enrichment of Bacterial Characteristics in Sea Ice

Characteristic	Spring Ice	Autumn				Winter Ice
		Ice	Slush	Surface Pond	Pore-Water	
Bacteria	10.2	5.11	16.6	19.2	1.86	—
Bacterial biomass	28.4	14.9	45.6	80.3	4.44	—
Average cell biomass	2.80	3.98	2.73	4.16	2.38	1.20
Bacterial cell production	—	0.466	0.607	12.4	7.31	15.3
Bacterial carbon production	—	17.8	16.5	4840	208	18.3
Bacterial growth rate	—	0.737	0.199	8.78	6.47	—

Estimated by determining the ratio of bacterial characteristics in various sea ice microhabitat to the underlying water during spring 1983 and autumn 1986 in the Weddell Sea and during winter 1985 in the Bellinghausen Sea. Values are the ratio sea ice: underlying water for each characteristic.

Source: From Kottmeier, S.T., Sullivan, C.W., *Deep-Sea Res.,* 37, 1311–1390, 1990. With permission.

heterotrophic flagellate biomass ranged from 7.6 μg C l^{-1} and averaged 24 μg C l^{-1}. Hewes et al. (1985) reported that at two stations in the Scotia Sea the ciliate biomass ranged from 1.7 to 7.3 μg C l^{-1}, accounting for about 40% of the total microplankton biomass.

A study of phytoplankton biomass and ciliate abundance by Heinbokel and Coats (1985) at Arthur Harbour showed that the chlorophyll biomass was dominated by a less-than-20-μm size fraction of the phytoplankton (65–87% of chlorophyll *a*) and ciliate abundances ranged from 1.7 to 5.1×10^3 cells l^{-1}. Nöthig et al. (1991), in studies from the eastern Bransfield Strait to the Orkney Islands, described phytoplankton assemblages dominated by nanoflagellates, prasinophytes, and cryptophytes. Heterotrophic biomass was dominated by heterotrophic dinoflagellates (58%) and non-loricate ciliates (42%).

The most comprehensive studies of epipelagic microbial community structure were made during the Antarctic Marine Ecosystem Research in the Ice Edge Zone (AMERIZ) in the waters of the Weddell and Scotia Seas. Seasonal data on

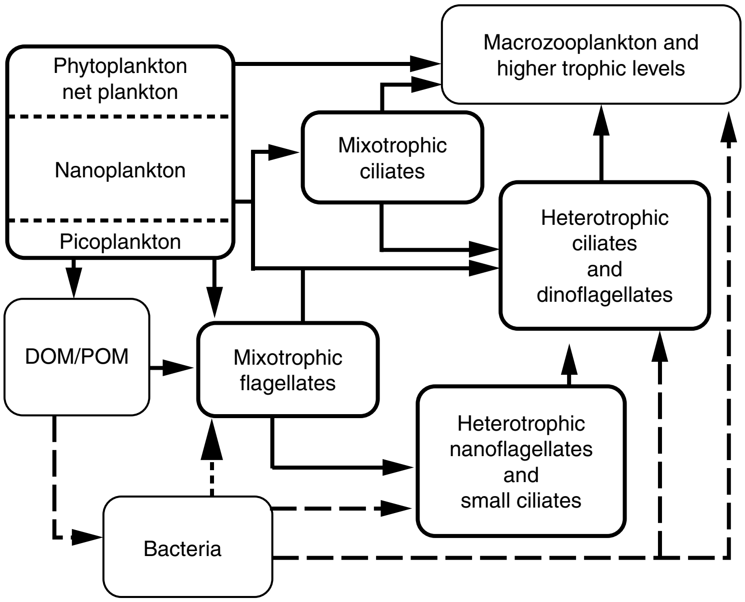


FIGURE 15.8 Conceptual model of the pelagic food web. Solid lines indicate the grazing food web. Broken lines indicate possible pathways from DOM sources through bacteria. Although it is not shown, Dom and POC are produced by all components of the food web. Compartments with lined margins indicate the major groups of organisms constituting the food web. DOM, dissolved organic matter; POM, particulate organic matter. (From Garrison, D.L. and Mathot, S., *Ant. Res. Ser.*, 70, 156, 1996. With permission.)

the community composition have been reported in Garrison and Buck (1989a, 1989b) and Garrison et al. (1991, 1993). Several conclusions were drawn from these studies: (1) The biomass of the protozooplankton is often a significant fraction of the total biomass in the nano- and microplankton assemblage. This percentage ranged from 6 to 11%, 8 to 19%, and 48 to 76% for the spring, summer, and autumn studies, respectively; (2) The protozooplankton biomass and abundance distributions appeared to reflect production gradients because most of the protozooplankton biomass (e.g., flagellates and ciliates) were found within the upper 100 m or so of the water column, and because biomass was found to vary directly with phytoplankton biomass and production, and bacterial biomass and production, in a gradient across the ice edge zone during both spring and autumn; and (3) Among the protozooplankton, the flagellates and ciliates (primarily non-loricate oligotrichs) were the major group making up the protozooplankton biomass. In these and other studies a seasonal bloom of autotrophs is followed by a seasonal increase in the biomass of heterotrophic consumers (Figure 15.9).

15.4.4 COMPARATIVE ROLES OF KRILL AND OTHER ZOOPLANKTON

Chapter 4 gave a general account of the zooplankton of the Southern Ocean. Here we shall consider their role in the pelagic ecosystem with special reference to the Seasonal Pack-Ice Zone, and the role of krill in relation to other zooplankton species. It has generally been considered that krill contribute 50% of the biomass of the zooplankton as a whole. However, in spite of the intensive decade of the BIOMASS programme directed at understanding the biology, distribution, and standing stock of krill, the number of krill is still uncertain. The situation is further complicated by a number of factors. Firstly, krill are discontinuously distributed both in space and time due to their aggregating and swimming behaviour. Variability in krill distributions will be discussed in detail. Secondly, there are other zooplankton species. Apart from the early life history, stages krill are largely found in the euphotic zone, whereas the copepods, which along with the euphausiids are the dominant zooplankton, are distributed from the euphotic zone to 1000 m plus. Thirdly, mucus feeders (predominately slaps) occasionally form dense swarms, but their role in relation to other zooplankton species is not well understood. They are a major component of the Ice-Free Zone communities away from the krill areas. However, current lack of knowledge about the rate processes of these organisms and their biology prevents consideration of their importance in biogeochemical cycles or their role in the ecosystem (Duhamel and Hureau 1985).

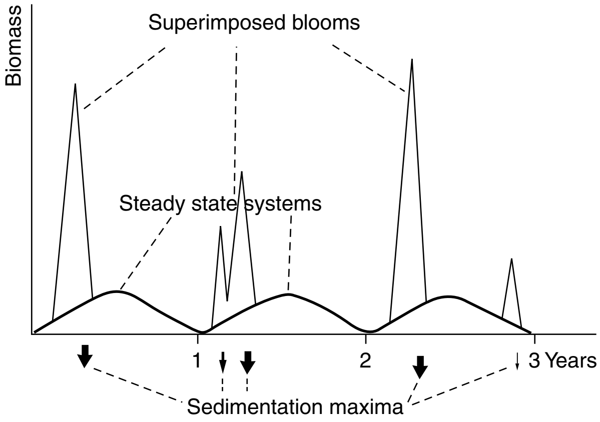


FIGURE 15.9 A hypothetical scheme illustrating the relationship between seasonality of the microbial network regenerating system (thick line) with superimposed "blooms" (thin lines). The latter exhibit more variability as they are induced by weather conditions operating on a scale of weeks. They are followed by a correspondingly variable sedimentatiration pulse. Based on Pace et al. (1984). (From Smetacek, V.S., Scharek, R., Nothig, E.-M., *Antarctic Ecosystems. Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Ed., Springer-Verlag, Berlin Heidelberg, 103, 1990.)

A remarkable feature of the Antarctic meso- and macrozooplankton is that the biomass in the upper 1000 m is mostly constant throughout the year (Foxton 1956, 1966; Hopkins 1971; Atkinson and Peck 1988).A few large copepod species, which reside over winter in the deeper layers in a dormant state, contribute the bulk of the stock. These copepods form an integral part of the microbial network, not only feeding on it as top predators, but also helping to maintain it by adding detritus in the form of fecal pellets and exuvia, as well as ammonia and microzooplankton in the form of nauplii.

Protozoan herbivores such as large dinoflagellates, many ciliates, heliozoans, radiolarians, and foraminiferans are common in Antarctic waters (von Brockel 1981; Hewes et al. 1983; Spindler and Dieckman 1986; Brandini and Kutner 1997; Nöthig 1988). These herbivores must exert considerable grazing pressure on the phytoplankton. However, they are grazed by the copepods, which have been shown to collectively feed on them in the presence of low phytoplankton biomass (Nöthig 1988). Therefore, the copepod biomass in any given region is largely geared to the microbial network and is not dependent on transient phytoplankton blooms.

There is considerable variability in the relative proportions of krill and other zooplankton species in the Southern Ocean (Table 15.5). As would be expected, compact krill swarms have a low percentage of other zooplankton species. In more diffuse swarms the proportion of these other species would be expected to be higher. In Chapter 3 where the swimming and feeding behaviour of krill were discussed in detail, it was noted that krill can swim for considerable distances as foraging swarms, and that when they locate a dense supply of phytoplankton they can graze it down and reduce the biomass of the preferentially grazed species (usually larger diatoms) to low levels. In this process they can change the species composition of the phytoplankton community and shift it towards one dominated by nanoplankton.

TABLE 15.5
Krill Biomass as a Proportion of Total Phytoplankton Biomass

Locality	Period	Biomass (% of total)
Scotia sea	24 Jan.–14 Feb.	
Total zooplankton		25
Excluding two swarms		
Western sector		6
Eastern sector		4
North of Elephant Island		
Total zooplankton	4–7 Mar.	70
	20–23 Mar.	72
Excluding large swarm	4–7 Mar.	40
	20–23 Mar.	24
Bransfield Strait	10–11 Mar.	
Total zooplankton		69
Excluding large swarm		40
South of Elephant Island	14–10 Mar.	25
East of Elephant Island		29
North of South Orkney Islands	14–19 Mar.	61
West of South Orkney Islands		4

Source: From Brinton, E., Antezana, T., *J. Crust. Biol.,* 4(Special Issue), 45, 1984. With permission.

Although the total standing stock of krill not known within any degree of certainty, it clearly is in excess of 100 million tonnes. By any standard this is an exceptionally large biomass for a single species. It is a species that is the product of a long evolutionary history in isolation, adapted to the strong seasonality and variability of the pack ice zone. Because of its swarming and foraging behaviour, it can seek out pelagic food in an environment where phytoplankton blooms can be very patchy in their distribution. Chapter 5 gave accounts of recent research that established, contrary to earlier opinions, krill have an ample food supply available in the winter in the form of the sea ice microalgae at a time when phytoplankton stocks in water column are low. This feeding behaviour is especially important to the furcilia stages that are particularly abundant within the pack ice.

Figure 15.10 depicts the energy flow through a krill stock to its consumers. The filtering basket and mouth parts of krill can cope with a food spectrum of 10 orders of magnitude in weight, ranging from nanoplankton to adult krill. Adult krill are very large in relation to other pelagic herbivorous zooplankton and its energy demands for metabolism are very high. When feeding in the euphotic zone, the principal food is phytoplankton, but in the process of filtering that they also certainly consume heterotrophic flagellates and ciliates, and probably other zooplankton. In spite of their large biomass, it has been estimated that in the areas where they occur krill consume at most 5% of the spring phytoplankton blooms, and often much less (see Chapter 5). The extent to which they also consume POM aggregates with their associated microbial community (the detrital–microbial complex) is unknown. In the process of "sloppy" feeding, they add to the POM and DOM pools within the water column. Excretion adds to the DOM pool and also N and P to the euphotic zone. As detailed in Chapter 14, krill exuiva and fecal pellets are a significant component of vertical flux of organic material.

Either directly or indirectly, krill support large populations of vertebrate consumers as depicted in Figure 15.10 (Everson 1984c). Krill also compete for the primary production of the euphotic zone with other zooplankton species, especially the copepods and the salps. The salps, as mucus-net feeders, are able to feed on much smaller-sized particles than krill such as bacteria and picoplankton, and thus may not directly compete for the larger diatoms. However, it is significant that dense swarms of salps and krill do not coincide, and areas where krill may have dominated in one season may be dominated by salps in the next.

15.4.5 THE ROLES OF GRAZING AND IRON IN PELAGIC ECOSYSTEMS

Smetacek et al. (2004) have addressed the roles of grazing and iron as selective forces operating on the structure and functioning of Southern Ocean pelagic ecosystems. As discussed in Chapter 2, Section 8.4, it is established that iron availability is a key factor in the initiation of phytoplankton blooms in the Southern Ocean. Smetacek et al. (2004) contrast the iron-limited, silica-sinking, open-ocean system with the iron-replete, carbon-sinking phytoplankton bloom system. Phytoplankton growth rates in areas of the Southern Ocean remote from land are limited by iron availability, whereas the higher-productive coastal shelf waters are supplied with iron from land run-off and shelf sources, and in land-remote areas from aeolian dust or melting icebergs.

Figure 15.11 illustrates the iron-limited, silica-sinking, open-ocean system. This system is characterised by the regenerating system comprising bacteria, pico- and nanophytoplankton, together with the protozoan grazers. Small copepods and salps are the top grazers on small phytoplankton cells. This system supports small diatoms, as well as heavily salicified diatoms that accumulate by sequestering nutrients from the microbial network. The diatoms are highly diverse in shape and comprise over one hundred species from a broad rage of the common diatom genera. In restricted regions along fronts where iron, albeit at low concentrations, is introduced to the surface in upwelling water, diatom biomass can exceed that of the microbial phytoplankton by a factor of two or more (Smetacek et al. 2002). About six species from disparate genera and *Phaeocyctis* colonies tend to contribute the bulk of the biomass. They are all giants of their respective genera and they can dominate diatom blooms in the Polar Frontal Zone at Si concentrations less than 5 mmol m^{-3} (Smetacek et al. 2002).

Figure 15.12 illustrates the iron-replete, carbon-sinking phytoplankton bloom system. This system is characterised by high growth rates of weakly salicified diatoms and

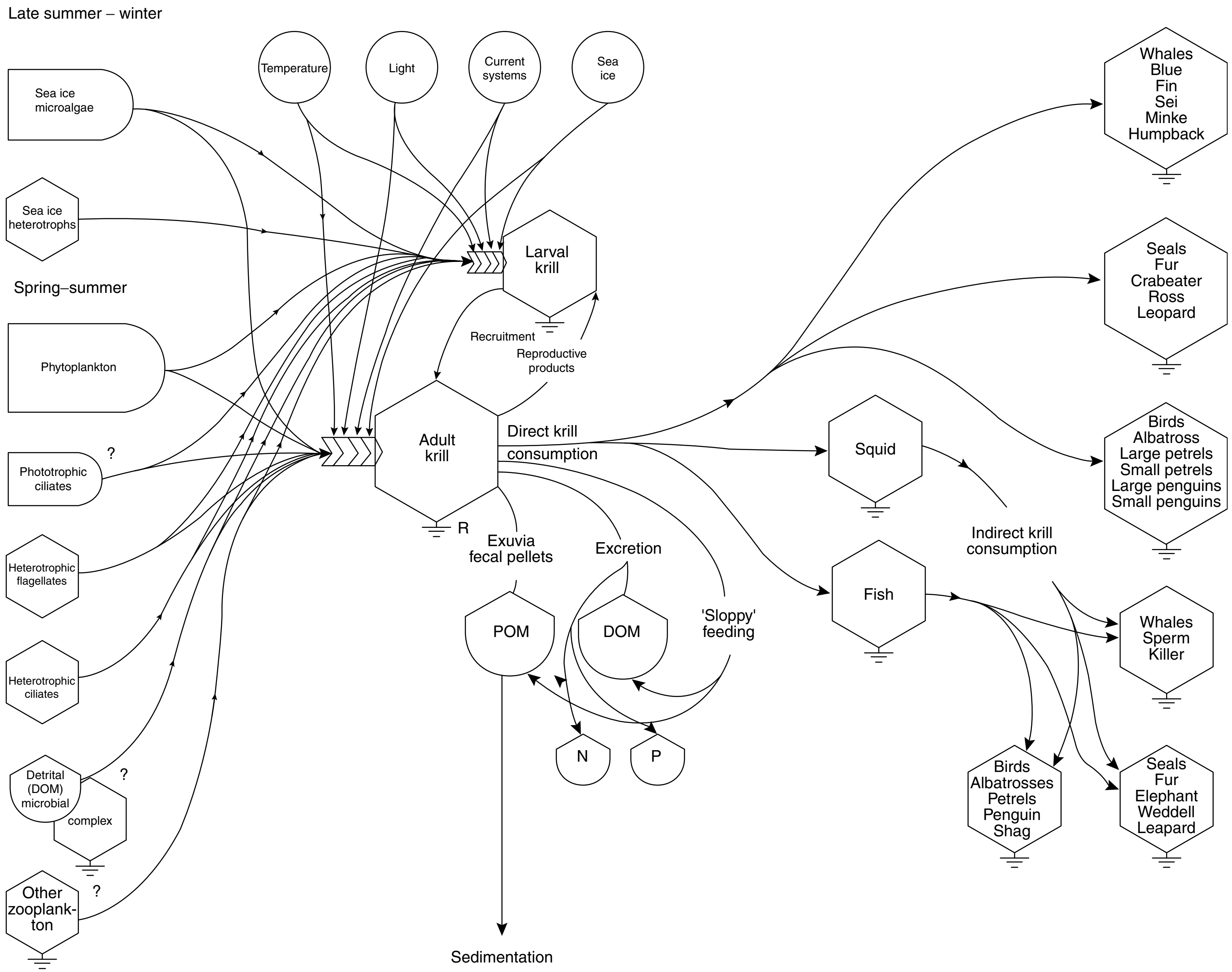


FIGURE 15.10 Model of energy flow through a krill stock and its consumers. With permission.

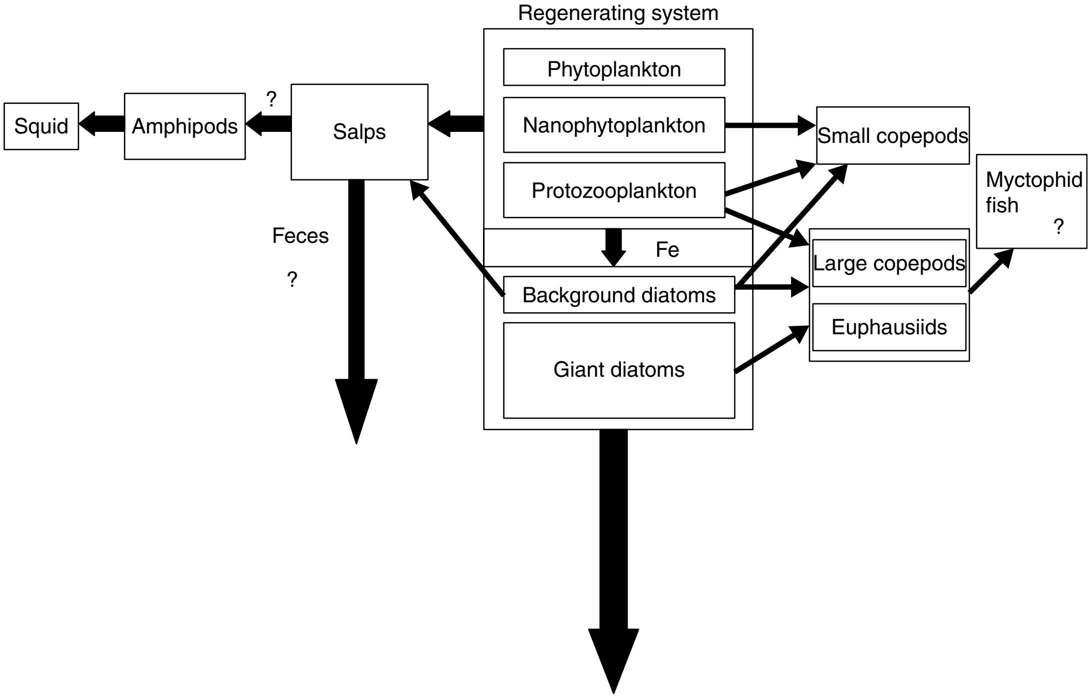


FIGURE 15.11 Schematic representation of the iron-limited, silica-sinking, open ocean system. The regenerating system comprises bacteria (not shown) and pico- and nanophytoplankton with their protozoan grazers. Salps and copepods graze on this system but also on the weakly-salicified background diatoms, whereas the giant diatoms are mainly grazed by large copepods and euphausiids. Vertical flux consists mainly of silica. (From Smertacek, V., Assny, P., and Henjes, J., *Ant. Sci.,* 16, 553, 2004. With permission.)

Phaeocyctis colonies resulting in the build up of the blooms that fuel the food chain of the giants (diatoms–krill–whales) and drive the carbon pump. The vertical flux comprises diatoms cells, phytodetritus of faeces of crustacean zooplankton with lower Si:C ratios than in iron-limited systems.

The Si:N ratio is reported to be up to twofold higher in iron-deficient diatoms as compared to iron-sufficient diatoms (Takeda 1998; Hutchins and Bruland 1998), which implies that the former make thicker frustules (Boyle 1998), or that their cells contain relatively less plasma than iron-sufficient diatoms, or both. Diatom biomass in the iron-depleted, open ACC although low, tends to be dominated by species that are larger and have thicker frustules or stouter spines than species that dominate the much higher diatom biomass in productive coastal waters. This difference in diatom community composition is reflected in the underlying sediments. Whereas biogenic silica (BSi) is dominated by the thick frustules of a few species, and contributes about 50–70% of the sediments underlying the low productive areas of the

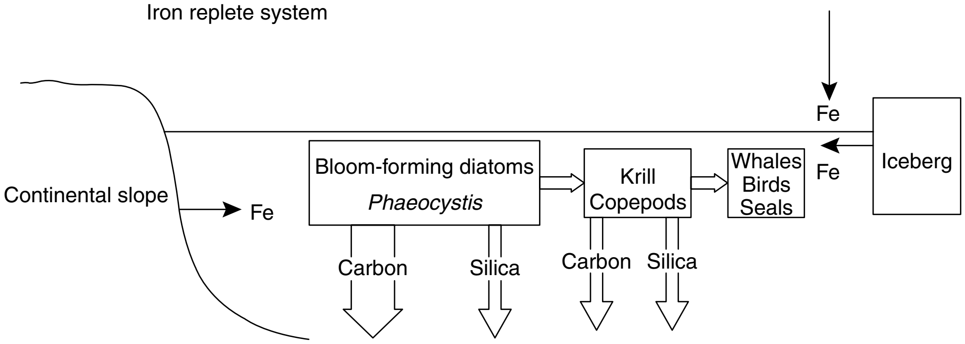


FIGURE 15.12 Schematic representation of an iron-replete, carbon-sinking phytoplankton bloom system. Iron is supplied from land run off and shelf sources, and in land-remote areas from aeolian dust and iceberg melting. Vertical flux comprises diatom cells, phytodetritus or feces of crustacean zooplankton with lower Si:C than in iron-limited systems. (From Smetacek, V., Assny, P., Henjes, J., *Ant. Sci.*, 16, 534, 2004. With permission.)

ACC, the sediments under the productive regions have lower BSi (10%), but twofold higher organic carbon percentage of bulk sediment (Berger and Herguera 1992). Most of the diatom frustules in coastal sediments are resting spores of the cosmopolitan genus *Chaetoceros*.

15.4.6 THE ROLE OF VERTEBRATES

The apex predators in the Southern Ocean include fish of several families (predominantly the Nototheniidae), the fur seals (Otariidae) the sea elephants (Phocidae), the baleen whales (Mysticetes), toothed whales (Odontocetes), and seabirds of various families, the most important ones being the penguins (Spheniscidae) and petrels (Procellariidae). Only a handful of warm-blooded vertebrates overwinter around the margins of the continent, the most well-known being the emperor penguins which breed during the austral winter. The warm-blooded vertebrate communities of the Southern Ocean can be sub-divided into two groups, shelf residents, and slope and oceanic water residents.

Permanently resident, high-trophic level predators in the pack ice over the shelves include the minke whale, four seals (Ccrabeater, Weddell, Ross and leopard) and five birds (emperor and Adélie Penguins, Snow and Antarctic petrels, and the South Polar skua) (Figure 15.13). Key prey species at the intermediate levels of the food web are the small euphausiid (*E. crystallorophias*), the pelagic silverfish (*P. antarcticum*), some pagotheniid fish, and a squid (*Psychroteuthis glacialis*) (Plotz 1986; Hopkins 1987; Thomas and Green, 1988; Ridoux and Offredo 1989). During the winter at the pack ice edge predators characteristic of the shelf are present, as well as the beaked whales (Ziphiidae), Antarctic fur Seals, elephant seals, chinstrap penguins, and several species of petrels (Procllariidae). Here *E. superba*, myctophid fish, pasiphaeid shrimps, and two squid species (*G. antarcticus* and *Galiteuthis glacialis*) are important prey (Ainley et al. 1984, 1988; Laws 1984a, 1984b). Mesoplagic fish, which are important consumers of krill, are ecologically very important in this food web (Lancraft et al. 1989).

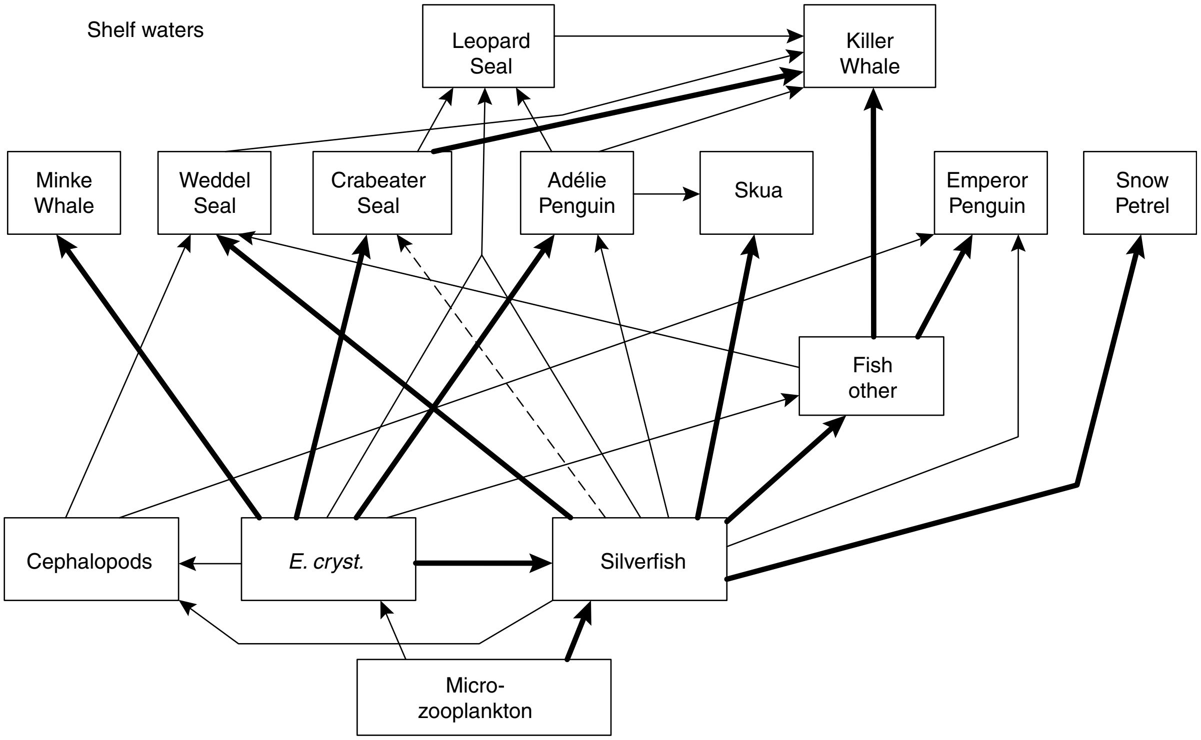
As the pack ice retreats in the summer, the surface waters of the Southern Ocean are invaded by a range of predators that feed on the abundant macrozooplankton and microplankton. In addition to the many species that resided at the ice edge during the winter, the ecologically important species include several large baleen whales (Balaenopteridae and Balaenidae), male sperm whales (*Physeter macrocephalus*) which feed in the mesopelagic zone, killer whales (*Orcinus orca*), and about ten seabird species, mostly belonging to the order Procellariformes (Laws 1977b; Ainley and Jacobs 1981). While *E. superba* is the dominant food item in the summer, some species such as the right whale (*Eubalaena australis*), prions (*Pachyptila* spp.), and diving petrels (*Pelecanoides* spp.) also feed on small copepods (Brown and Lockyer 1984; Ainley and DeMaster 1990) (Figure 15.13B).

Ainley and DeMaster (1990) have discussed the factors that concentrate these predators and their prey in specific locations. These concentrations occur at the Marginal Ice-Edge Zone (Fraser and Ainley 1986) in association with polynyas, at continental shelf-break fronts (Ainley et al. 1985; Veit and Braun 1984) and insular fronts.

Perissinotto and McQuaid (1992) have discussed the impact of land-based predators on the vertically migrating zooplankton and micronekton in the waters surrounding the Prince Edward Archipelago. The Prince Edward Archipelago has a breeding population of twenty-nine bird species and three seal species (Condy 1981; Cooper and Berruti 1989), estimated at 4–6 million individuals. Studies have revealed diurnal vertical migration of the major prey species (the euphausiid *Euphausia vallentini* and the myctophic fish *Kreftichthys andersoni*) of the land-based predators, resulting in advection of the prey over the shelf. The predators have a major impact on their prey species (fish, crustaceans, and squid) (Table 15.6). It was estimated that 3200 tons of zooplankton and 310 tons of myctophid fish were carried over the shelf every 24 h. Predators in the archipelago consume roughly 900 tons of crustaceans and 1700 tons of fish a day^{-1}. The daytime decrease in biomass on the shelf relative to deep water was about 35% of the total zooplankton (almost exclusively due to migrating crustaceans) and over 80% of the fish. Macaroni and rockhopper penguins are zooplankton feeders, and they account for roughly 85% of the total crustacean consumption in the archipelago. However, mesopelagic fish and squid form 52% of the macaroni penguin diet. Seals are predominantly squid feeders. It is thus clear that land-based vertebrates can have a major impact on their food resources.

van Francker (1992) investigated energy flow through the top predators (birds, seals, and whales) in the Confluence and Marginal Ice Zones of the Weddell and Scotia Seas. Figure 15.14 shows the distribution of bird biomass as a function of distance from the ice edge. Average bird biomass in Open Water Zones ranged from 5 to 11 kg km^{-2} (0.8 kg^{-2} in the Subantarctic Zone), while in the Sea Ice Zones it ranged from 32 to 56 kg^{-2} due mainly to Adélie Penguins. According to Briggs et al. (1987), bird biomasses of about 50–100 kg^{-2} are the upper limits reached in the most densely populated regions worldwide.

Figure 15.15 diagrams the energy and food requirements of the top predators in the different zones of the area investigated. Bird, seal, and probably also whale requirements were highest in ice-covered areas. Densities generally increased further into the ice. In the pack ice, combined energy requirements of the top predators often amounted to about 200,000 kJ day^{-1}, or 45 kg of fresh food, indicating high abundance and availability of prey under the ice. Turbinosed birds concentrated along the ice edge in the early summer, but they moved north to open water during December, leaving the area of maximum phytoplankton biomass associated with the retreating ice edge. This pattern matched northward movement of krill swarms. Figure 15.13 shows that the food requirement of the top predators increased with distance into the pack ice.



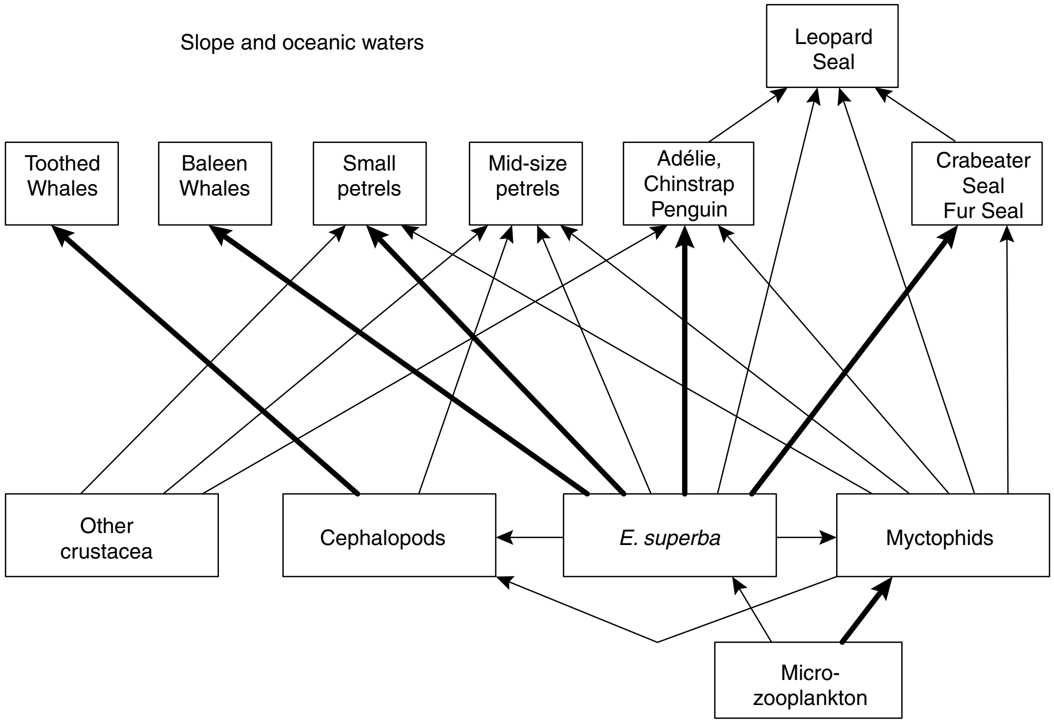


FIGURE 15.13 Summary of the major energy flows in the upper trophic levels of the ice influenced, shelf and slope/oceanic waters in the Antarctic. Data from Ainley et al. (1984), Ainley and Fraser (unpublished), DeWitt and Hopkins (1977), Nemoto et al. (1985), Siniff and Stone (1985), Williams (1985a), and Offredo and Ridoux (1986). (From Ainley, D.G., DeMaster, D.P., *Ecology*, 61, 522, 1990. With permission.)

TABLE 15.6
Daily Food Consumption (t wet wgt) of the Main Land-Based Predators at the Prince Edward Archipelago

Predator	Fish	Crustaceans	Squid	Total
King Penguin *Aptenodytes patagonica*	1599	Trace	177	1776
Macaroni Penguin *Eudyptes chrysolophus*	82.7	331	95.3	509
Rockhopper Penguin *Eudyptes chrysocome*	8.82	113	2.56	124
Gentoo Penguin *Pygoscelis papua*	1.94	2.11	0.08	4
Penguins, Family Spheniscidae (total)	1692	446	275	2413
Seals, Order Pinnipedia	27.1	1.07	66.8	94.9
Petrels and Prions, Family Procellaridae	150	147	74.2	391
Wandering Albatross *Diomedia exulans*	0.47	0.47	3.70	4.64
Total	1870	614	420	2904

For penguins only figures based on seasonal consumption for the period of the investigation. All other values were calculated from estimates of annual food requirements given by various sources.

Source: From Perissonotto, R., McQuaid, C.D., *Mar. Ecol. Prog. Ser.,* 80, 25, 1992. With permission.

15.4.7 STABLE ISOTOPES

Early studies of the diets of organisms in Antarctic food webs involved investigations of stomach contents enumerating either the numbers or biomasses of the individual species consumed. Such analyses suffered from a number of defects. Firstly, identification of partially digested remains was often difficult; secondly, many soft-bodied animals were often not identifiable; and thirdly, the contribution of the different items consumed to the animals' energy budget could not be assessed. However, more recently the measurement of stable isotope ratios ($^{13}C/^{14}C$ and $^{15}N/^{14}N$) in animal biomass has, under certain circumstances, proven useful to elucidate feeding relationships in a variety of marine settings. As reviewed by Fry and Sherr (1988) and Wada and Hatton (1990), the utility of such measurements for marine food web studies lies in the fact that stable isotope abundances of carbon and nitrogen in an animal are largely determined by the isotope abundance of the animal's food. Therefore, large differences in isotope abundances among animals within a community can provide evidence of significant differences in diet among those

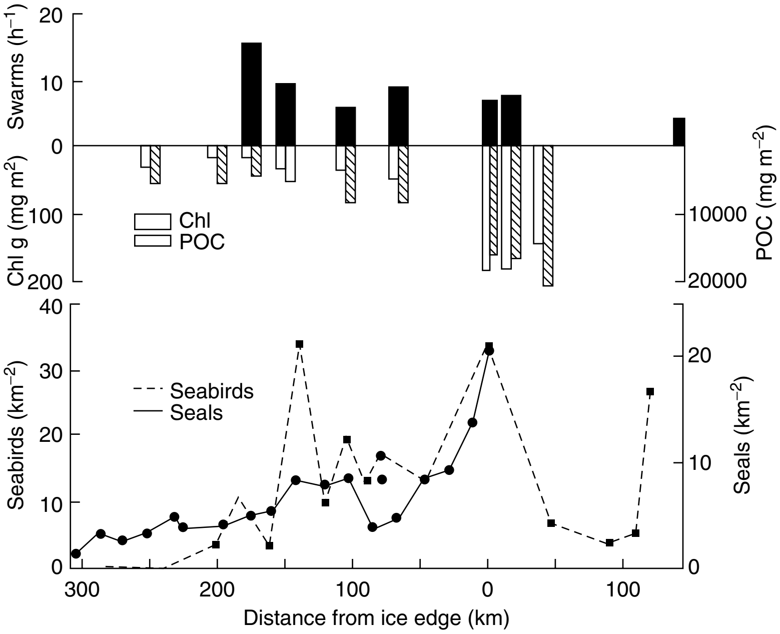


FIGURE 15.14 Bird biomass as a function of distance from the ice edge. EPOS Leg 2, all counts ($n=704$). Numbers at the x-axis refer to outer limits of areas for which data have been pooled (25 = 0–15 km; 75 = 25–75 km, etc.). (From van Frankner, J., von Falkner, A. *Polar Biol.,* 12, 99, 1992. With permission.)

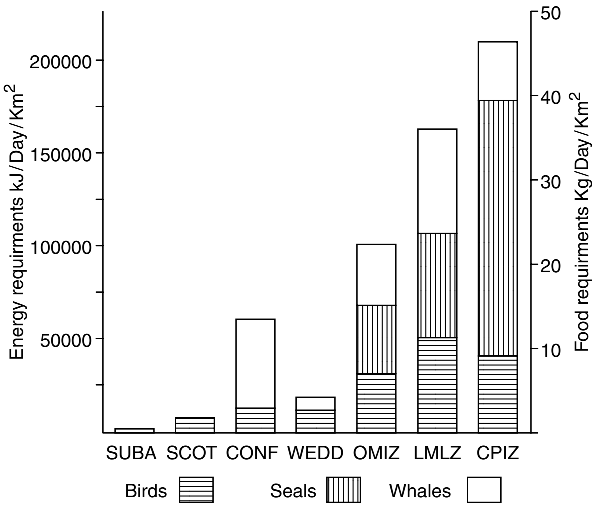


FIGURE 15.15 Energy and food requirements of top predators in different zones of the Eeddell and Scotia Seas. EPOS Leg 2, all counts ($n = 704$). Birds; seals, whales. (From von Frankner, A. *Polar Biol.,* 12, 101, 1992. With permission.)

consumers. Conversely, similarities in isotope abundances among animals signify similar diets, provided that different combinations of isotopically contrasting food items have not by chance led to identical ^{13}C/^{12}C and ^{15}N/^{14}N among consumers.

Metabolic isotopic fractionations that occur within animals also need to be considered. It has been shown that marine invertebrates are measurably enriched in their heavier isotopes (especially ^{15}N) relative to their food (Minagawa and Wada 1984). This is apparently the consequence of isotopically selective excretion or respiration of the lighter isotopes. Elevations in an animal's ^{13}C/^{12}C, and particularly ^{15}N/^{14}N relative to those of the community food base, can thus infer a consumer's trophic distance from that food base (Rau 1981; Minagawa and Wada 1984; Hobson 1991). Indeed, Wada et al (1987) used this approach to study lower animal trophic levels in the Ross Sea. ^{13}C and ^{14}N natural abundances have also been used to investigate the ecology and biogeochemistry associated with high-southern-latitude seabird rookeries (Wada et al. 1981; Moors et al. 1985; Mizutani and Wada 1988). Isotopes have been successfully applied to Southern Ocean pelagic food webs (Wada et al 1987; Burns et al 1998) and particularly to the pelagic fauna and top predators of the Weddell Sea (Rau et al. 1991a, 1991b, 1992).

Rau et al. (1991a) investigated biomass δ^{13}C, δ^{15}N, and C/N were measured for each of 29 taxa of the pelagic invertebrates from the Weddell Sea. The δ^{13}C values of the invertebrates ranged from -33.2 to -23.9%, and a significant logarithmic relationship was observed between these values and biomass C/N. This implied that the relative proportions of carbon-rich δ^{13}C-depleted lipid in these animals significantly influenced the δ^{13}C of their bulk biomass. No such relationship with C/N was evident with respect to biomass δ^{13}N, where values ranged from -1.2 to $+7.3$%. This spread of values reflected a wide diversity of food sources and trophic positions among the species analysed. Isotopic abundances of krill *E. superba* varied with individual length, apparently reflecting dietary changes during growth. Isotope values in *E. superba* from the Weddell Sea overlapped those of krill from other southern locations in the Scotia Sea/Drake Passage (Rau et al. 1991a), the Ross Sea (Wada et al. 1987), and Prydz Bay.

Rau et al. (1992) investigated δ^{14}C, δ^{15}N, and C/N ratios in tissue samples from twelve bird, four seal, and four fish species in the Weddell Sea. δ^{13}C values ranged from -31.3 to 22.0% and, in the case of fish and seal samples, varied inversely with C/N. This implied that lipid concentration significantly influenced these vertebrates' δ^{13}C measurements. No such relationship was found between C/N and δ^{15}N, where the latter values ranged from $+4.4$ to $+11.2$% with considerable overlap between the taxonomic groups measured. Significant feeding on vertebrate biomass was indicated by the δ^{15}N enrichment of the southern giant fulmar and several snow petrel individuals. Some diet separation among the crabeater, Antarctic fur, leopard, and ross Seals was also evident. Nevertheless, the overlap in δ^{15}N values among most Weddell Sea vertebrates, coupled with an observed range of vertebrate values that was considerably narrower than that of their potential prey, supported the hypothesis that many of these higher consumers shared a small number of common food resources (krill and several species of copepods and amphipods) and trophic levels.

Nyssen et al. (2002) analysed stable isotopes on ninety species belonging to different benthic communities in the eastern Weddell Sea. The ranges of isotope ratios from each taxon—grouped by phylum, class, or order followed by the number of samples, as well as that of suspended organic matter (SPOM)—are shown in Figure 15.16 and Figure 15.17. The analyses revealed a considerable range in both δ^{13}C and δ^{15}N values for the benthic species. Stable carbon isotope ratios ranged from -32% for the SPOM to -16.1% for the anthozoan *Thourella* sp. δ^{15}N values were generally less variable than δ^{13}C values, and a step-wise increase with trophic level ranged from 2.6% for SPOM to 16.1% for the fish *Pagonophryne barsukovi*, suggesting a food web composed of about five trophic levels (Michner and Schell 1994; Hobson et al. 1995).

The SPOM isotope data were typical of high-latitude northern and southern hemisphere food webs with δ^{13}C and δ^{15}N-depleted food bases (Wada et al. 1987). The high values displayed by some sponge species (-22.3 and 12.5% for δ^{13}C and δ^{15}N, respectively) compared to SPOM ratios could reflect an assimilation of sea ice POM by these benthic suspension feeders. Another hypothesis to explain the great enrichment between POM and POM grazers is assimilation by suspension feeders of benthic, re-suspended organic matter that originates from a strong microbial loop—the period of sampling (post-bloom, late-summer period) corresponding to the maximal activity (Karl 1993)—through which fixed carbon is first cycled through flagellates and microzooplankton before being consumed. The amphipod stable isotope ratios corresponded fairly accurately to the trophic classification based on gut contents, and reflected their wide spectrum of feeding types from suspension-feeders to deposit-feeders, to scavengers and predators.

15.5 ECOSTYSTEM MODELS

To obtain a coherent picture of the functioning of a marine ecosystem, we need to summarize the available information quantitatively and in a systematic manner. Over the past two decades, systems analysis and simulation models have become increasingly important analytical tools to complement field and laboratory techniques in an attempt to understand the dynamic behaviour of aquatic ecosystems. Early models of the Antarctic marine ecosystem, or rather components thereof, were directed at assessing the abundance of marine resources, and their behaviour and distribution, and at ascertaining the responses of these resources to exploitation and possible environmental change. Notable among these were the models developed for the International Whaling Commission on the stocks of

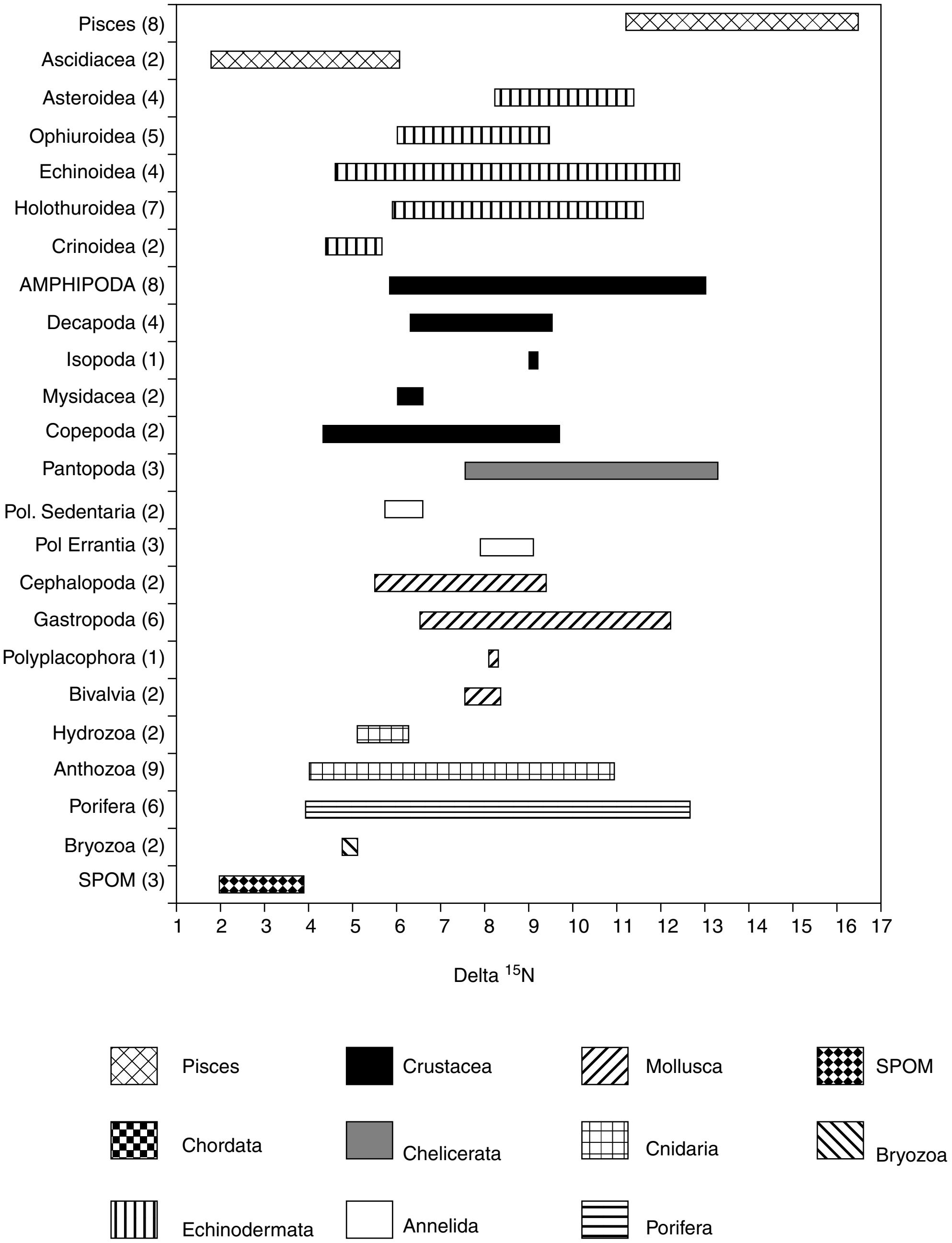


FIGURE 15.16 Range of $\delta^{13}C$ values (%) for SPOM, benthic invertebrates and vertebrates from the eastern Weddell Sea shelf. Numerals in parentheses indicate the amount of analysed species. (From Nyssen, F., et al., *Polar Biol.,* 25, 283, 2002. With permission.)

whales and the impact of different levels of exploitation. For example, Beddington and Cooke (1981), and Cooke and Beddington (1982), developed a model for assessing sperm whale abundance based on length composition. Other models (e.g., Kirkwood 1981) investigated the relationship between whale catch per unit effort and true abundance.

Modelling of Southern Ocean ecosystems, apart from Green-Hammond (1981b) model of the Ross Sea pelagic ecosystem, has been a much-neglected aspect of research into the functioning of Antarctic ecosystem. However, the establishment of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) has increased interest in model development as an aid in decision making.

15.5.1 The Role of Sea Ice in Structuring Antarctic Ecosystems

A dominating feature of the Southern Ocean is the sea ice canopy, which covers up to 20×10^6 km^2 during the winter and recedes to less than 4×10^6 km^2 extent in the austral

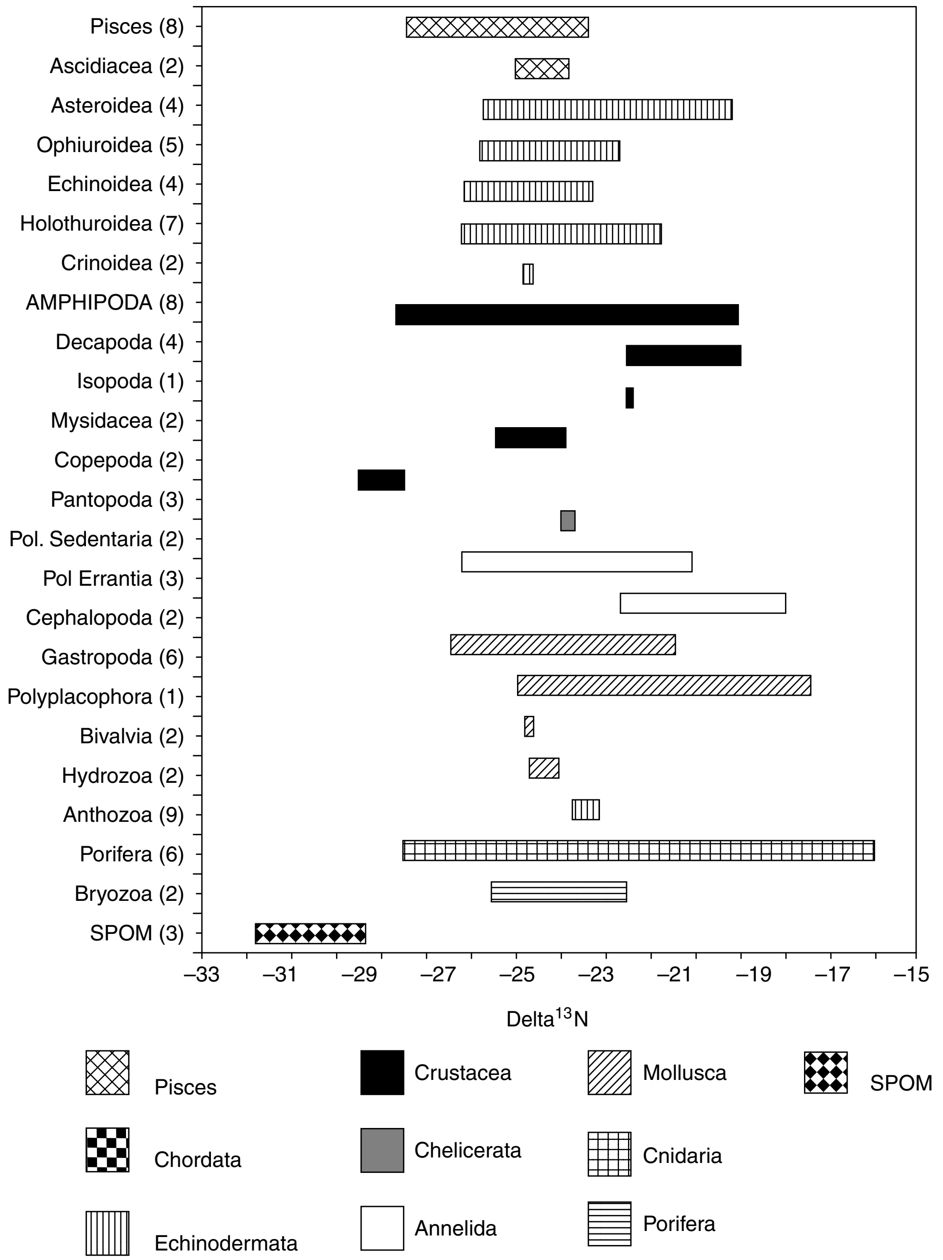


FIGURE 15.17 Range of δ^{15}N values (%) for SPOM, benthic invertebrates and vertebrates from the eastern Weddell Sea shelf. Numerals in parentheses indicate the amount of analysed species. (From Nyssen, F., et al., *Polar Biol.,* 25, 284, 2002. With permission.)

summer (Zwally et al. 1993a, 1993b). Its significance for Antarctic biology has long been recognized (Hempel 1985a, 1985b; Garrison et al. 1986). Eicken (1992) has discussed in detail the role of sea ice in structuring Antarctic ecosystems. The sea ice canopy regulates the light regime in the underlying water through two principal mechanisms. During the formation of the ice, large amounts of brine are expelled from the ice while a fraction is retained in channels in the ice (Weeks and Ackley 1982). The cold brines ejected from the sea ice are denser than the underlying water, inducing thermo-haline convection and deepening of the mixed layer (see review by Carmack 1986) (Figure 15.18). With typical mixed layer depths of 50–200 m in the Weddell Sea during winter and spring, growth of phytoplankton is retarded (Scharek 1991; Nöthig et al. 1991). On the other hand, the summertime melt of the desalinated ice (Weeks and Ackley 1982; Eicken and Lange 1989) stabilizes and shallows the mixed layer, thus enhancing phytoplankton growth (Smith and Nelson 1986; Sullivan et al. 1988). Backscatter and absorption within the sea ice and snow cover reduces the amount of light available to the phytoplankton in the water column by a factor ranging between 50 and 1000 (Buckley and Trodahl 1987). Thus, the presence of the ice favours the growth of phytoplankton that is specifically shade adapted (Sakshaug and Holm-Hansen 1986; Rivkin and Putt 1987). However, the ice provides a more favourable environment for the growth of the sea ice microalgae.

The sea ice cover is a habitat that allows for maximum utilization of sunlight, because the ice microalgae are exposed to radiative fluxes higher than anywhere in the water column below the ice. As a consequence, standing stocks of microalgae can be of the same order of magnitude within the sea ice as in the entire water column below. The two important factors structuring the sea ice community are those of light, as discussed above, and of temperature. While the surface of an ice floe generally corresponds to the ambient air temperature, the ice at the floe bottom generally remains at the freezing point of seawater (−1.8°C). The colder the ice, the more salt solution retained when the ice freezes (Weeks and Ackley 1982). Consequently, salinities with in the brine rises as high as 143 as temperature drops to −10°C (Cox and Weeks 1983). Organisms living within the sea ice not only have to cope with low temperatures, but also have to withstand high osmotic pressures. Studies by Grant and Horner (1976), Kottmeier and Sullivan (1988), and Bartsch (1989) have shown that ice diatoms are physiologically active at temperatures as low as −7.5°C and salinities as high as 100. A most important aspect of temperature is its control on brine volume, i.e., the environmental spaces available to organisms in the ice. As a result, pores of different sizes are created. The composition and biomass of the microbial communities within these pores is a function of their size.

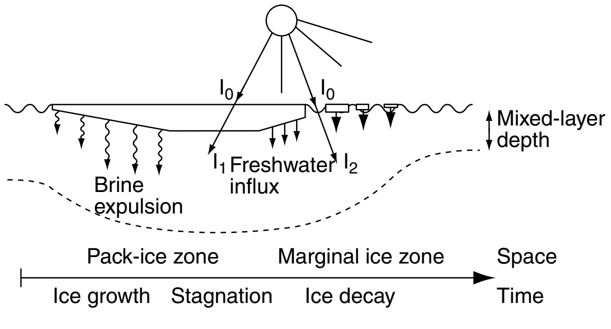


FIGURE 15.18 Temporal and spatial evolution of a sea ice cover and its influence on mixed-layer depth and irradiation fluxes into the mixed layer ($I_0 > I_2 > I_3$). (From Eicken, H., *Polar Biol.,* 12, 4. With permission.)

Antarctic sea ice is essentially a two-dimensional environment. This has important consequences for grazers up to the highest trophic level. In the sea ice, motile grazers have to expend little energy in encountering prey. Krill *E. superba*, which have been shown to feed on sea ice microalgae during the winter and spring (Bergstrom et al. 1990; Daly 1990), can exploit the microalgae in the bottom layer of the ice or in larger openings in the ice (Stretch et al. 1988). Birds and mammals similarly profit from the ice association with krill, since they can encounter their prey in high concentrations within a rather confined volume. Besides feeding on the sea ice underside, penguins and seals depend on the sea ice as a platform for resting and reproduction. The fast ice that girdles the continent plays an important role in providing the emperor penguin (*Aptenodytes forsteri*) and the Weddell Sea (*Leptonychotes weddellii*) with a breeding substrate.

As discussed above, the zonal distribution of the sea ice and its seasonal variation have resulted in creation of a series of major zones, as typified by the Weddell Sea. These are the Seasonal Pack Ice Zone, Coastal Zone and the Perennial Pack-Ice Zone. This is part of the circum-Antarctic seasonal pack ice belt, bordered by the Marginal Sea-Ice Zone on the north and the Coastal Zone in the south. The Coastal Zone typically is composed of four subunits: the ice shelf, the fast ice, the seasonal coastal polynyas, and the pack ice boundary. The fast ice, which persists for the greater part of the season, and may last several years, is of extreme importance for seals and penguins. The polynyas are a dominating feature of the Coastal Zone. They are regions of high productivity, and they provide food resources for the breeding populations of seals and penguins. The pack ice boundary is a zone of highly deformed ice. Ridges, which may account for 50% and more of the ice cover, represent a most favourable habitat for krill and other metazoans that graze within the voids created by the ridged floes (Marschall 1988; Smetacek et al. 1990).

The sea ice cover of the western Weddell Sea persists throughout the year, forming the Perennial Pack Ice Zone. As in the fast ice cover of the Coastal Zone, the sea ice in the western Weddell Sea provides penguins and seals with a resting and reproduction platform. The Marginal Sea-Ice Zone has been discussed in detail in Section 15.2 and Section 15.5.2.3. It is a narrow zone that moves south as the sea ice melts and decays. It is a region of high primary production and large concentrations of zooplankton and higher predators. As such it has a major impact on the ecosystem structures and patterns of energy flow.

The growth, deformation, drift, and decay of sea ice cause an increase in the variability of environmental factors relevant to Antarctic marine ecosystems. Consequently, the spectrum of ecological niches within the Antarctic marine environment is widened substantially, and the carrying capacity of the system may be increased. As the result of the seasonal changes which occur in the sea ice cover, new resources are continually exposed to krill and other grazers at different times and locations The presence of sea ice may increase the robustness of Antarctic marine ecosystems, because they favour the growth and dispersal of organisms which are highly tolerant of, or particulary adaptive to, fluctuations in the environment.

15.5.2 CONCEPTUAL MODELS OF ANTARCTIC MARINE ECOSYSTEMS

15.5.2.1 Model of the Three Major Zones of the Southern Ocean

Section 15.2 discussed the three major Southern Ocean zones of the Ice Free Zone, the Seasonal Pack-Ice Zone, and the Permanent Pack-Ice Zone. Marchant and Murphy (1996) have diagrammed the major energy flows in the microbial system in these three zones (Figure 15.19).

Northern Zone (Ice Free Zone). In this region, production is generally low, although macronutrient levels are high. The pycnocline is deep in this area of high-wind stress. Other factors that may restrict production are low levels of trace elements, low ammonium levels, and restrictive grazing. Copepods, salps, chaetognaths, and amphipods dominate the zooplankton with herbivorous and carnivorous species at various stages of their life cycle producing complex food webs (Smith and Schnack-Schiel 1990). Much of the production is produced and recycled within the smaller microbial components of the system. In the winter the water column is homogeneous with a deep thermocline, and although stratification occurs in the summer the thermocline remains relatively deep (Jacques 1989).

Intermediate Zone (Seasonal Pack-Ice Zone). In this region the amount of light reaching the water column is very low because of the low angle of the sun and the attenuation by the sea ice and its frequent cover of snow. As the ice edge recedes in the spring, the surface water is stabilized by a layer of less saline water released from the melting sea ice (Sullivan et al. 1988). This nutrient-rich, high light, shallow mixed layer provides optimal conditions for phytoplankton growth. This ice edge zone plays a major role in the enhancement of biological activity at all trophic levels (Ainley et al. 1991). Seeding of this Marginal Ice Edge Zone by the sea ice community as the ice melts is likely to contribute to the developing planktonic production (Garrison

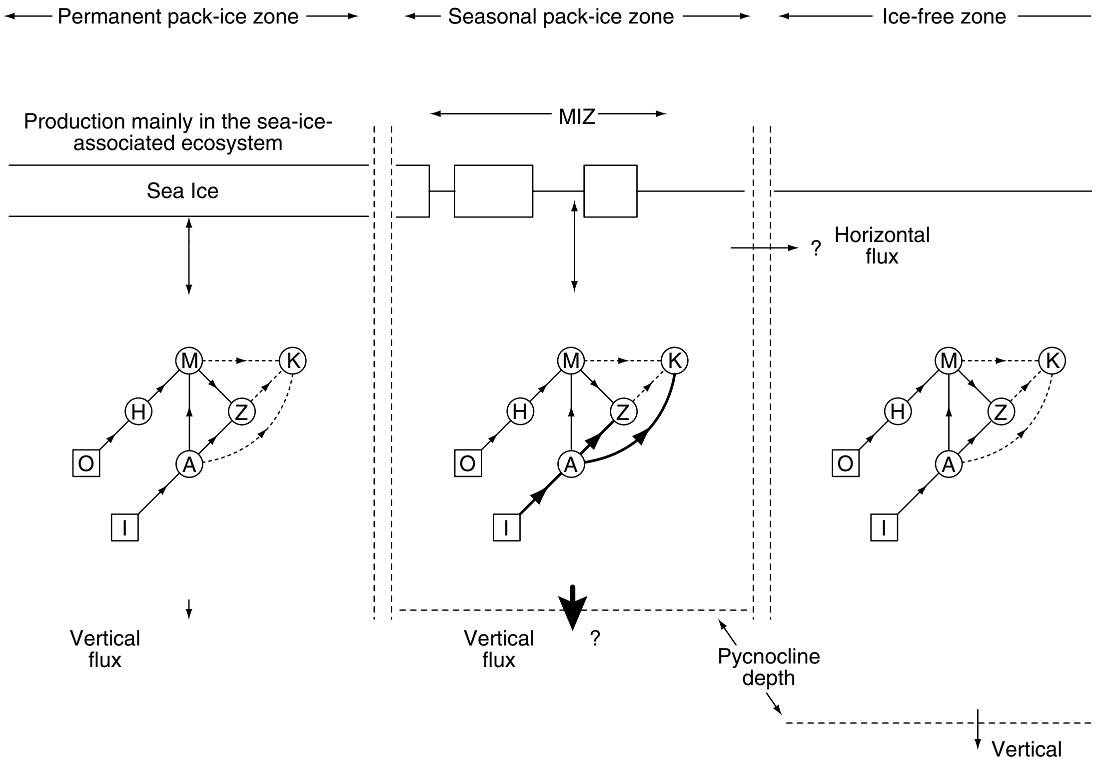


FIGURE 15.19 Schematic representation of the three major zones of the Southern Ocean that characterizes much of the large-scale variation in operation of the lower trophic level networks. O, organics; I, inorganics; A, autotrophs; H, heterotrophs; M, microzooplankton; Z, zooplankton other than krill; MIZ, marginal ice zone. (From Marchant, H.J. and Murphy, E.J., *Southern Ocean Ecology: The BIOMASS Perspective*, El Sayed, S.Z., Ed., Cambridge University Press, Cambridge, 276, 1996. With permission.)

et al. 1987), although the extent to which this occurs has been questioned (Riebesell et al. 1991). This southward-moving region of high phytoplankton production (Smith and Nelson 1986) is utilised by the higher trophic levels (Ainley et al. 1991), thus sustaining large populations of zooplankton, birds, and mammals (Sakshaug and Skjoldal 1989). A substantial amount of the biogenic production sinks rapidly from the eutrophic zone (Smith and Nelson 1986; Karl et al. 1991b; Riebesell et al. 1991). This Seasonal Pack Ice Zone is highly variable over all scales, from the interannual changes in sea ice extent (Smith et al. 1990; Eiken 1992), through seasonal changes in ice edge position, to the high variability in the Marginal Ice Zoneposition.

Southern Zone (*Permanent Pack-Ice Zone*). In this region the ice persists from year to year, and there is little production associated with the pelagic environment under the ice. In addition, there is very little vertical structure in the water column under the ice except in the layer immediately below the ice, which is influenced by melting and brine expulsion. The highlight absorption by the ice results in a rapid attenuation of the light. The majority of the production occurs within the sea ice. The sea ice ecosystem shows high variability over small scales, resulting in patchiness in the microbial community (Murphy et al. 1988; Vincent 1988; Eicken 1992).

15.5.2.2 The Pack-Ice Pelagic Ecosystem

Figure 15.20 is a model of carbon flow in the upper water column of the pack ice in the winter-early spring, before the melting of the ice floes. The sea ice microbial community (SIMCO) is represented at the top left. Chapter 3 and Chapter 12 discuss this community in detail. The sea ice microalgae and associated organisms (bacteria, sea ice heterotrophic protozoa, and small metazoans) are consumed by members of the cryopelagic community (i.e., fish, especially larval forms and amphipods; see Figure 3.20). As discussed in Chapter 5, furcilia and adult krill graze extensively on the SIMCO when the phytoplankton in the water column is low.

In the water column beneath the ice, the sparse phytoplankton community is dominated by nano- and picophytoplankton which are fueled by nitrate-*N* (“new”-*N*) and ammonium-*N* (“regenerated”-*N*), the latter being derived from the metabolism of the water column microbial community. The higher consumers are dominated by fish, principally myctophids and cephalopods, and some penguins

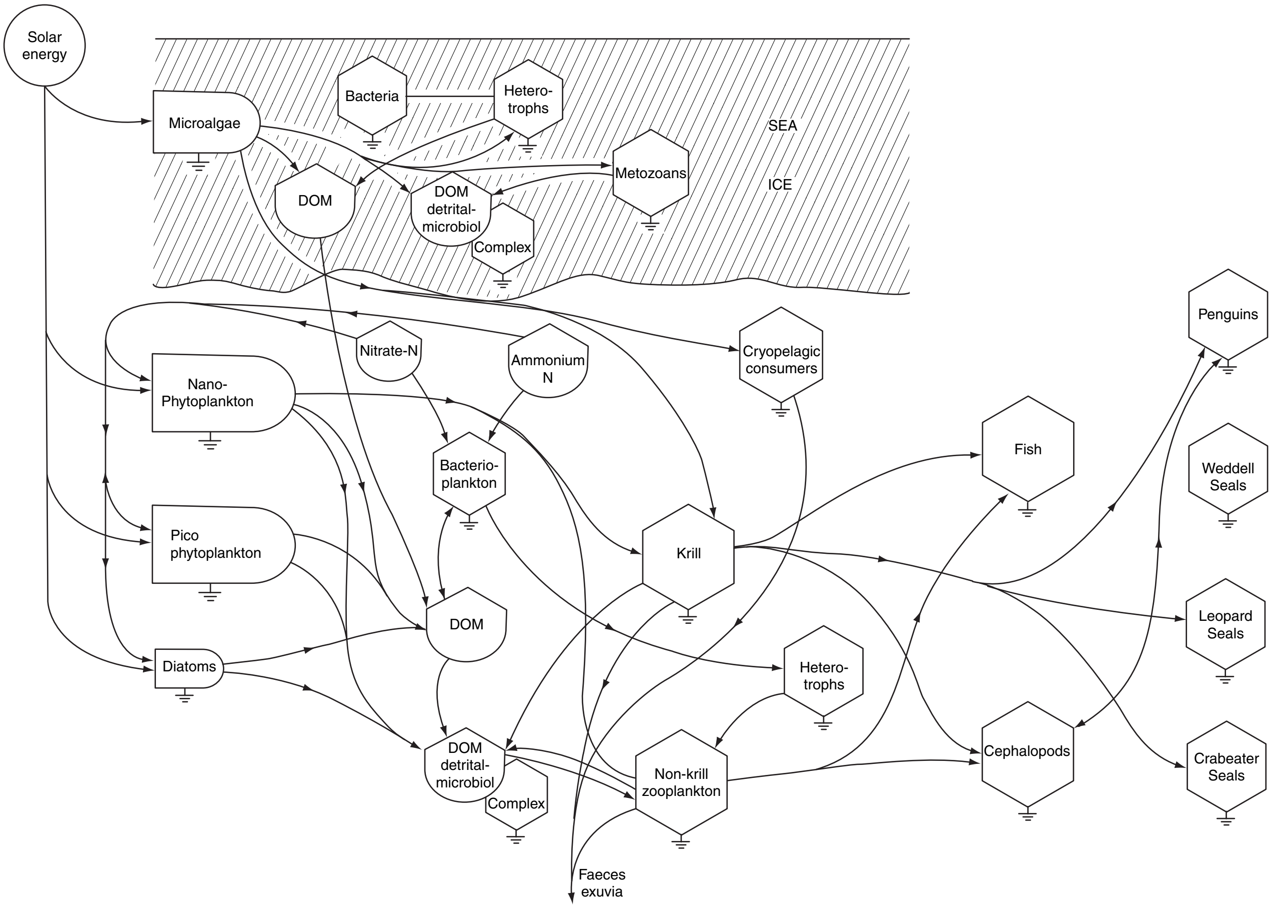


FIGURE 15.20 Energy flow in the pack ice zone ecosystem in the winter and early spring before the melting of the sea ice.

and petrels and the ice seals, principally crabeater and leopard Seals.

Based on research carried out in the region west of the Antarctic Peninsula, Garrison and Mathot (1996) have modelled the community structure and carbon flow of the pelagic system in the pack ice zone over the period from spring to winter as observed during the AMERIEZ and EPOS Programs (Figure 15.21). Carbon utilization by heterotrophic nanoflagellates (H. Nano), heterotrophic dinogflagellates (H. Dinos), and ciliates was based on observed population densities and individual clearance rates from the literature. These calculations and the underlying assumptions are discussed in Garrison and Buck (1989a). Sources of production data for the AMERIEZ Program are cited in Garrison and Buck (1989a), Garrison et al. (1993), and Smith and Nelson (1990). Data for the EPOS 2 cruise are cited in Mathot et al. (1992), Becquevort et al. (1992), and Billen and Becquevort (1991). The diagrams suggest the potential for microbial consumers to utilize production by their prey items. The fraction of the bacterioplankton and phytoplankton production that cannot be utilized by heterotrophic flagellates is available to the larger zooplankton. Vertical flux was low in November (inner ice edge), low in the first December cruise (inner ice edge), and March (ice edge); high in November (ice edge bloom); low in the second December (ice edge bloom); and very low in July–August (ice edge). The high vertical flux in the November ice edge bloom is due to the colony-forming diatom *Thalassiosira gravida*.

Phytoplankton biomass values (mg C m^{-2}) ranged from 696 in November [inner ice edge; *Phaeocystis* (mobile) and small diatoms], 176 in the first December cruise [inner ice edge, nanoplankton dominated, mainly flagellates

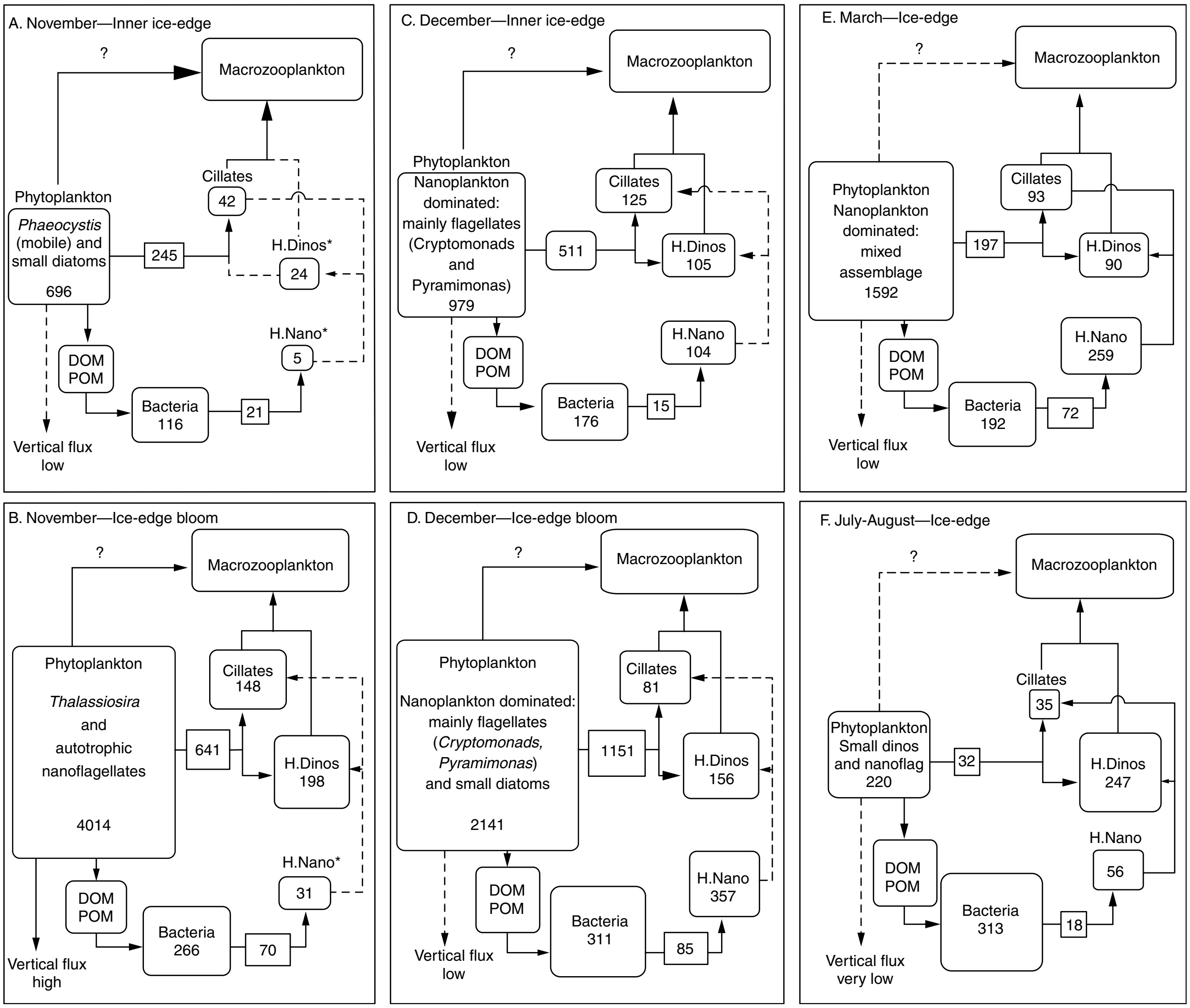


FIGURE 15.21 Diagrammatic representation of community structure and potential carbon flow through the pelagic food web as observed during AMERIEZ (November, March, and July–August) and EPOS 2 December programs. See text for detailed explanation. *Abundance and biomass (and potential grazing rates) underestimated. Carbon flow is suggested by arrows. Arrows with broken line for shaft indicate negligible flow. Smallest solid-shaft arrow shown indicates approximately 10% of carbon from source. Carbon flow is proportional to the width of the shaft. (From Garrison, D.L. and Mathot, S., *Ant. Res. Ser.,* 70, 165, 1996. With permission.)

(Cryptomonads and Pyraminimas)], 192 in March [ice edge, nanoplankton dominated, mixed assemblage], 4014 in November [ice edge bloom, dominated by diatoms (*Thalassiosira*) and autotrophic nanoflagellates], 2141 in December [ice edge bloom, nanoplankton dominated, mainly flagellates (Crypromonads, *Pyramimona*) and small diatoms], and 220 in July–August [ice edge, small nanoflagellates and dinoflagellates]. Production peaked during the ice edge bloom, and community composition changed over the year.

The biomass of the other components of the food web also varied in a similar manner. Bacterial biomass peaked in November and December (266 and 311) during the ice edge bloom, but also was high in July–August post-bloom. Ciliates and heterotrophic dinoflagellates followed a similar pattern. This model emphasizes the important role played by the components of the microbial community.

15.5.2.3 A Coastal Fast-Ice Ecosystem

Chapter 3 and Chapter 12 discussed some aspects of the coastal fast ice ecosystem. This section deals with overall ecosystem model. Figure 15.22 is a model of the carbon flow in the mouth of the McMurdo Sound at the edge of the McMurdo Ice Shelf. This model uses the energy circuit language developed by H. T. Odum, and the basic symbols used in the model are explained in the Appendix. The various components and flows in the model are expressed in terms of carbon equivalents. By the use of appropriate conversion factors they can be converted into energy units (kcal or kJ).

This carbon flow model is divided into five levels: (1) primary producers; (2) dissolved organic matter (DOM); (3) the detrital–microbial complex (particulate organic matter (POM) plus its microbial community); (4) invertebrate consumers; and (5) vertebrate consumer. The horizontal line separates sediment processes from those occurring in the water column. Four major and two minor producer units are shown. The detrital–microbial complex compartment includes detritus of plant and animal origin and the organisms associated with it (unicellular algae, bacteria, yeasts, fungi, protozoa, and microscopic invertebrates). The invertebrate consumers include the planktonic heterotrophs, zooplankton, cephalopods, benthic epifauna, and benthic fauna, while the vertebrate consumers include fish, birds, seals, and whales.

A number of minor pathways have been excluded in order to simply the model. Additionally, the model does not portray predation within compartments. For example, within the benthic invertebrate compartment considerable predation occurs, such as several species of asteroids on the abundant sponges (Dayton et al. 1974). In spite of this the model is still complex, but could be further simplified by combining compartments and omitting some of the smaller flows to produce a model suitable for simulation. Submodels of this model could also be developed. As it stands, in spite of the shortcomings discussed below, it is a realistic model of the McMurdo Sound marine ecosystem. The value of such a model from the conversation/management point of view is that the relative importance of the various flows are clearly evident, and simulation could be used to predict changes that might occur following alterations to producer inputs, or declines and increases in consumer populations.

Estimates of the biomass values for the carbon storages and for the flows between compartments have, where possible, been derived from data obtained by various investigators working in the McMurdo Sound region. Where data was unavailable, estimates are based on studies carried out elsewhere in Antarctic, or data in the general literature on marine ecosystems.

Phytoplankton succession in McMurdo Sound has been described in Section 15.3.4. Estimates for primary production for eastern McMurdo Sound and for the entire sound are given in Table 15.7. For the purposes of calculating the total phytoplankton production the January–February diatom bloom is estimated at half the value given by Smith and Nelson (1986) for the ice edge bloom in the waters to the north of McMurdo Sound. The total annual phytoplankton production for McMurdo Sound has been calculated by Knox (1990), as 16.6 g C m^{-2} for the *Phaeocystis* bloom, plus 22.8 g C m^{-2} for the later diatom bloom, plus 5 g C m^{-2} at other times, making a total of 43.9 g C m^{-2}, which is more than three times that calculated by Holm-Hansen et al. (1977) for the open waters of the Southern Ocean.

There are three pools of DOM: the sea ice pool, the water column pool, and the sediment pool. The major sources of the water column organic matter are the release of extracellular organic carbon by the sea ice microalgae, the phytoplankton, and the benthic microalgae. In shallow water the benthic macroalgae can contribute substantial amounts of DOM. Figure 15.23 depicts the water column detrital microbial complex. As illustrated, the water column POM is derived from a great variety of sources: from the sea ice microbial community after the melting of the sea ice; from the phytoplankton, epiphytic microalgae, and the benthic microalgae; and from contributions from all the other water compartments. Fecal pellets from the zooplankton and faeces from the higher consumers are a major input. Crustacea exuiva, the unconsumed remains of zooplankton and the dead bodies of the consumers, also contribute to the water column POM. Berkman et al. (1986) have postulated that sediment resuspension by wind-generated waves during periods of open water, and by anchor ice or current when there is ice cover, is an important mechanism for introducing organic matter into the water column in the shallow waters of McMurdo Sound. All of this POM is colonized by a rich microbial community. In addition to the bacteria attached to the POM, there are the free-living bacteria of the bacterioplankton.

Microalgal Carbon Flux. Figure 15.24 is an attempt to diagram the microalgal carbon flux in McMurdo Sound. Some of the estimates are speculative and these are prefaced by question marks. Nevertheless, they are probably of the right order of magnitude. Some 20% of the sea ice macroalgal net production (NP) is released as extracellular organic carbon (DOM). This extracellular carbon is either released to the water column, or utilized by bacteria attached to the

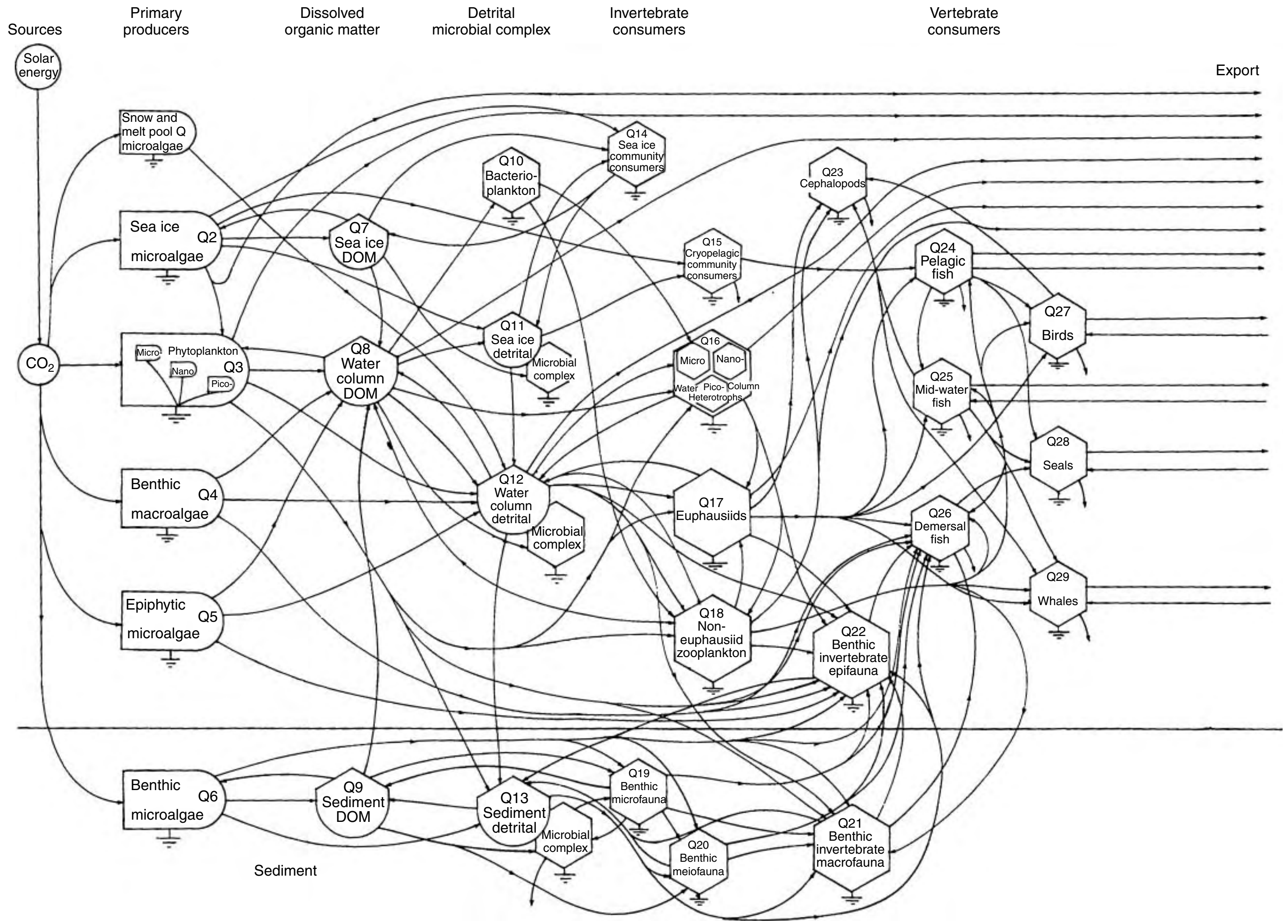


FIGURE 15.22 Energy flow in the coastal fast ice ecosystem of McMurdo sound.

TABLE 15.7
Primary Production in McMurdo Sound

Compartment	Annual Net Production (g C m^{-1}yr^{-1}) (Eastern Sound)	Total Annual Production (C yr^{-1}) (for the Whole Sound)
Snow and meltpool microalgae	Not known	Not known
Sea ice mircroalgae	11.83	500–700,000
Phytoplankton		
Phaeocystis	16.10	
Other species	27.8	
Total	43.9	1.5–2.25 million
Benthic microalgae	Not known	Not known
Epiphytic mircroalgae	Not known	Not known
Benthic microalgae		
East sound	26.0	25–30,000
West sound	3.0	2–3,500

Assuming that phytoplankton production in the Western Sound is half of that in the Eastern Sound.

Source: From Knox, G.A., *Antarctic Ecosystems: Ecological Change and Conservation,* Kerry, K.R., Hempel, G., Eds., Springer-Verlag, Berlin Heidelberg, 145, 1990. With permission.

diatoms or POM, or by free-living bacteria. Of the sea ice microalgal biomass produced (NP-exudates), it is estimated that 7% becomes POM after death of the cells, 2% is consumed by the sea ice sympagic community, and 11–16% is consumed by the cryopelagic consumers. Thus, of the microalgal biomass 75–80% is released into the water column upon ice melt.

The phytoplankton production and its fate is depicted in Figure 15.25. The phytoplankton, on average, release 10–12% of their net production into the water column as DOM (exudates). Of the phytoplankton biomass produced (NP-exudates) only 3% is estimated to be consumed by the zooplankton and the water column heterotrophs, while some 8% after cell death is estimated to contribute to the water column POM and by lysis to the water column DOM. The remaining 89% sediments through the water column to the sea bottom. Depending on the depth of the water column, a percentage of this will be remineralized as it sinks to the sediments. In the shallower depths it is estimated that about 10% of the biomass is consumed by the epifaunal suspension feeders. Thus, in order of 75% of the original phytoplankton biomass, at least in the shallow water, reaches the surface of the sediments.

Invertebrate Consumers. Chapter 3 and Chapter 12 discussed the food web of the sea ice microbial community and the associated cryopelagic community. Water column heterotropic protozoa have as yet not been studied in McMurdo Sound but are likely to be similar to those of other fast ice regions. It is probable that the total heterotropic protozoan biomass is in the order of 50–300 mg C m, and they form an important link in the transfer of carbon from the extracellular C secreted by the phytoplankton via the bacteria that they consume to higher trophic levels (Hewes et al. 1985, 1990).

Chapter 12 discussed the zooplankton of McMurdo Sound. The zooplankton is dominated by copepods and pteropods; other species include ostracods, euphausiids, mysids, amphipods, chaetognaths, pelagic polychaetes, the larvae of benthic polychaetognaths, and larval and post-larval stages of the mid-water fish *P. antarcticum. E. superba* is not present, and although *Thysanoessa macrura* occurs sparsely in the early spring, the principal euphausiid present throughout the summer is the small *E. crystallorophias*. Hicks (1974) estimated zooplankton net weights of 0.073–3.309 mg m^{-2} during January and early February in the vicinity of Cape Armitage. Forster (1989a, 1989b), in the same area in early November to early December, recorded biomass values ranging from under 1 to 5.0 mg m^{-2} wet weight, with a mean of 2.5 mg m^{-2}. Further north in McMurdo Sound in February Hopkins (1987) recorded higher densities and estimated the zooplankton biomass at 1.5–3.5 g dry wt m^{-2}. The biomasses of postlarval *E. crystallorophias* and *P. antarcticum* were estimated at 0.21 (10.16 − 0.33) (5.63% of the zooplankton biomass) and 0.82 (3.69 − 0.18) g dry wt m^{-2}, respectively. Euphausiid biomass in McMurdo Sound is much lower than recorded from other parts of Antarctic coastal waters (Hopkins 1985a, 1985b). In addition, salps and myctophid fish, which are prominent elsewhere, are virtually absent.

The diets of the McMurdo Sound zooplankton have been discussed in Chapter 4 Section 6, where it was noted that the total zooplankton consumption was only about 2% of the phytoplankton biomass. While ciliates and other heterotrophic microorganisms consume an as-yet undetermined amount of phytoplankton, the total phytoplankton consumption is not likely to exceed 3%. Thus, at least 97% of the standing crop remains unconsumed by the grazers.

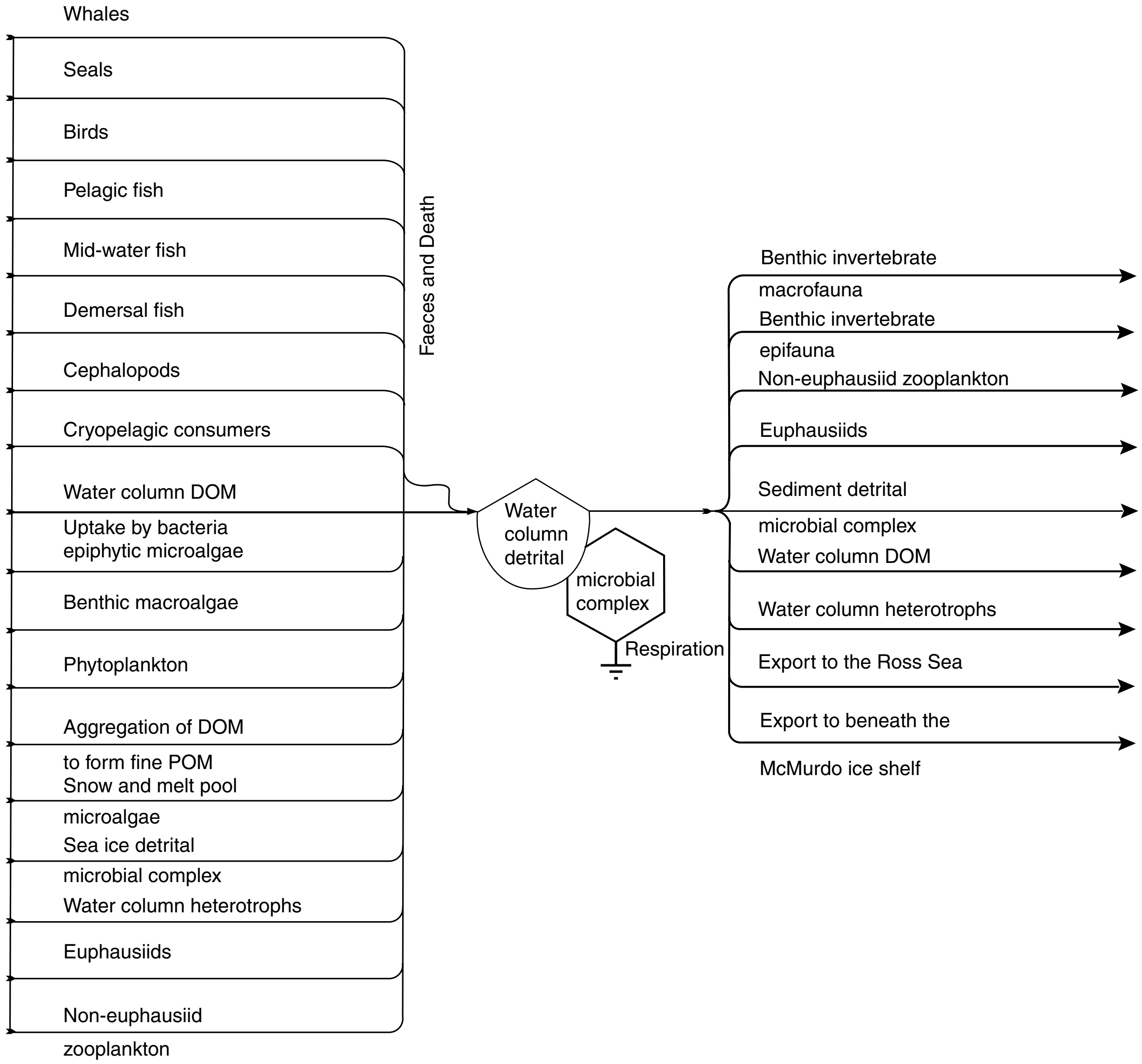


FIGURE 15.23 Energy flow through the detrital–microbial complex compartment in the energy flow model depicted in Figure 15.22.

Figure 15.26 depicts the non-euphausiid zooplankton compartment.

Much more research needs to occur before carbon flow through the benthic epifauna and infauna can be quantified. In shallow water the benthic microalgae are important producers at the base of the food web. The epifaunal filter-feeders obtain their food from sedimenting phytoplankton from resuspension from the sediments. Feeding is largely restricted to the short summer phytoplankton blooms, during which food reserves are laid down to enable the species to survive for the rest of the year. While benthic filter-feeders also feed in a similar manner, detrital feeders have food available to them throughout the year.

Higher Consumers. Nothing is presently known concerning the distribution and abundance of cephalopods in McMurdo Sound. The diets of many fish species are reasonably well known, but there is little information available on the population densities of the fish, so that it is not possible to quantify carbon flow through their stocks. Only a single species of seal, the Weddell seal, occurs in McMurdo Sound and while it would be possible to estimate their food consumption, the scanty data on the fish stocks makes it impossible to evaluate their impact. While killer and minke whales penetrate into McMurdo Sound in the late summer, after the ice breakout, their impact is not likely to be large. Of the birds, McCormick skuas and Adélie Penguins feed in the sound when there is open water, but they do so in relatively small numbers.

15.5.2.4 The Marginal Ice-Edge Zone

Hopkins et al. (1993a, 1993b) have discussed the trophic structure in the open water of the Marginal Ice Edge Zone in the southern Scotia Sea during spring. Top predators in the

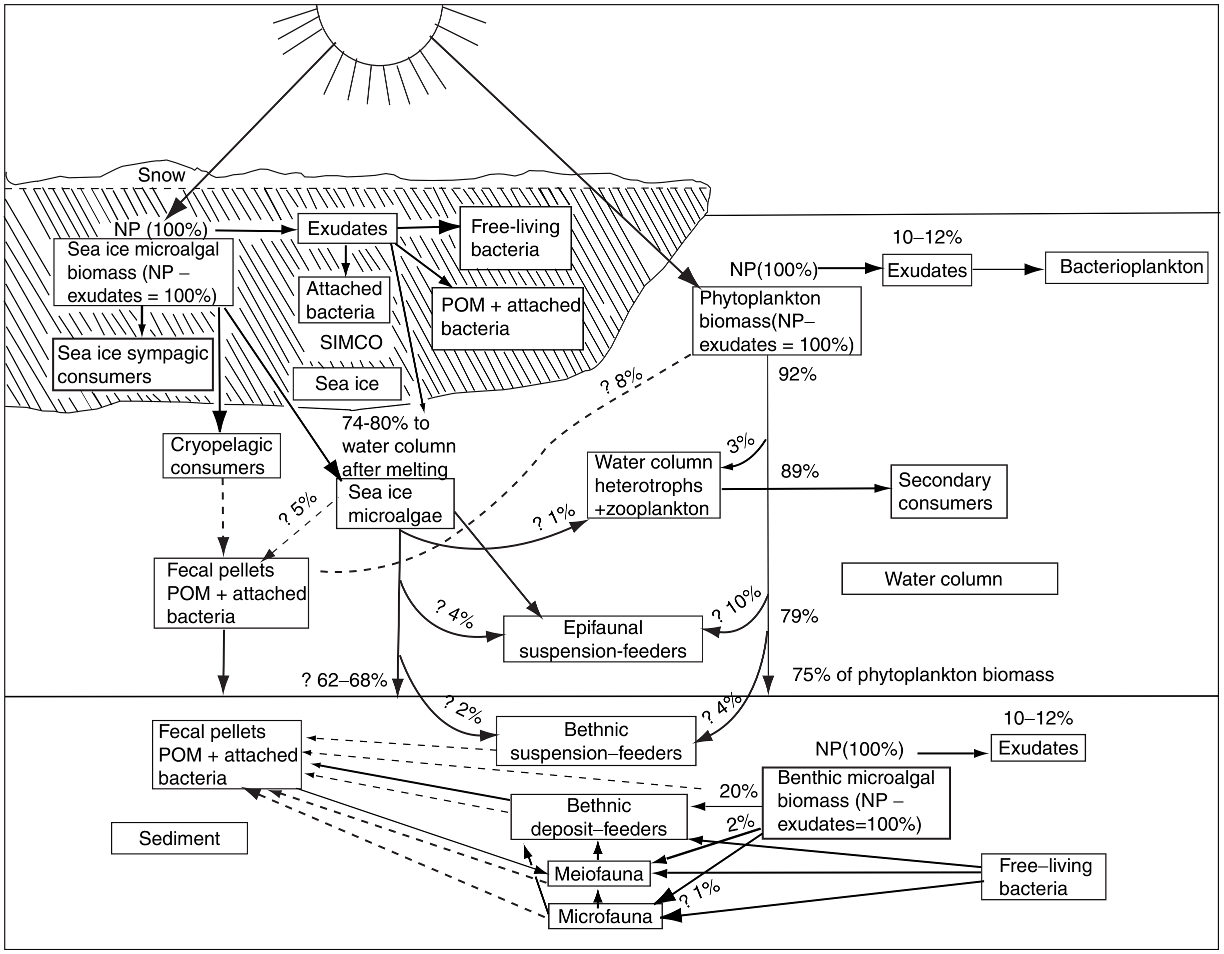


FIGURE 15.24 Microalgal carbon flux in the coastal fast ice ecosystem of McMurdo sound. Solid arrows represent energy flow (consumption) and sedimentation. Dashed arrows represent POM production. The percentages are the percentage of the microalgal biomass (NP-exudates) that is either consumed or sedimented. NP = net production of the microalgae.

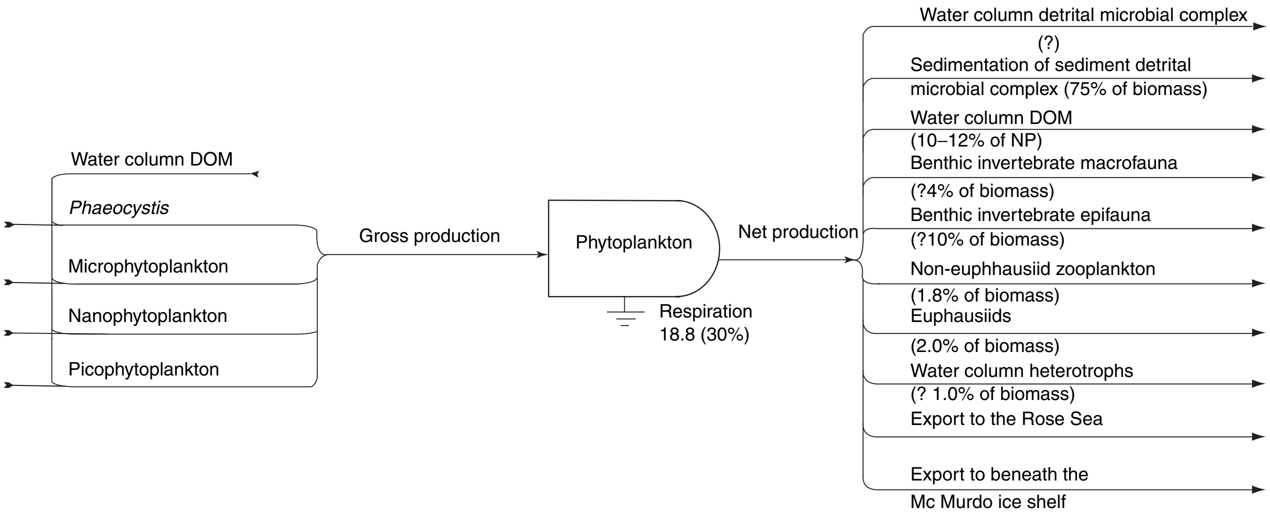


FIGURE 15.25 Energy flow through the phytoplankton compartment in the energy flow model depicted in Figure 15.22.

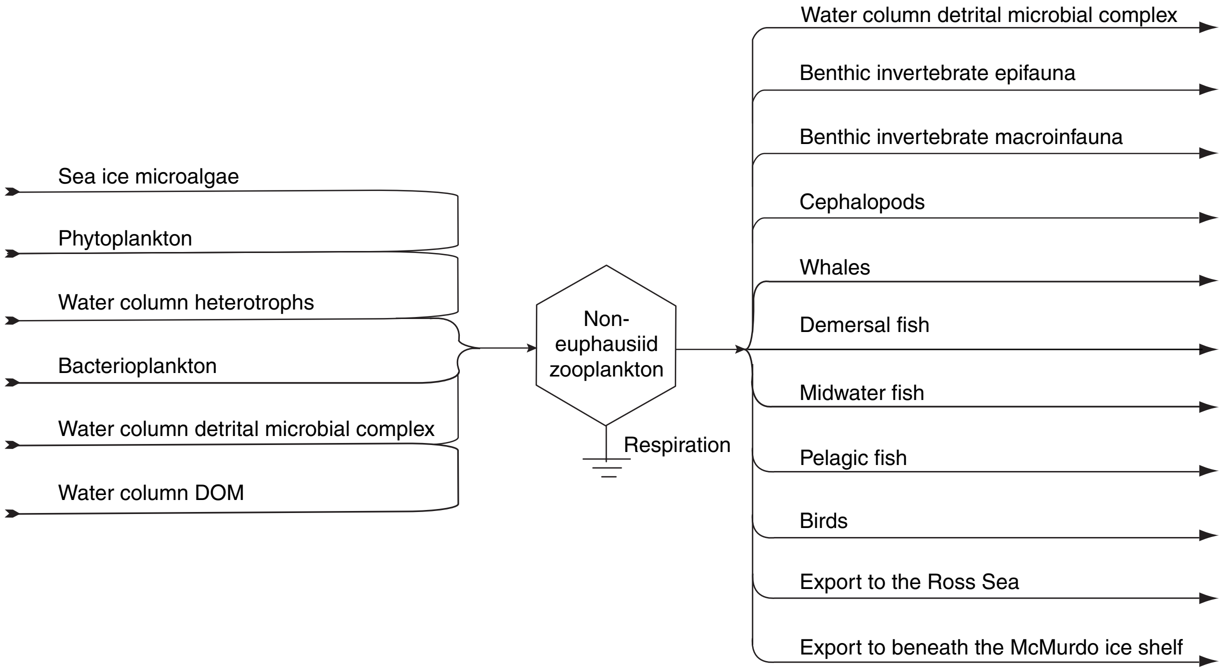


FIGURE 15.26 Energy flow through the non-euphausiid zooplankton compartment in the energy flow model depicted in Figure 15.22.

Marginal Sea-Ice Zone were the Antarctic fur seal (*Arctocephalus gazella*) and the minke whale (*Balaenoptera acutorostrata*). Other dominants, such as the crabeater seal and all the species of penguins, occurred either deeper in the pack or further at sea (Ribec et al. 1991; Ainley et al. 1992). Diets were determined for the dominant zooplankton, micronekton, and flying seabirds, and then aggregated by cluster analysis into feeding groups. Most zooplankton were omnivorous, feeding on phytoplankton, protozoans, and in some cases small metazoans (copepods). Only two species were found to be exclusively herbivorous, *Calanus acutus* and *Rhincalanus gigas*. Micronekton were carnivorous, with copepods being the dominant prey in their diets. The midwater fish *Electrona antarcticus* was the dominant food item in seven of the nine seabird species. Cephalopods, midwater shrimps, and carrion were also important in the diets of a few seabird species.

Figure 15.27 depicts the major trophic pathways from phytoplankton to apex predators in the open waters. Energy from water column production (phytoplankton, protozoans) flows through copepods and krill to the top predators. The diagram also highlights the importance of the intermediate trophic levels, the fish and the cephalopods, to energy flow through the pelagic ecosystem. In addition, it strongly suggests that relatively few taxa account for most of the biomass and energy flow through this region of the Southern Ocean. Lower latitudes, in contrast, are characterized by higher biological diversity. For example, the upper 600 m of low latitude "gyre" ecosystems have over 200 copepod species, 25–30 euphausiid species, 30–40 decapod shrimp species, and more than 200 species of midwater fish. The combined diversity of those groups exceeds that in the Scotia-Weddell region by more than a factor of six. The biomass and energy flow at intermediate and top trophic levels in the Scotia Weddell area can be accommodated by less than 20 species.

Figure 15.28 attempts to construct a carbon flow model of a Marginal Ice-Edge Zone ecosystem in the Seasonal Pack-Ice Zone during a phytoplankton bloom. Although the model is complex, it does not completely represent the complexity of the system. Nevertheless, the major energy flow pathways are depicted. The horizontal line separates the euphotic zone from the upper mesopelagic zone below. The model is divided into levels (from left to right): (1) primary producers; (2) organic matter and bacterioplankton; (3) first level (primary) consumers, including invertebrates and heterotrophic protozoans; and (4) higher level consumers. The dotted lines represent vertical migrations.

When the sea ice melts the sea ice microalgae, bacteria, protozoans, and micrometazoans, as well as the sea ice DOM and POM, are released into the water column. With the seeding of the euphotic zone by the sea ice microalgae and the resulting stability of the surface layer due to the freshwater input, coupled with the increase that occurs in PAR, an ice edge phytoplankton bloom develops rapidly. This bloom is dominated by diatoms, and/or *P. antarctica*, and is supported in the first instance primarily by "new"-*N*, although "regenerated"-*N* is often preferentially used if available. The dominant diatoms require large amounts of silica, and although the stocks of silica, along with those of nitrate-*N*, may be considerably reduced, they do not become limiting to phytoplankton growth. The release of large amounts of extracellular carbon by the microalgae results in an increase in the DOM pool. The bacterioplankton and

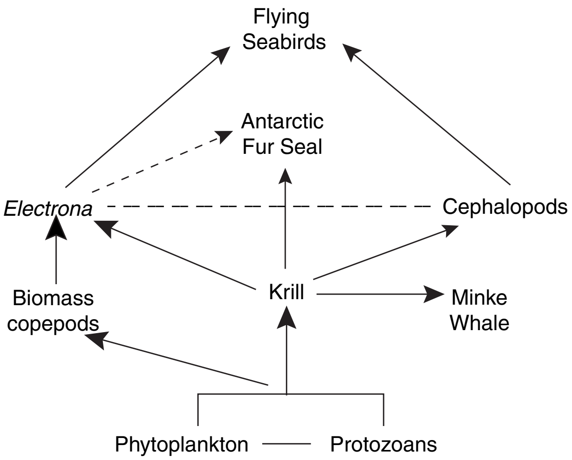


FIGURE 15.27 Principal trophic pathways in open water adjacent to the marginal ice zone of the southern Scotia Sea in spring 1988. (From Hopkins, T.L., Lancraft, T.M., Torres, J.J., Donnelly, J., *Deep-Sea Res.,* 40, 296, 1993. With permission.)

the attached bacterial of the water column detrital–microbial complex utilize this DOM, but their growth is kept in check by the grazing of the heterotrophic flagellates and ciliates.

The major consumers of the diatoms are krill. Although the krill swarms can rapidly graze down patches of phytoplankton, the overall proportion of the primary production consumed does not exceed 5%. Other grazers on the phytoplankton include the protozoa and the zooplankton other than euphausiids, especially the copepods and salps. Their consumption, however, does not exceed that of the krill. Consequently, a large proportion of the phytoplankton production sediments out of the euphotic zone, and either contributes to the mesopelagic detrital–microbial complex or, via senescence and autolysis, to the mesopelagic DOM pool which supports the growth of the mesopelagic bacteria. Some of the sedimenting phytoplankton cells will be consumed by the mesoplankton zooplankton (principally copepods and salps). The detrital–microbial complex (with its associated bacteria, microalgae, fungi, flagellates, and ciliates) is a complex of detrital aggregates of varying sizes derived from a multiplicity of sources (phytoplankton, regurgitations, fecal pellets, crustacean exuvia, and dead animals, etc.). Where *Phaeocystis* blooms occur they contribute to these aggregations in the manner outlined above.

The principal consumers of the krill are cephalopods, fish, petrels, penguins, leopard and crabeater Seals, and baleen whales. The cephalopods, myctophid fish and some of the copepod species regularly undergo vertical migrations between the euphotic and mesopelagic zones. Toothed whales feed on fish and cephalopods both in the euphotic and mesopelagic zones. The vertical migrating cephalopods and the micronekton are consumed in the surface waters by the petrels and penguins.

Figure 15.29 depicts a model of the euphotic zone in the "post-bloom" situation. Diatoms are now a minor component of the phytoplankton that is dominated by nano- and picophytoplankton (mainly flagellates). Primary production is now largely supported by "regenerated"-*N* (ammonium). Krill are largely absent and the zooplankton is dominated by copepods. Krill and many of the higher consumers have migrated southwards following the retreating ice edge blooms.

15.5.2.5 The Ross Sea Plankton System

Hecq et al. (1998) have developed a conceptual and numerical model of the Ross Sea plankton ecosystem (Figure 15.30). In the Ross Sea, temperatures never exceed values higher than 3–4°C in the summer and they approach -2°C in the winter. The principal cause of the variability of the Ross Sea ecosystem is the existence of the Southern Ross Sea polyna generated by strong winds which are advect to the ice cover (Zwally et al. 1983) and by sensible heat coming from the ocean (Jacobs and Comiso 1989). During the winter and at the beginning of spring, the ice-free surface propagates from south to north (Hecq et al. 1993). Another source of variability is due to local wind conditions. Strong katabatic winds can increase the depth of the mixed layer and impose a decrease of phytoplankton biomass.

High phytoplankton concentrations and massive blooms from 10 to 40 mg chlorophyll *a* have been observed in the Ross Sea polyna (Smith and Nelson 1985a; Hecq et al. 1993, 1998; Smith and Gordon 1997; Arrigo and McClain 1994) in November when other austral regions are ice-covered. These high chlorophyll *a* concentrations are among the highest observed in the Southern Ocean. However, nutrient concentrations are high and never limit primary production (Catalano et al. 1997). In winter nitrate, phosphate, and silicate concentrations can exceed 30 and 100 mmol m^{-3}, respectively. *Phaeocyctis* dominates the concentrations in the major part of the southern Ross Sea. High diatom concentrations dominate in the coastal regions. Microphytoplankton consisted of large-celled diatoms that dominated the Periantarctic Marginal Ice Zone. Nano- and pico-phytoplankton were more abundant in the Periantarctic Ice-Free Zone.

The principal characteristics of the Ross Sea zooplankton are the comparative absence of benthic larvae, the low diversity (poor in species, rich in individuals), the existence of diurnal and seasonal migrations (Mackintosh 1973), and the reproduction of species which coincides with the seasonal pulse of phytoplankton production occurring over a restricted period (Knox 1994). Other important characteristics are the large size of many of the zooplankters (typified by *E. superba* but also other groups such as copepods), and their slow growth and long life cycle. Herbivorous zooplankton mostly occurs in the upper 50 m of the water column (i.e., the mixed layer) and consists largely of protozoans, and larval and juvenile stages of copepods. Herbivorous copepods (*Calanus propinquus* and *C. acutus*), krill, and the pelagic mollusc *Limacina helicina* dominate the macrozooplankton. The maximum grazing pressure on large-sized diatoms is due to the herbivorous macrozooplankton.

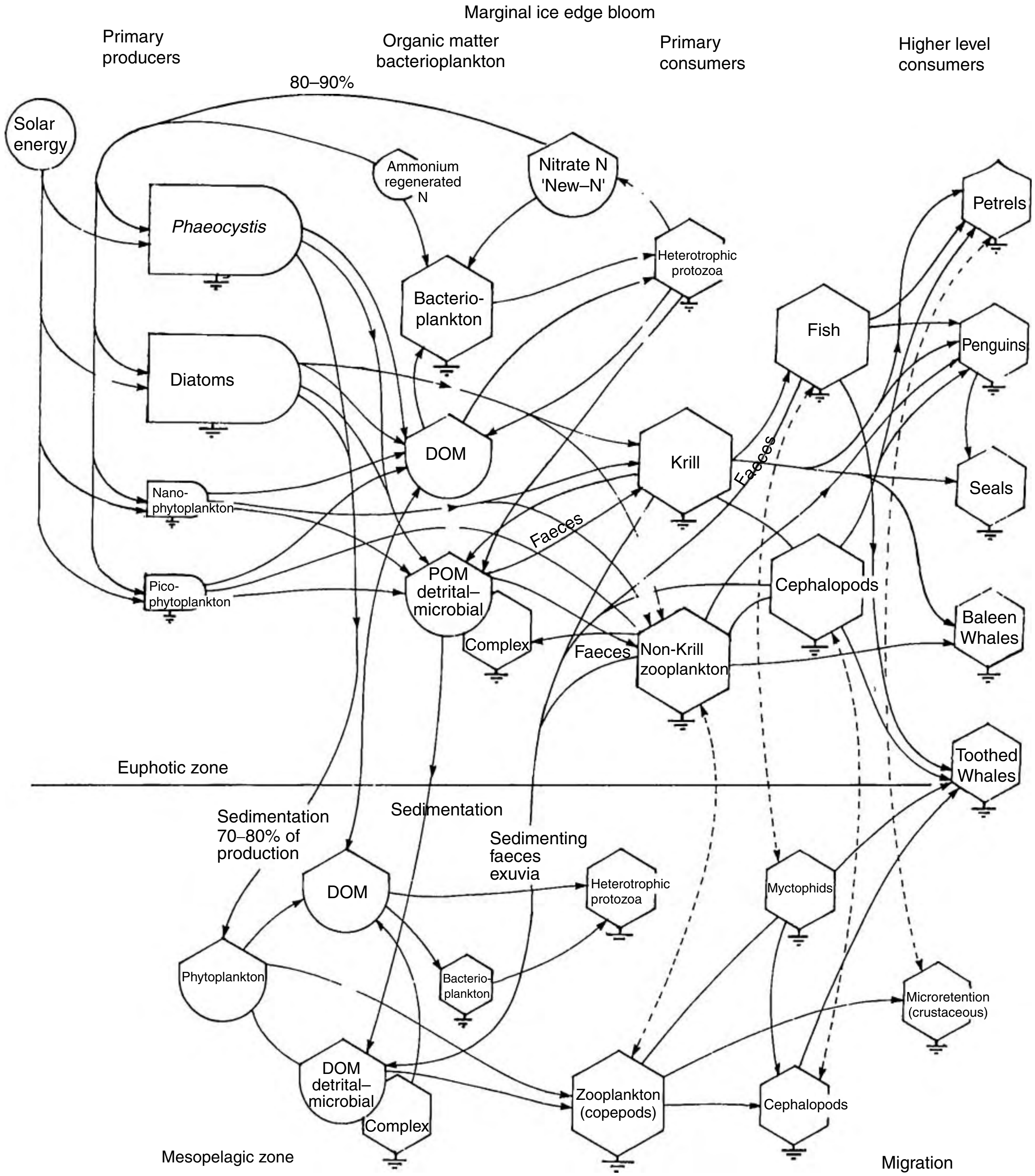


FIGURE 15.28 Energy flow in the marginal ice-edge zone ecosystem during a phytoplankton bloom. Dashed arrows show vertical migration.

Omnivorous forms are present below 50 m and are dominated essentially by the copepod *Metridia gerlachi*, amphipods, and ostracods, respectively in coastal and offshore waters. Copepods (*Euchaeta antarctica*), molluscs (*Clione* sp.), chaetognaths, and larvae of *P. antarcticum* dominate the carnivorous zooplankton in the Coastal Zone and *E. superba* in off-shore areas. Salps are essentially restricted north of the Antarctic Divergence. As discussed in Chapter 5, krill populations in the northern parts of the Ross Sea are as abundant as those in the Atlantic and Indian sectors (Azzali and Kalinowski 1998).

In the model in Figure 15.30 the principal variables, processes, and forcing functions identified in the Ross Sea seasonal ice shelf are included. The atmospheric forcing, sun

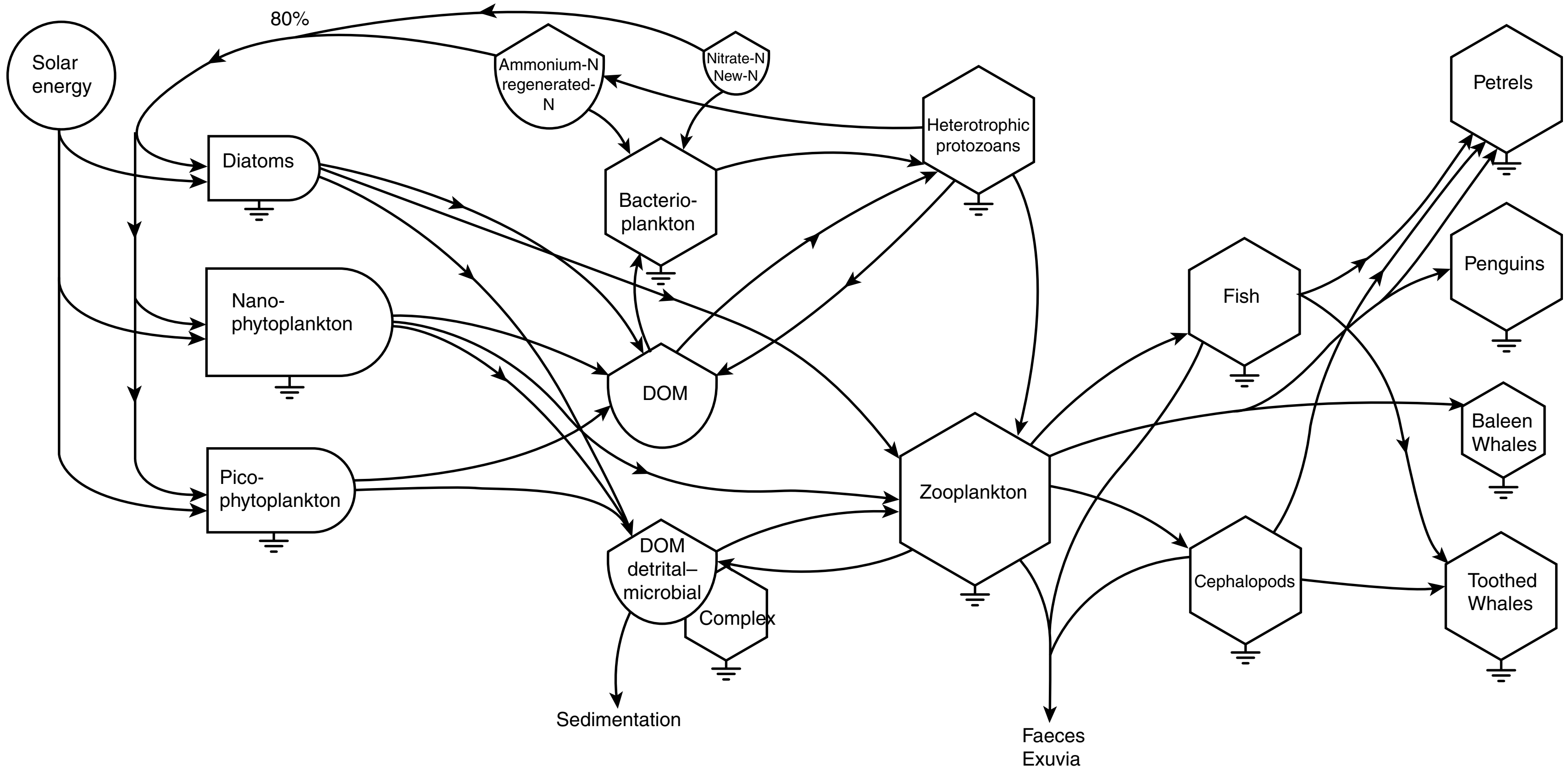


FIGURE 15.29 Energy flow in the "post-bloom" situation in the marginal ice-edge zone.

energy, cloud cover, air temperature, and wind stress act on the ice-melting process and the liberation of low salinity water; water turbulence, mixed-layer depth, and stratification will also indirectly affect the release of ice algae and primary productivity. The ice algal growth is also explicitly parametized. The model takes into account the control of the plankton ecosystem by ice cover; ice edge dynamics; atmospheric forcing and surface circulation, nutrients being non-limiting factors; ice-edge thickness, retreat, and melting to determine the initial conditions for the spring bloom (ice algal concentration, vertical structure of the water column) and to allow the biological processes of primary production in the water column to start. The combined effects of wind and solar irradiance determine the depth of the upper-mixed layer and quantitatively control photosynthetic levels. Simulation of the model was used to determine a standard state of the Ross Sea plankton system and numerical results accurately simulated the vertical stabilization of the water column within the Ross Sea Marginal Ice Zones during the ice-melting period and the biological structure of the upper layers. It simulated primary production and selection of the type of phyto- and zooplankton communities.

15.5.2.6 The South Georgia Region

A considerable amount of research has been carried out in the South Georgia region. This has been synthesized by Atkinson et al. (2001). South Georgia is a region characterised by high biomass and productivity of phytoplankton, zooplankton, and vertebrate predators. Important commercial fisheries have

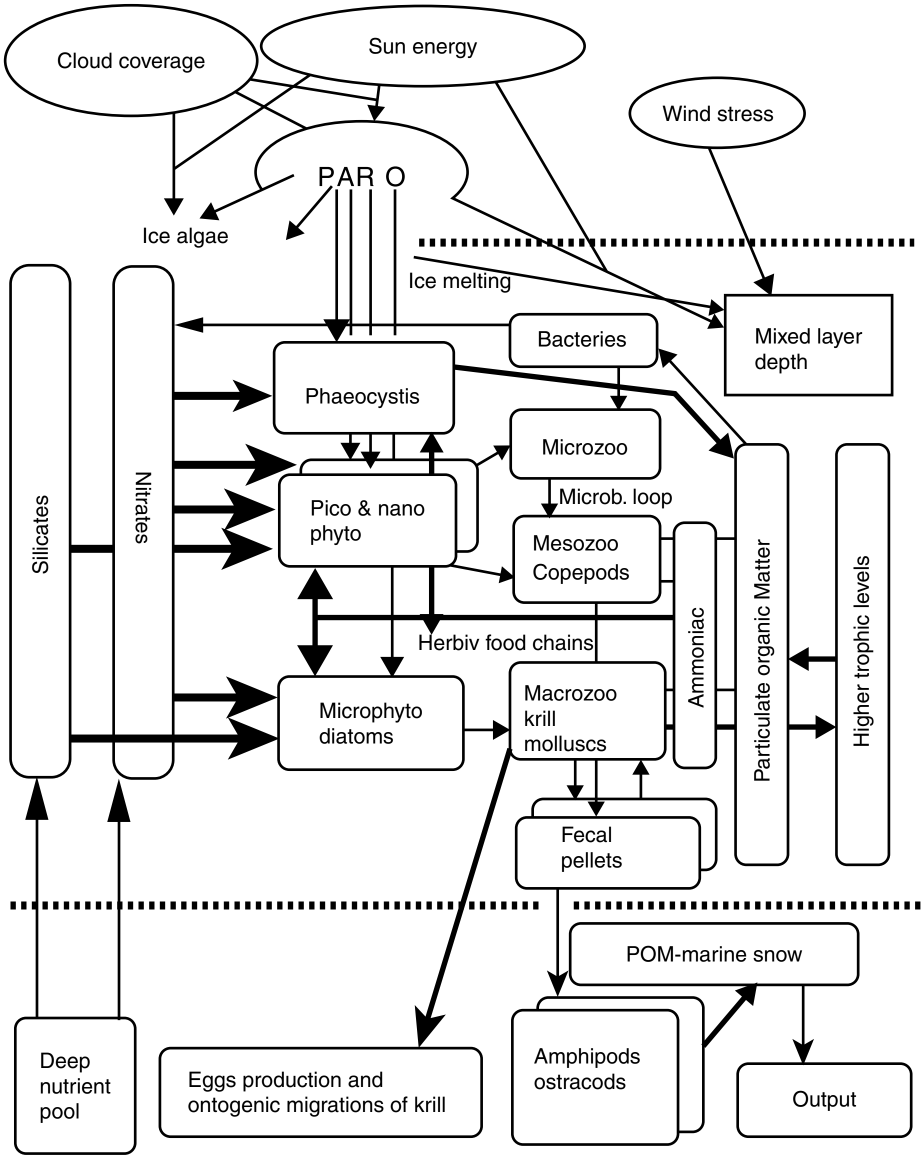


FIGURE 15.30 Conceptual model of the Ross Sea plankton ecosystem. (From Hecq, J.H., et al., *Progress in Belgian Oceanographic Research Proc. Workshop on Belgian Oceanogr. Res.,* Academy of Sciences, Brussels, 402, 1993. With permission.)

been based around the island since the late 1700s, initially exploiting seal and whales, and currently harvesting finfish and krill. The island lies within the Antarctic Zone of the ACC, to the south of the Polar Front. The offshore waters to its north and east are affected by a northward deflection of the Southern Antarctic Circumpolar Current Front, together with waters from the Weddell-Scotia Confluence. Although macronnutrients are not limiting, silicate concentrations of <1 mmol m^{-3} are growth-limiting in some summers.

Primary production is high (>20 mg chlorophyll *a* m^{-3}). Atkinson et al. (2001) have summarized primary production values for the region. They range from a mean of 0.57 g C m^{-3} day^{-1}(0.069–1.2) (Owens et al. 1991) in December to February, a mean of 1.72 (0.323–8.9) (Owens et al. 1991) in December to February, 1.08–6.58 (Moline and Prezelin 1992) in neritic regions in spring-summer, to 0.49 (0.17–0.98) (Smith and Nelson 1990) in spring in the seasonal ice zone. The growth season is long and blooms of greater than 2 mg chlorophyll *a* m^{-3} occur for four to five months. The high phytoplankton concentrations may be linked to an enhanced supply of iron or reduced forms of nitrogen (up to ~ 3 mmol ammonium m^{-3}). Phytoplankton blooms round South Georgia invariably comprise large colonial diatoms, mostly centric forms such as *Eucampia antarctica, Odontella weisfloggii, Chaetoceros socialis*, and *Thalassiosira* spp. (especially *T. scotia* and *T. tumida*). The patchy diatom blooms are superimposed on a more constant background of smaller autotrophs and heterotrophs, dominated by small diatoms with prymnesiophytes and dinoflagellates also contributing. Of the total microbial biomass of 2.3–4.5 g C m^{-3} in the upper mixed layer, heterotrophic nanoplankton and microplankton comprised about 20% of total microbial biomass at shelf and shelf-break stations, but greater than 50% at oceanic stations. Of the heterotrophic fraction, between 14 and 39% were bacteria, the remainder being mainly dinoflagellates. The biomass of protozoans is at the upper end of the range of Antarctic summer values.

A combination of factors appears to enhance phytoplankton growth at South Georgia. These include: (1) possibility of enhanced supplies of iron; (2) rapid recycling; (3) temperatures that can be elevated over the shelf due to seasonal warming; and (4) local inshore conditions providing shallow stable stratification for bloom formation.

Copepod growth rates are related to enhanced microplankton biomass. On the other hand, copepod mortality is probably high due to a wide variety and number of predators. These include vertebrates such as prions and diving petrels (Reid et al. 1997), as well as fish larvae (North and Ward 1989), and a wide range of invertebrates. These include euchaetid copepods, the amphipod *Thermisto gaudichaudii*, and also krill. Krill eat other zooplankton, especially during non-bloom conditions. Copepod abundance is severely affected by the presence of krill (Atkinson et al. 1999).

Several studies have suggested that rates of krill removal by land-based predators are high relative to the krill stocks at South Georgia (Croxall et al. 1985; Boyd and Croxall 1996). Atkinson et al. (2001) have estimated the biomass of krill removed during January from the western end of South Georgia. The land-based predators on krill include fur seals and macaroni penguins. It has been estimated that the average demand for krill by the South Georgia population of both of these species was 32,000 tonnes fresh mass day^{-1} (Boyd and Croxall 1996). Compared to estimates of krill biomass, Atkinson et al. (2001) estimated the removal rate by both species at $\sim 3\%$ day^{-1}.

Hydrography, nutrient concentrations, phytoplankton, copepod, and krill biomasses fluctuate between years. Periodically (once or twice a decade) shortages of krill in summer result in breeding failures among many of their predators. This occurred in 1977/1978, 1983/1984, 1900/1991, 1993/1994, and 1998/1999 when krill biomass was only ~ 5–10% of the mean values in other years (Murphy et al. 1988; Brierley and Goss 1999). In these years there was widespread declines in breeding success, particularly of gentoo penguins and Antarctic fur seals (Croxall et al. 1985, 1999). However, other krill predators such as macaroni penguins appeared to be able to switch to alternative prey such as the amphipod *T. gaudichaudii*, and they did not suffer such breeding failure (Croxall et al. 1999).

Atkinson et al. (2001) note that if high rates of energy flow are needed to support the large stocks of grazers in the system, it would be latently unstable without some kind of feedback preventing overgrazing. The fact that actual measurements of grazing impact do not exceed 50% of daily primary production, and that summer chlorophyll *a* concentrations rarely fall below 1 mg m^{-3}, supports the feedback concept. Figure 15.31 diagrams the possible feedback mechanisms that help prevent overgrazing of phytoplankton by krill. As phytoplankton becomes less abundant the krill switch to feeding on herbivorous zooplankton. This reduced the grazing on the phytoplankton, and nutrient regeneration stimulates phytoplankton growth Figure 15.32.

Biomass of krill plus net-caught zooplankton in summer is around 15–20 g dry mass m^{-2} equally dominated by krill and copepods. Mesozooplankton biomass is clearly much greater at South Georgia than elsewhere in the Southern Ocean; it is high compared to productive northern shelves. Mean krill biomass of ~ 59 g wet mass m^{-2} (Brierley et al.

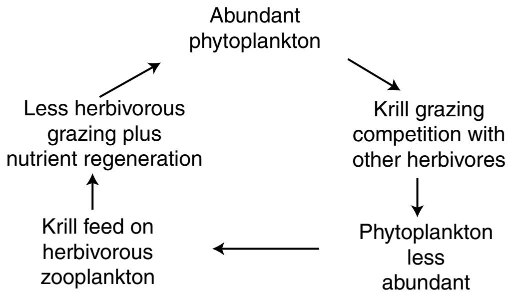


FIGURE 15.31 Hypothetical feedbacks that potentially help to prevent overgrazing of phytoplankton in localized regions of abundant krill at South Georgia. (From Atkinson, A., et al., *Mar. Ecol. Prog. Ser.,* 216, 2001. With permission.)

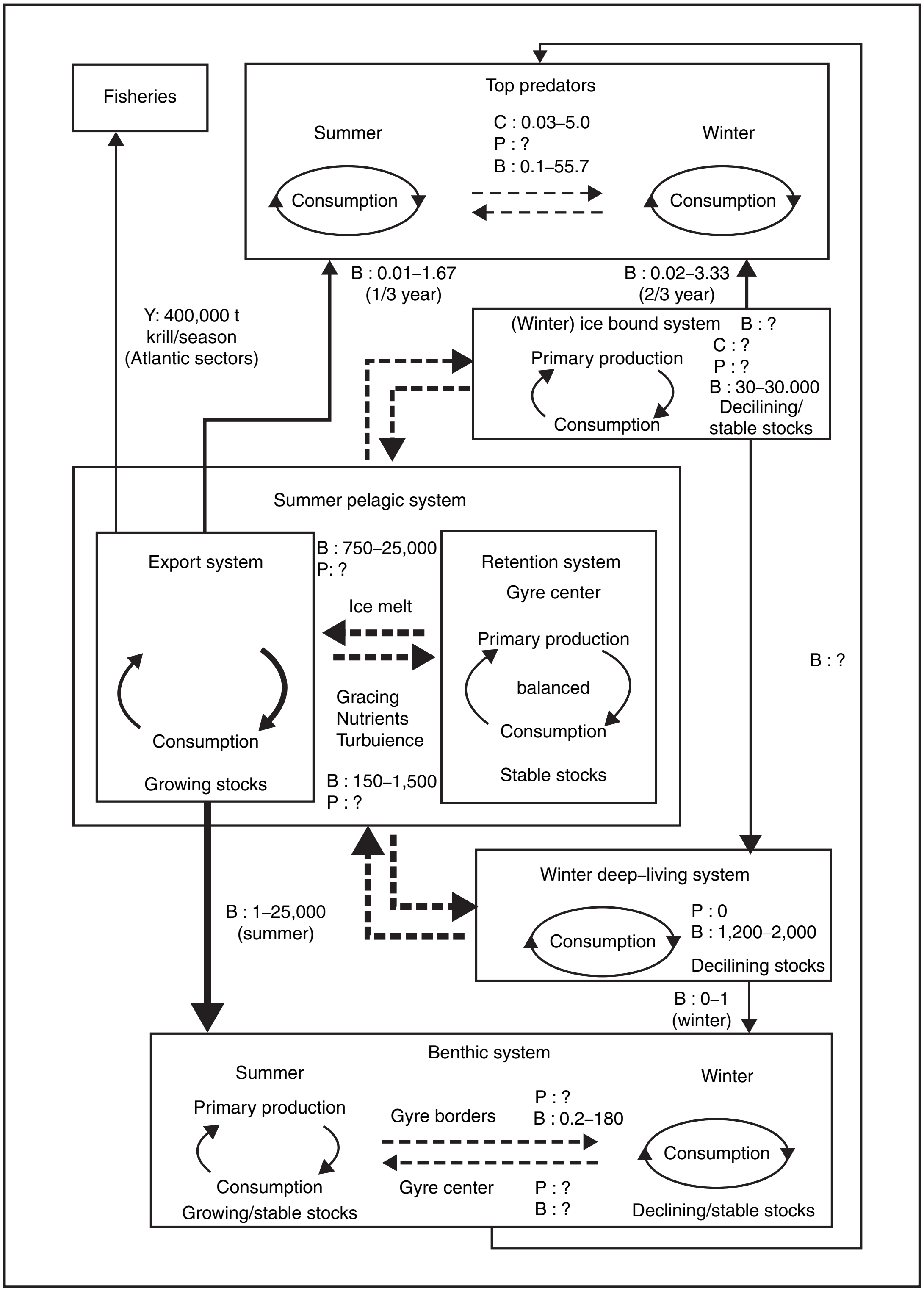


FIGURE 15.32 Components of the Weddell Sea ecosystem model. C, consumption (mg C m^{-2} year^{-1}); P, production (mg C m^{-2} year^{-1}); and B, biomass (mg C m^{-2}). (From Schalk, R., et al., *Trophic Models of Aquatic Ecosystems,* Christensen, V., Pauly, D., Eds., International Center for Living Resources Management, Makati, Phillipines, 324, 1993. With permission.)

1999), or ~14 g dry mass m^{-2} is of a similar value to that for mesozooplankton . Copepods comprise greater than 60% of the biomass caught with ring nets at South Georgia, in common with other Antarctic zones. Also in common the rest is mainly small euphausiids, pteropods, amphipods (mainly *T. gaudichaudii*), and chaetognaths (Atkinson and Peck 1990; Pakhomov et al. 1997). However, salps are not as prominent as in higher latitudes. Salps have only been prominent in three of the previous fifteen summers. Copepod biomass is dominated by the large Antarctic and Subantarctic species, *C. acutus, R. gigas*, and *C. simillimus*. Small species, particularly of the genera *Oithona* and *Ctenocalanus*, are moderately abundant around the island. The small neritic species *Drepanopus forcipatus* is very numerous, particularly close to the island.

While krill are a species characteristic of the Seasonal Sea-Ice Zone, South Georgia is an atypical habitat, being near the northern limit of their distribution and almost always in areas free of pack ice. Zooplankton, and particularly krill, appear to play a pivotal role in regulating energy flow in the South Georgia food web through selective grazing and possibly also nutrient regeneration. Abundances of krill and copepods are negatively related across a wide range of scales, suggesting direct interactions through competition or predation. Evidence suggests that when phytoplankton stocks are low, energy flow through krill is maintained by their feeding on the large populations of small copepods. Metazoans and higher predators at South Georgia can feed across several trophic levels according to prey abundance, and they regenerate substantial quantities of reduced nitrogen. These groups, therefore, have a controlling influence on lower trophic levels, both stabilising population sizes and maintaining high rates of energy flow.

15.5.2.7 Weddell Sea Ecosystems

Schnack et al. (1993) have constructed a comprehensive series of conceptual models of the biomasses and energy flows through the various trophic levels and compartments of the Weddell Sea ecosystem, comprising pelagic, benthic, and sea ice habitats. Figure 3.32 depicts the various components of the Weddell Sea ecosystem model. The Weddell Sea ecology is dominated by the distribution of water masses, ocean currents, and frontal systems (see Chapter 7 Section 7.1. and Figure 1.8). The compartments identified in the model comprise: (1) the *summer pelagic ecosystem*, subdivided into, 1.1. the *export system* based on >new production= and 1.2 the *retention system* based on > regenerated production (Smetacek et al. 1990); (2) the *winter ice bound system*; (3) the *winter deep-living system*; (4) the *benthic system*; and (5) the *top predators*.

Summer Pelagic System. Differently structured pelagic systems exist at various spatial and temporal scales, their patchiness and functioning depending on history and local events. Two major pelagic systems that are identified are pelagic systems based on new production (*export systems*, Figure 3.33) and regenerated production (*retention systems*, Figure 3.34) on the basis of the level of primary production, consumers, and carbon export (Smetacek et al. 1990).

Retention systems (Figure 15.34) are characterised by small flagellates, low primary production rates (<100 mg C m^{-2} day^{-1}), and low biomass of grazers (10–200 mg C m^{-2}), as well as small (3–80 mg C m^{-2}) and large predators (<1 mg C m^{-2}). Accordingly, consumption rates are low, and carbon is recycled almost without any export.

Export Systems. Export systems (Figure 15.33) may occur in frontal areas at the northern part of the Weddell Sea gyre, the shelf areas in the south and southwest, near islands, and in the ake of the melting ice edge. They change into relatively poor retention systems due to (micro) nutrient exhaustion, vertical mixing in the photic layer, and/or heavy grazing pressure by various heterotrophs and vice versa as a result of water column stabilization, ice-edge seeding, or mixing of water masses. As a consequence of this switching, the export vertical flux to the deep-sea and bottom communities has a pulsed character, with the main peaks in the spring-summer period (November–February) (Figure 15.34).

Winter Pelagic System. Pelagic primary production is confined to the short spring/summer period (roughly four months); during the remainder of the year the water column is low in primary production. As the result of zooplankton community overwintering strategies, the community disperses in winter into a deep-living community (Figure 15.35) and a surface ice-bound community (Figure 15.36) (Marschall 1988; Stretch et al. 1988). Grazers that maintain a more or less constant biomass throughout the year and have an insufficient capability to reduce metabolic demand (krill, some copepods) switch to ice algae in the sea ice system (Kottmeier and Sullivan 1987). A majority of the herbivorous copepods migrates to deeper water layers (>500 m) and hibernates (Voronina 1972, 1978), followed by predators (e.g., chaetognaths, siphonophores). The two grazers (krill and salps) that may occur in high densities in the summer pelagic system have the capability to switch to a carnivorous diet (Price et al. 1988; Huntley et al. 1989). When summer pelagic or winter ice microlagal production is insufficient, krill switch to carnivory to satisfy their metabolic demands (Price et al. 1988).

Sea-Ice System. The sea ice cover is an important component of the pelagic system as it influences and governs critical factors such as hydrography and the light regime in the water column and supports a stock of microalgae, which is an energy source for grazers during the winter. Figure 15.36 depicts the consumption, production, and biomass of the ice-bound system.

Vertical Carbon Flux. The pattern of vertical flux rates, and the amount and composition of the particle, varies in space and time. Recorded vertical flux varies from 1.1 to 130 g C m^{-2} yr^{-1} (see Table 4, Schalk et al. 1993). Krill grazing is considered to be responsible for much of this variability.

Benthic system. (Figure 15.37) Broadly, the Weddell Sea benthic system can be divided into three depth-related compartments (Knox and Lowry 1977; Picken 1985a): (1) The ice-affected shallow littoral and sublittoral (above approx. 30 m) around the tip of the Antarctic Peninsula and the islands to the north; (2) the narrow continental shelf and slope (down to about 3000 m); and (3) the deep sea compartment that is situated partially below the Weddell Gyre.

With the exception of the shallow areas in the north, where benthic primary producers are present, the Weddell Sea benthos depends on food supply from the pelagic zone. Sedimentation rates are high from the export systems in the northern and southern border areas and extremely low in the centre of the gyre. The input is largely limited to the brief phytoplankton bloom period. In the sublittoral zones of the islands there is a particularly rich algal cover down to about 30 m depth with macroalgal biomasses up to 80 g C m^{-2}. The annual production:biomass ratios are in the range of 0.1–1.8 (see Brey and Clarke 1993). Along the continental borders of the Weddell Sea Gyre, several distinct communities are recognized (Voβ 1988), which are similar to the

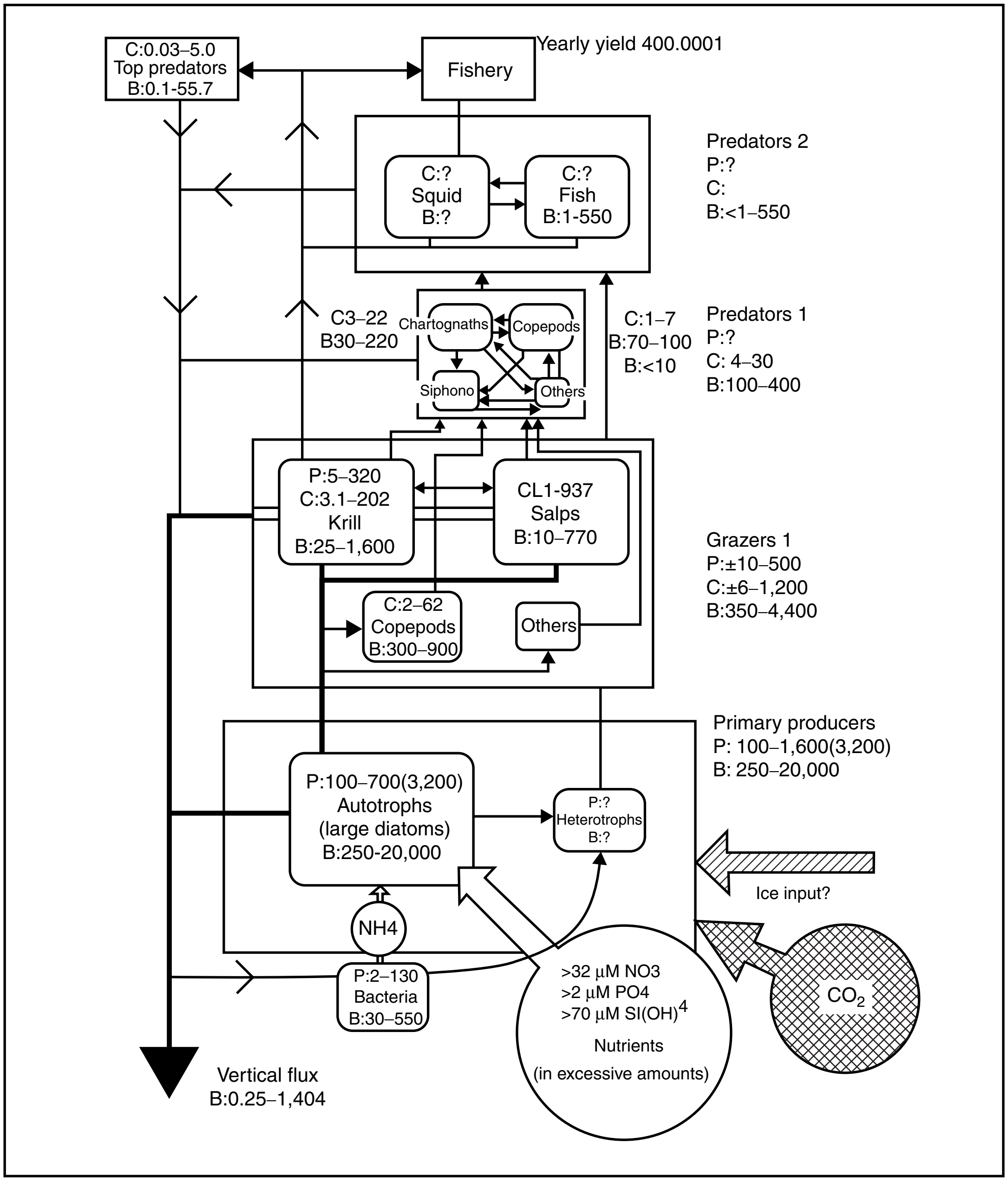


FIGURE 15.33 The pelagic export system component of the Weddell Sea ecosystem model. C, consumption (mg C m^{-2} day^{-1}); P, production (mg C m^{-2} day^{-1}), and B, biomass (mg C m^{-2}). (From Schalk, R., et al., *Trophic Models in Aquatic Ecosystems,* Christensen, V., Pauly, D., Eds., International Center for Living Resources Management, Mataki, Phillipines, 326, 1993. With permission.)

epifaunal communities found in other Antarctic regions. Biomass estimates of Weddell Sea benthic communities range from less than 0.1 to greater than 180 g C m^{-2} above 1200 m, with lesser biomasses in the deeper areas.

Top Predators. Seabirds, seals, and whales are the top predators. Bird and sea communities are highly variable in different areas and seasons. Krill, *E. superba*, seems to be the overall main food of the top predators around the islands in the north and in the Seasonal Pack Ice Zone of the East Wind Drift. Further south, in shallower coastal waters, it is replaced by the smaller *E. crystallorohias*. Both of these species form the main food of squid and the abundant midwater fish *P. antarcticum*. The impact of the top predators shows distinct spatial and seasonal difference as ice cover has a major influence on distributions. Overall biomass and consumption of the top predators in the Scotia-Weddell Sea Confluence zone are estimated at 24.5 mg C m^{-2} and 1.79 mg C m^{-2} day^{-1}, respectively.

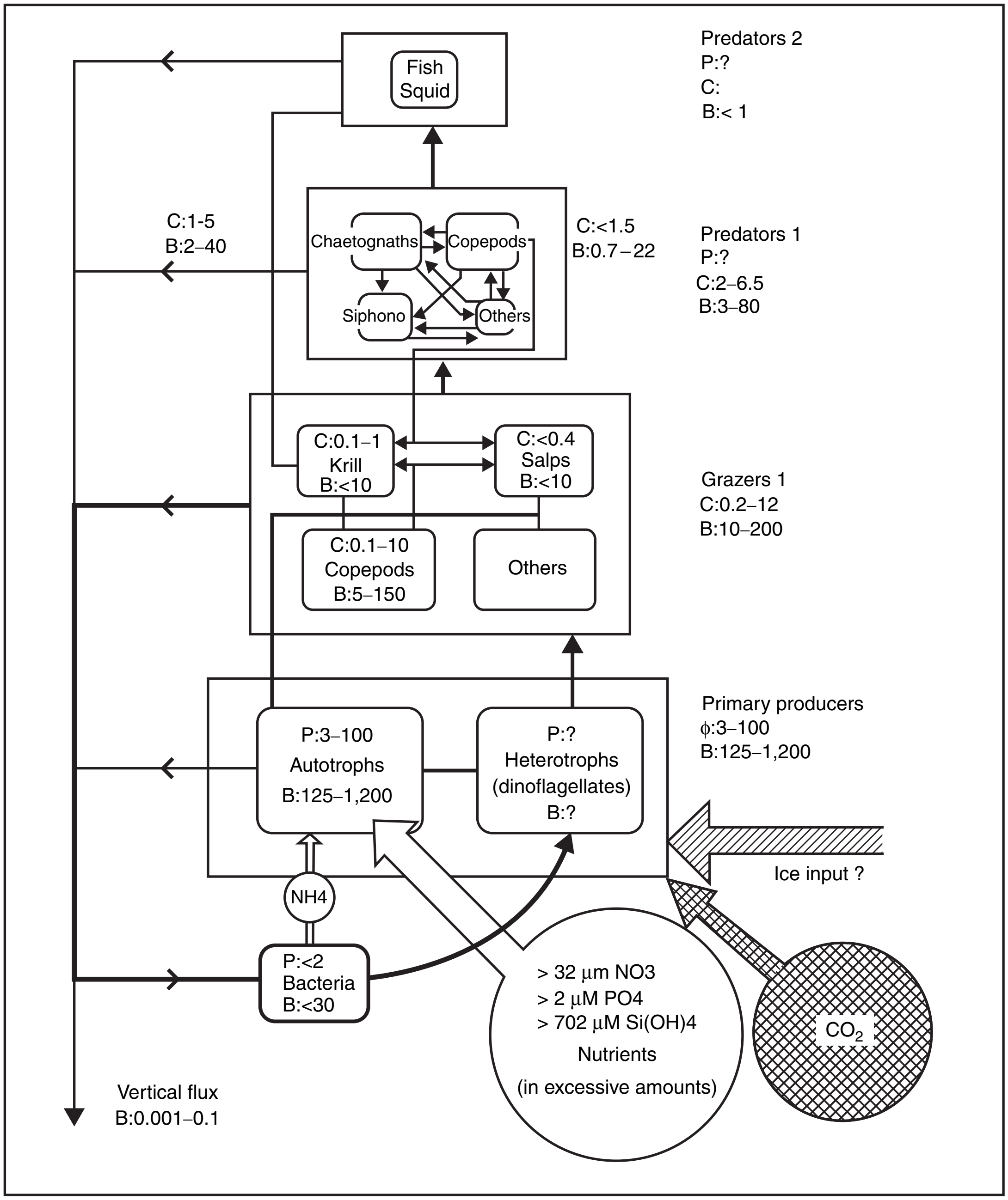


FIGURE 15.34 The pelagic retentive system component of the Weddell Sea ecosystem model. C, Consumption (mg C m^{-2} day^{-1}); P, production (mg C m^{-2} day^{-1}); B, Biomass (mg C m^{-2}). (From Schalk, R., et al., in *Trophic Models in Aquatic Ecosystems*, Christensen, V., Pauly, D., Ed., International Center for Living Resources Management, Mataki, Phillipines, 328, 1993. With permission.)

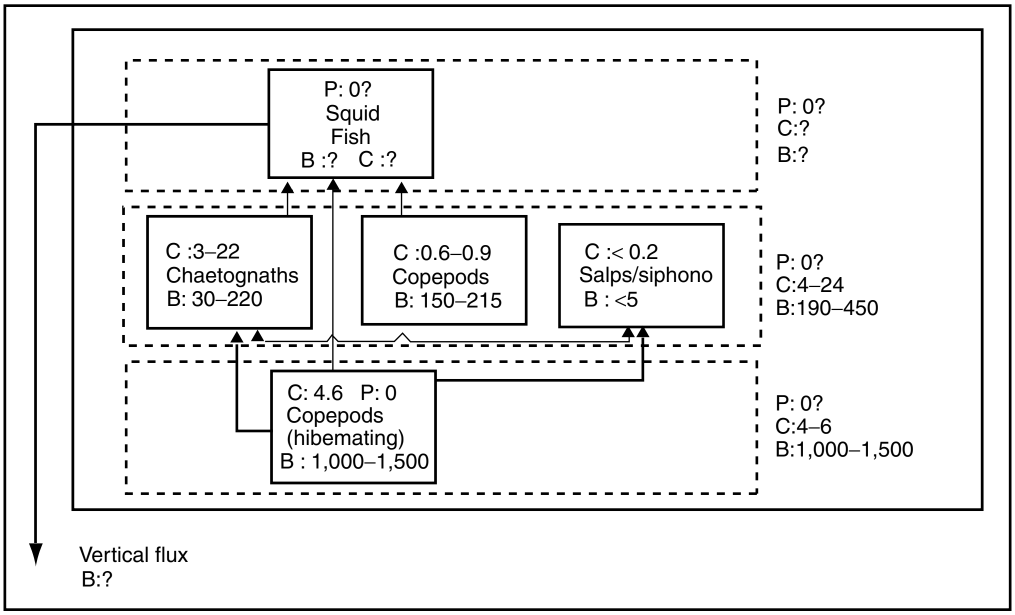


FIGURE 15.35 The winter deep-living system component of the Weddell Sea ecosystem model. C, consumption (mg C m^{-2} day^{-1}); P, production (mg C m^{-2} day^{-1}); and B, biomass (mg C m^{-2}). (From Schalk, R., et al., *Trophic Models in Aquatic Ecosystems*, Christensen, V., Pauly, D., Eds., International Center for Living Resources Management, Mataki, Phillipines, 329, 1993. With permission.)

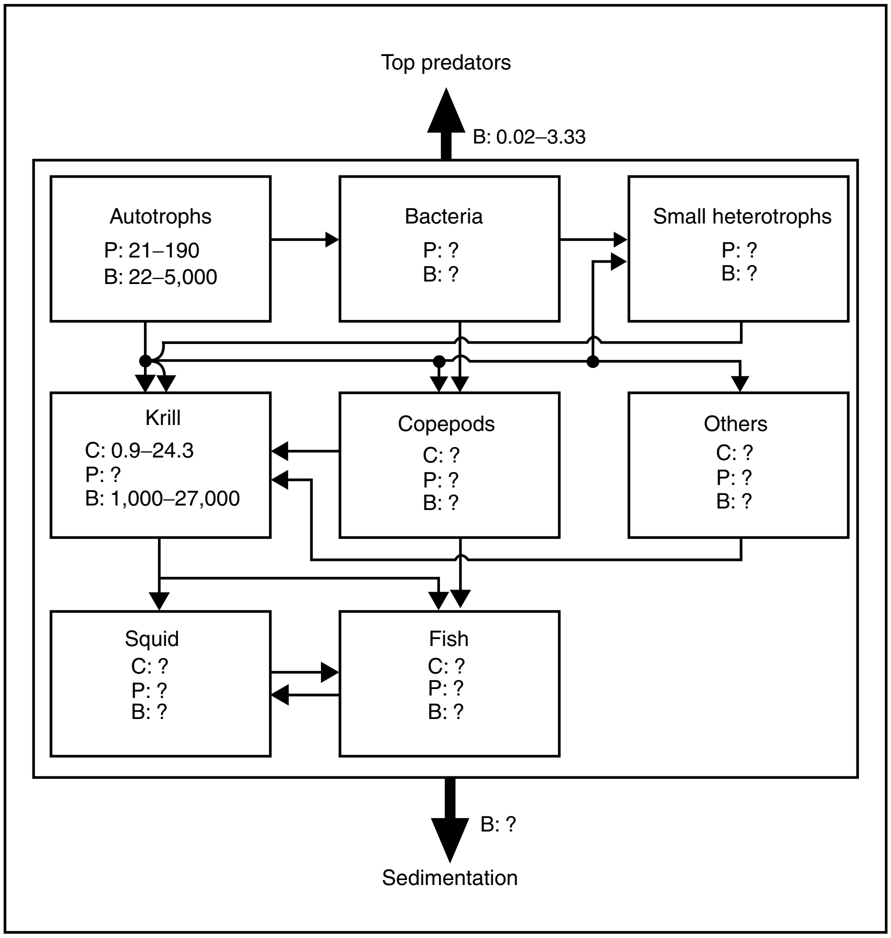


FIGURE 15.36 The ice bound system component of the Weddell Sea ecosystem model. C, consumption (mg C m^{-2} day^{-1}); P, production (mg C m^{-2} day^{-1}); and B, biomass (mg C m^{-2} day^{-1}). (From Schalk, R., et al., *Trophic Models in Aquatic Ecosystems,* Christensen, V., Pauly, D., Eds., International Center for Living Resources Mangement, Mataki, Phillipines, 329, 1993. With permission.)

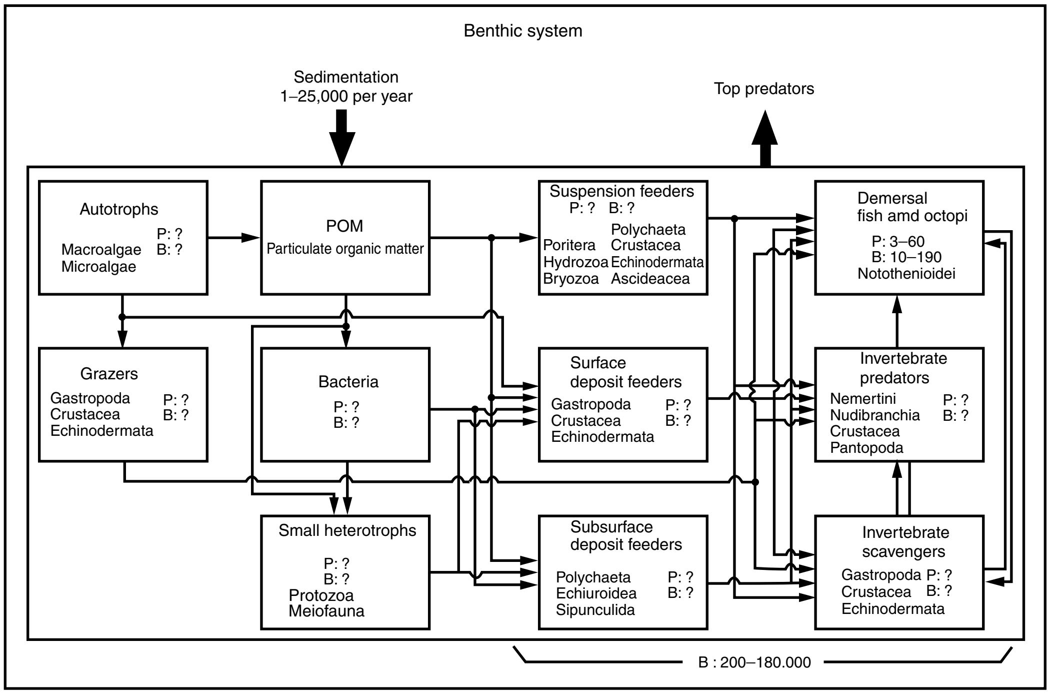


FIGURE 15.37 The benthic component of the Weddell Sea ecosystem model. C, consumption (mg C m^{-2} day^{-1}); P, production (mg C m^{-2} day^{-1}); and B, biomass (mg C m^{-2}). (From Schalk, R., et al., *Trophic Ecology in Aquatic Ecosystems,* Christensen, V., Pauly, D., Eds., International Center for Living Resources Management, Mataki, Phillipines, 331, 1993. With permission.)

15.6 SOUTHERN OCEAN ENVIRONMENTAL VARIABILITY AND ITS IMPACT ON THE PELAGIC ECOSYSTEM

15.6.1 Introduction

In 1987 CCAMLR and IOC jointly sponsored a Seminar on "Antarctic Ocean and Resources Variability" Sahrhage (1988a), with the support of SCAR and SCOR. The Seminar discussed the following questions:

- What is known on the variability of the Antarctic Ocean circulatory system?
- What are the possible causes for such variations?
- To what extent and how does the ocean variability influence primary productivity, zooplankton, and other organisms?
- To what extent and how does this variability influence krill distribution and abundance?
- What are the effects on krill predators (seals, penguins, fish, etc.)?

Significant interannual variability occurs in ecosystems that are coupled tightly to local physical processes (Smith et al. 1990). Examples from marine systems include upwelling systems (Barber and Smith 1981), intertidal communities (Dungan et al. 1982), the Bering Sea (Niebauer 1980), the Fram Strait (Smith et al. 1987), and coral reefs (Woodley et al. 1991).

The seminar focussed on meso- and large-scale variability and identified future research needs.

15.6.2 Meso/Large-Scale Variability in the Southern Ocean

As Sahrhage (1988a) points out, meteorologists and oceanographers tend to use average values of parameters in their investigations to describe the structure and processes of the atmosphere and ocean. However, it is the interannual change and seasonal abnormality in the weather, ice, and hydrographic conditions that have the greatest influence on distribution, growth, reproduction, and mortality of living organisms. Thus, biologists are mainly interested in the environmental conditions during a specific year, or season, and the environmental extremes.

15.6.2.1 Variations and Trends in Temperatures

Unfortunately, there are few long-time series of observations available for the Antarctic and most of these are from a few localities, mostly at or close to the Antarctic Peninsula. Records from the South Orkney Islands (Jacka and Budd 1998) show that from 1908 until 1949 the 10-year annual running means of annual air temperature were below the overall long-term average (−4.3°C), with a particularly cold period between 1922 and 1935. On the other hand, temperatures well above the long-term average were measured from

1950 to the present. Evidence of increases in sea surface temperatures is inconclusive. While particularly cold and warm periods can be identified in the Antarctic Peninsula area, these do not coincide with such years in other parts of Antarctica (Jacka and Budd 1998). Data from 22 years of observations in the Indian Ocean Sector have revealed interannual variations in the position of the Antarctic Polar Front Zone and the position of the northernmost edge of the 0°C isotherm (Nagata et al. 1988).

15.6.2.2 Circulation Patterns

Reviews of spatial and temporal variation in the Southern Ocean circulation patterns, water mass distributions, and frontal positions (Gordon 1988), and for specific areas such as the Drake Passage (Sievers and Nowlin 1988), the Antarctic Peninsula and Southwest Scotia Sea (Stein 1988), and the Indian Ocean Sector (Nagata et al. 1988) have provided evidence of large variability between seasons, from year to year, long-term trends, and also differences from one region to another.

The Southern Ocean is not radially symmetrical, and many circulation and water mass features vary markedly with latitude, as well as being influenced by topographic features (ridges, islands). The Antarctic Circumpolar Current displays significant temporal variation ranging from mesoscale features such as meanders and eddies to broad regional low frequency variations (Klinck and Hofman 1986; Gordon 1988). The importance of wind-induced variations in the circulation patterns was stressed by contributors to the seminar. Such wind-induced variations, perhaps coupled to changes in the freshwater balance, would also influence the vertical stability of the water column, the vertical heat flux, and the extent of sea ice cover.

15.6.3 THE SOUTHERN OSCILLATION

One phenomenon which influences the air pressure distribution over the Southern Hemisphere, and which impacts on the oceanic circulation patterns, is the irregular Southern Oscillation, resulting in the El Niño off Peru (van Loon and Shea 1987). While the influence of El Niño/Southern Oscillation (ENSO) events on the Southern Ocean are likely to be significant, the precise influence is not yet firmly established. Smith et al. (1988) have discussed the possible effects on primary production at the ice edge while Croxall et al. (1988a) and Priddle et al. (1988) point out that the seasons 1977–1978 and 1983–1984, when krill was scarce around South Georgia and land-based predators experienced poor breeding success, both followed years with strong ENSO events. Barry and Dayton (1988) have drawn attention to the correlation between ENSO events and the extent of fast ice off McMurdo Sound.

15.6.3.1 Variation in the Extent and Timing of the Advance and Retreat of Sea-Ice Cover

As discussed in Chapter 2 and Chapter 3, the sea ice is a major environmental variable influencing the distribution and production of the biota in the Southern Ocean. Mackintosh (1972) evaluated information on ice limits in the Southwest Atlantic Sector over the periods 1926–1939 and 1950–1951. He found that there was an anomalous northward extension of the ice edge during the cold season of 1930–1931, and a decrease in ice cover during the relatively warm seasons of 1929–1930, 1932–1933, and 1936–1937. Variations in the latitude of the northward extent of drift ice in the Scotia Sea that were identified in the study were probably related to the outflow of water from the Weddell Sea.

Carleton (ms) found that the substantial annual variations in the rate of ice advance and retreat, and the timing of the maximum and minimum extent, were linked with large-scale variations in atmospheric circulation, particularly cyclonic activity. During the period 1973–1977, the mean positions of the ice edge in the Southwest Atlantic Sector were found increasingly further south, while during the following years they were shifting back north, and they remained in average, rather stable, latitudes during the 1980s (Sahrhage 1988a) (Figure 15.38). Variations in the annual position of the fast ice edge in McMurdo Sound have been documented by Barry (1988).

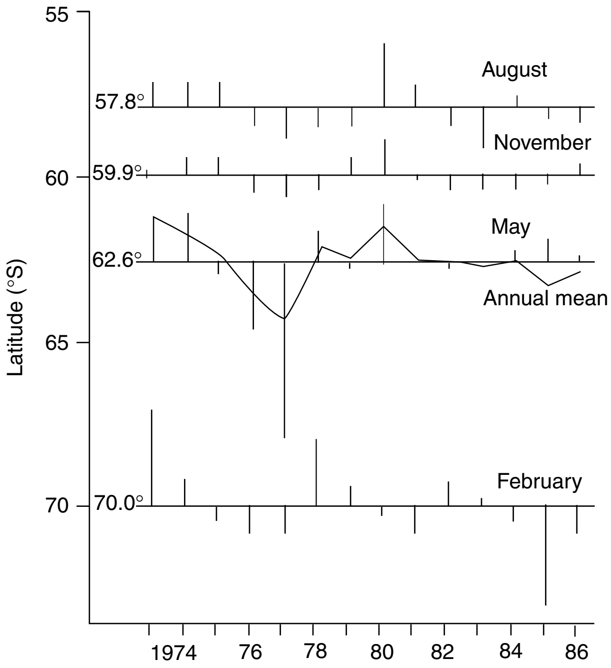


FIGURE 15.38 Mean positions and annual variations of the ice edge in the Southern Ocean between 0 and 60°W at the end of the months February, May, August and November, 1973–1986. Data source; Weekly ice charts of the Navy/NOAA Joint Ice Center, USA. (From Sahrhage, D., *Antarctic Ocean and Resources Variability,* Sahrhage, D., Ed., Springer-Verlag, Berlin Heidelberg, 33, 1988. With permission.)

15.6.4 MESO/LARGE-SCALE VARIABILITY IN THE SOUTHERN OCEAN BIOTA (RELATED TO THE ENVIRONMENT)

Many publications have discussed the relationships between water mass circulation and the distribution of krill and other living organisms in the Southern Ocean (e.g., Maselenkov 1980; Amos 1984; Lubimova et al. 1984). The conclusions of the seminar participants on variations in primary production in relation to environmental variability are summarized in the next two sections.

15.6.4.1 Phytoplankton

El-Sayed (1988a) has analyzed information collected during the past twenty-five years on spatial and temporal variabilities in the distribution and abundance of phytoplankton in the Drake Passage/Scotia Sea, the Bransfield Strait/Elephant Island, and Ross Sea areas of the Southern Ocean. The general picture that emerged was one of great variability in phytoplankton biomass and primary production. This spatial variability (up to two orders of magnitude) tends to overshadow that of seasonal differences. The timing of the peak phytoplankton abundance also varied from year to year. El-Sayed concluded that seasonal variability was much more pronounced than interannual variability.

15.6.4.2 Primary Production in the Marginal Ice Zone

As detailed in Chapter 13, large accumulations of phytoplankton (Smith and Nelson 1985a, 1985b; Smith et al. 1988), zooplankton (Marr 1962), seabirds (Ainley and Jacobs 1981; Fraser and Ainley 1986), and marine mammals (Laws 1985) are associated with the Marginal Ice Edge ZoneMarginal Ice Edge Zone. Smith et al. (1988) have considered the interannual variability of the estimated primary productivity of the Antarctic Marginal Ice Edge Zone. This was considered to be substantial, with the maximum productivity being 50% greater than the minimum. While it appears that there is a significant potential for interannual variability in the primary productivity in the Marginal Ice Edge Zone, it does not appear to be as great as that observed in some pelagic ecosystems, e.g., the Peruvian upwelling ecosystem (Chavez and Barker 1987). The variability that does occur is directly related to the advance and retreat of the seasonal pack ice, which can be highly variable from year to year (Zwally et al. 1983a, 1983b).

15.6.5 KRILL VARIABILITY IN RELATION TO THE ENVIRONMENT

Investigations of the patterns of the distribution and abundance of krill have been discussed in Chapter 5. As seen, krill form an important component of the Southern Ocean pelagic food web. They account for a substantial proportion of the diet of many predators, some of which rely exclusively on krill for food during their breeding period. Recent studies summarized by Priddle et al. (1988) have provided direct evidence of substantial interannual changes in the abundance of krill in certain parts of the Southern Ocean, particularly in the Southwest Atlantic Sector. Parallel data on the breeding success of land-based krill predators (breeding seabirds and seals) have provided additional evidence over a longer time scale (see below).

15.6.5.1 Large-Scale Fluctuations in the Distribution and Abundance of Krill

Studies by British Antarctic Survey scientists revealed that the stocks of krill around South Georgia in August 1983 were very much lower (3%) than expected from a comparison with those found in December 1981 (Heywood et al. 1985). In contrast, the stocks of other zooplankton approximated to anticipated levels, after allowing for seasonal change. Krill biomass in September 1983 was also much lower than in February 1982 along three transects across the Scotia Sea.

The SIBEX cruises in the following summer (1983–1984) in the Bransfield Strait area also showed very greatly reduced krill biomass (Mujica and Asencio 1985; Witek et al. 1985). Both studies also noted the predominance of salps in their samples. Wormuth (1987), in comparing samples taken near Elephant Island in 1981 and 1984, found that the four dominant copepod specis (*C. propinquus, C. acutus, M. gerlachii*, and *R, gigas*) were more abundant by factors of 101. 807, 20 and 1,000, respectively, while the salp *Salpa thompsoni* was 10.5 times more abundant in 1984 than in 1981. In contrast, the biomass of krill in the Southern Scotia Sea appears to have been normal during the 1983–1984 season (Everson 1988). The Prydz Bay region also had a lower than expected krill biomass during the same period (Miller 1985, 1986a; Terazaki and Wada 1986). Krill biomass in the Bransfield Strait returned to the expected levels in the second year (1985–1986) of the BIOMASS SIBEX survey after the low biomass of the 1984–1985 season. Two larger data sets on krill predators suggest that low krill biomass episodes in the Bransfield Strait-South Georgia region may occur two or three times in a decade (Priddle et al. 1988; Croxall et al. 1988a, 1988b).

According to Priddle et al. (1988), it seems most unlikely that the changes described above could be ascribed to features of krill biology. Simple models of recruitment failure or mortality could explain the observed changes, and alterations in small-scale distribution patterns were not indicated from the available data. They considered that the more probable mechanisms must involve large-scale changes in the distribution of krill brought about by ocean-atmosphere processes. They postulated that a breakdown of the hydrographic structure in the surface waters over a large area would drastically reduce the residence time of krill, and that it would take some time to reestablish the former high-krill density.

15.6.5.2 Mesoscale Changes in the Distribution of Krill

The presence of krill in the open ocean such as the seas around South Georgia is dependent largely on the transport of animals to the area by ocean currents. Mesoscale hydrographic features impinging on krill distribution in this region are the ACC and the Weddell Sea Gyre. Bottom topography of the submarine ridges and the associated islands of the Scotia Arc deflect these currents northwards in the vicinity of South Georgia. Meridional transport in this region of the Southern Ocean is therefore slowed, and this, combined with the numerous eddies which are formed in the Drake Passage and the western edge of the Scotia Sea, would provide conditions that may retain or concentrate planktonic organisms including krill (Angel and Fasham 1983).

Influx of krill to the Scotia Sea is a second factor of major importance in determining the distribution and abundance of krill in the region. Animals are brought into the Scotia Sea from two main sources: in water from the Weddell Sea Gyre; and in water from the Southwest Pacific Basin, carried through the Drake Passage in the ACC.

One process that could redistribute krill in the region and give rise to low abundances near South Georgia is a southward shift of the Polar Frontal Zone under the influence of windforcing produced by atmospheric depressions which track across the region. Priddle et al. (1988) note that synoptic charts of sea-surface temperatures derived from satellite remote sensing data (NOAA) show that the Polar Frontal Zone (and hence the ACC) is a highly mobile feature of the Scotia Sea. The tracks of mesoscale eddies must be similarly affected. Southward displacement of could be sufficient to remove krill beyond the foraging ranges of seals and seabirds breeding at Bird Island, South Georgia. Breakdown of the eddy system would release krill into the main current flow to be dispersed downstream. While these mesoscale processes provide mechanisms by which krill may be distributed in the Scotia Sea region, their impact would be for only a comparatively short time and does not explain the six-nine month period of krill paucity noted in 1983–1984.

However, if the changes outlined above acted together with the eddy structure breaking down when the polar frontal system moved south to the southern limit of its range, krill would then be both displaced from the South Georgia region and released from the eddies to pass down current and to the east of the Scotia Sea. When the frontal zones returned to more northerly positions, replenishment of the Scotia Sea krill biomass would depend on the influx of animals carried by the Weddell Sea surface water and the surface water in the ACC derived from the Southeast Pacific Basin. Such “reseeding” of the area would clearly take longer than the original loss of animals form the area.

Maslennikov and Solyankin (1988) have analyzed data on the hydrometeorlogical conditions in the Atlantic Sector of the Southern Ocean over the period 1903–1975. “Cold” and “warm” epochs were identified. Sea surface isotherms during the cold period (1911–1937) and the warm period (1959–1979) were compared (Maslennikov 1979). These comparisons revealed a northward extension of water from the Weddell Sea during the cold period. This would have increased the concentrations of krill in the vicinity of South Georgia. The reverse would have occurred during the warm period.

15.6.5.3 Krill Variability Detected from Predator Studies

Measuring the reproductive effort of seabirds that during their breeding season feed predominately on krill has been suggested as a means of providing good indices of the state of the local marine system and of the local krill biomass (Everson 1977a; Croxall and Prince 1979; see Chapter 18). Recent relevant studies undertaken at South Georgia and Signy Island over the period 1976–1987 have been analyzed by Croxall et al. (1988a, 1988b). Changes in reproductive success need to be considered in relation to human exploitation of the marine resources, especially of seals, whales, fish, and krill. The changes in the magnitude of the catches of whales, fish, and krill, and the changes that occurred in penguin species and Antarctic fur seals at Signy Island and South Georgia over this period are shown in Figure 15.39 and Figure 15.40. Here, however, we are concerned with the interannual variations in reproductive success over the period for which data is available.

Birds. The data presented by Croxall et al. (1988a, 1988b) show that not all seabird populations are currently increasing. The pattern at South Georgia (Figure 15.39) over the past decade has been one of substantial fluctuation. A common feature was an abrupt decline in breeding numbers after 1978, which persisted for several years and which was succeeded either by a gradual increase or by further fluctuations. Another notable decrease occurred after 1984, although that of the gentoo penguin actually started in 1984. Fluctuations at Signy Island have not followed a similar pattern. Over the period 1979–1987 Adélie Penguins at Signy have increased, averaging 4% per annum, whereas chinstrap Penguin numbers did not change significantly. Breeding numbers of both species decreased abruptly in 1981 and, after a rapid recovery, chinstraps decreased again in 1983–1985. Breeding success of the wandering albatross, which breeds in the winter and eats fish and squid, has remained constant, while the population size has declined gradually but significantly. The other species which breed at South Georgia in the summer and which feed extensively on krill have shown major fluctuations in some, or all, of the following parameters; breeding population size, foraging trip duration, and offspring growth rate.

Seals. The reproductive behaviour of seals at South Georgia have been studied at Bird Island by Croxall and Prince (1979), Croxall et al. (1985), Doidge and Croxall

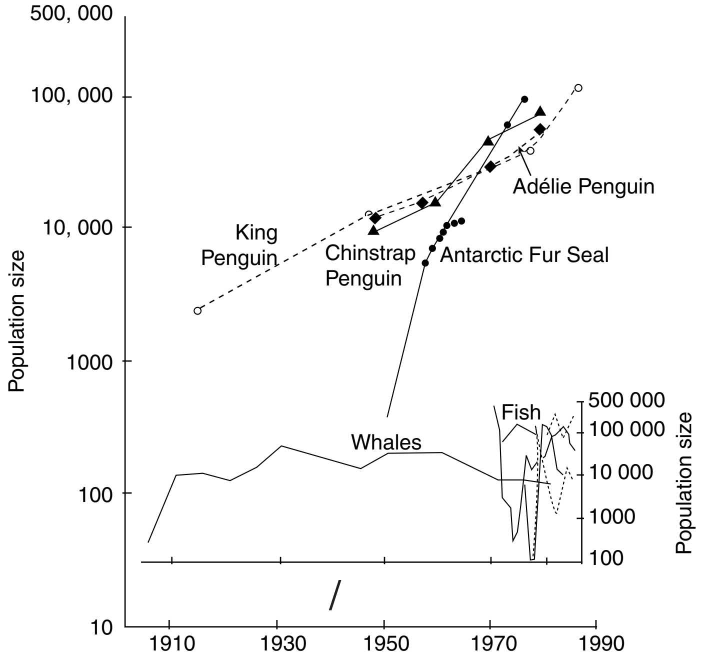


FIGURE 15.39 Changes in population size of Adélie and Chinstrap Penguins (breeding pairs; Signy Island, South Orkney Islands), king penguins (adults: South Georgia) and antarctic fur seals (pups: South Georgia), in relation (*inset*) to commercial harvests of Antarctic whales (individuals; from Bonner 1984), fish and krill (tonnes; CCAMLR 1986) on the South Georgia and South Orkney Islands. Note log scale. (From Croxall, J.P., McCann, T.S., Prince, P.A., Rothery, P., *Antarctic Ocean and Resources Variability,* Springer-Verlag, Berlin Heidelberg, 261, 1988. With permission.)

(1985), and Doidge et al. (1986). Variability in attendance patterns of the breeding females has been identified in these studies. These patterns comprise three elements:

1. The period between the birth of the pup and the mother's departure to sea (perinatal attendance).
2. The foraging trips at sea.
3. The interval between these trips when the pups are suckled.

Data for these elements over the period 1979–1987 are summarized in Figure 15.41. This figure identifies a number of points. First, the duration of the shore visits varies little between the years, and although the visits were significantly longer in 1984 and 1985 than in other years, this is not matched by variations in other parameters. Second, perinatal attendance was significantly shorter, and much more variable, in 1979 and 1984 than in other years, which show no obvious pattern. Third, foraging trips to sea were very long in 1979 and 1984, and were exceptionally so in the latter. Bengtson (1988) has examined the foraging patterns of seals at Bird Island over the period 1962–1981 by analysing the growth layers in the canine teeth. He found that over the twenty-year period the number of feeding trips made by the females varied markedly. His analysis confirmed 1979 as a year in which there was a significant decrease in the number of foraging trips.

Possible Explanations for the Variation in Reproductive Performance. From the data discussed above, it is clear that 1984 in particular was an anomalous year with reduced breeding success in Antarctic fur seals, grey-headed albatrosses, black-browed albatrosses, macaroni penguins, and gentoo penguins. The breeding populations of albatrosses, fur seals, and macaroni penguins were depressed in the following year, but generally seemed to have recovered by 1986 and 1987. While the data for the earlier years is not complete, it is evident that in 1978 seabird breeding success was very poor and that the Antarctic fur seal growth rates were low. The fact that in these years several species of different ecologies were affected is indicative of some environmental change that impacted them.

Croxall et al. (1988a, 1988b) note that there is evidence of medium- to large-scale environmental anomalies in both 1978 and 1984. In 1978 a variety of fishing and research vessels failed to locate krill concentrations around South Georgia (Bonner et al. 1978), with the only abundant planktonic crustacean being the amphipod *Thermisto gaudichaudii*. Krill was, however, present around the South Shetland and South Orkney Islands. Events leading up to the 1984 summer season are well known (Heywood et al. 1985; Priddle et al. 1988) with evidence of substantial oceanographic anomalies and very low numbers of krill over a wide area, and possibly for a long time. Krill predators would need to stay away foraging for a longer time than usual

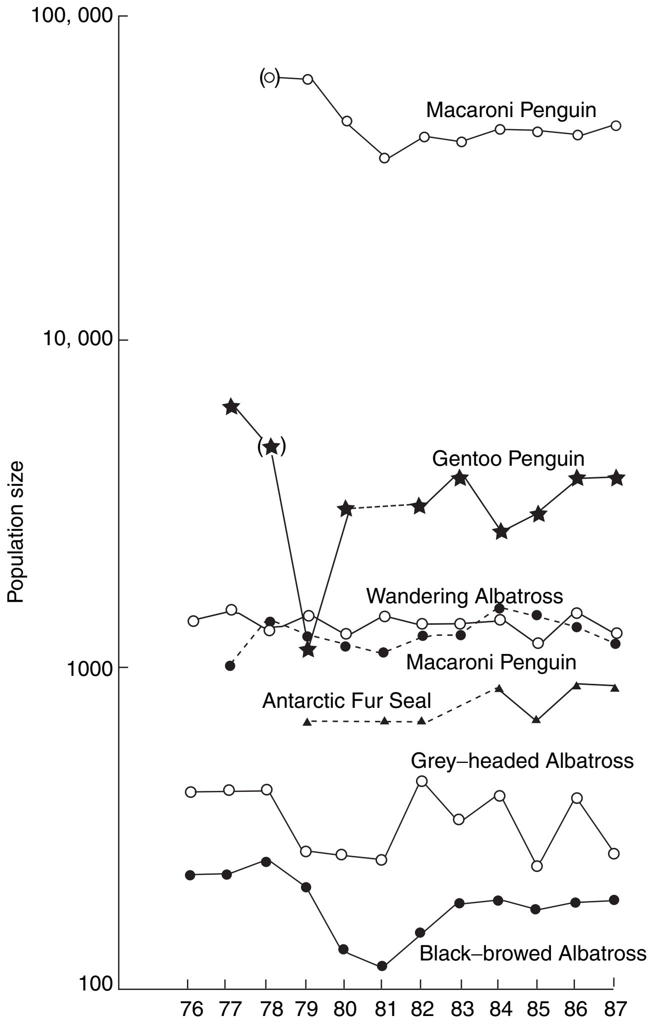


FIGURE 15.40 Changes in population size of seabirds (breeding pairs) and Antarctic fur seals (pups born) at Bird Island, South Georgia, 1976–1987. Values in *parentheses* are estimates from incomplete data sets. Note log scale. (From Croxall, J.P., McCann, T.S., Prince, P.A., Rothery, P., *Antarctic Ocean and Resources Variability,* Springer-Verlag Heidelberg, 161, 1988. With permission.)

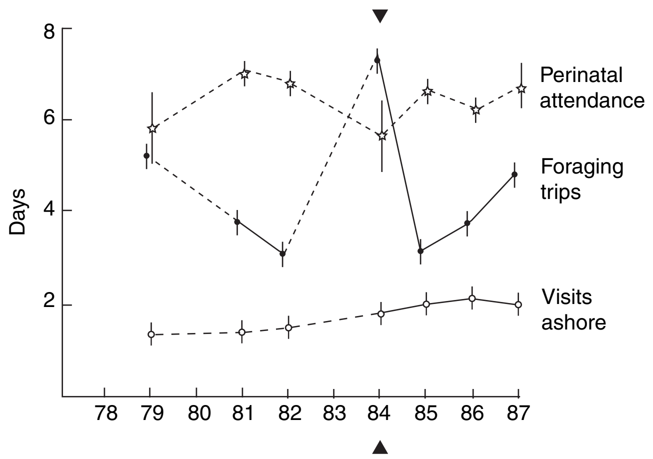


FIGURE 15.41 Duration of attendance periods ashore and foraging trips to sea in Antarctic fur seals at Bird Island, South Georgia, 1989–1987. Values are means 2 s.e. Arrow-heads indicate anomalous years. (From Croxall, J.P., McCann, T.S., Prince, P.A., Rothery, P., *Antaerctic Ocean and Resources Variability,* Springer-Verlag, Berlin Heidelberg, 161, 1988. With permission.)

until they had met their own requirements and collected enough extra food to make the return to their offspring energetically worthwhile (Charnov et al. 1976a) Because the food shortage persisted for a long period, it resulted in major offspring mortality and, eventually, adult mortality judging by the reduction in the breeding population size in the following year.

Croxall et al. (1988a, 1988b) drew attention to the fact that the two years in which there was evidence of food shortages and diminished breeding success were both one year after strong (massive in 1983) ENSO events. If in the future such phenomena are consistently detectable one year after an ENSO event, then this will have profound effects on resource management.

16 Resource Exploitation

CONTENTS

16.1 INTRODUCTION

The total world fish catch (including shellfish) reached a plateau in the early 1970s at about 70 million tons per annum, and has since remained steady or declined. Estimates of the total world potential of conventional marine living resources indicate that the total sustainable catch is of the order of about 100 million tons per annum (Gulland 1976). With the rapid increase in the world's population over the past few decades, and the increased demand for protein, attention has been focussed on currently unexploited resources, in particular, the harvesting of unconventional resources. Of the latter, many consider Antarctic krill as the most promising resource. Fishing restrictions placed on many fishing nations by the establishment of 200-mile Exclusive Economic Zones (EECs), and the declines which have occurred in the stocks of some major fisheries in the Northern Hemisphere, provide stimuli for the exploitation of Southern Ocean living resources. This has resulted in many Northern countries having an under-utilized or surplus fishing capacity.

The magnitude and distribution of Southern Ocean living resources and their potential for exploitation have been the subject of a number of recent reviews (Gulland 1970, 1983a, 1983b, 1986; Moiseev 1970; Lubimova et al. 1973, 1980; Nemoto and Nasu 1975; El-Sayed 1977; Everson 1977b, 1978, 1981; Bengtson 1978, 1985a; Knox 1983, 1994, 1987; McWhinnie and Dennis 1978b; Lubimova 1983; Budzinski et al. 1985; Kock and Shimadzu 1996). However, in spite of the comparatively large body of information that is available, the magnitude of the resources and the possibilities of their sustained exploitation are still subject to considerable speculation.

The exploitation of the Southern Ocean living resources started with sealing in the nineteenth century. The effects on Antarctic fur seal stocks in particular were drastic, although the impact on the ecosystem as a whole was not great. In contrast, whaling, specifically the depletion of larger baleen whale stocks, has had considerable impact, resulting in increases in the populations of competing species. These interactions will be discussed further in the next chapter. Exploitation is now concentrated on krill and demersal (bottom-living) fish. Although several fish stocks have already been greatly reduced from their original level, the stocks of krill have so far been minimally altered.

16.2 KRILL

Some time ago, an article appeared in a New Zealand newspaper, titled “Soviet Scientists Argue the Case for Krill Harvest.” An extract from this article follows:

> Soviet scholars have achieved major success in evaluation of the reserves of Antarctic krill… The area of krill domination has been set at 13–17 million square kilometres, with the total area of the Antarctic standing at 45 million square kilometres. It has also been established by modelling the life-cycle of the krill population that their average annual output in the domination zone ranges from 24 to 17 g per sq. m, while the annual aggregate krill mass is estimated at up to a billion tons.
>
> According to the latest Soviet and foreign experts, the volume of krill consumption by the principal consumers (whales, seals, fish, birds, and squid) stands at 200–300 million tons a year. It is obvious that in the ecological system where krill is the dominant species its annual growth exceeds the volume of consumption by other species.
>
> …This means that a certain part of the krill mass can be used by man for obtaining valuable food products without damage to the ecological system.

Soviet experts evaluate the potential krill catch on the basis of the results of many years of direct mature krill stock surveys in the individual areas of krill domination at 15–30 million tons per year, which is a safe minimum that cannot cause any damage to the optimal reproduction of krill and to the adequate food supply of its consumers.

In this and the succeeding chapter, we will evaluate the accuracy of the conclusions arrived at in the above statement, and assess the likelihood of the development of large-scale sustainable exploitation of krill.

16.2.1 THE DEVELOPMENT OF THE ANTARCTIC KRILL FISHERY

The krill fishery was the most recent fishery to develop in the Southern Ocean It also appeared to be potentially the largest and most attention attracting fishery. The earliest reports of krill fishing are for the 1962–1963 season, showing that three tons were caught by the USSR (Budkovskiy and Yaragov 1967). Further USSR exploratory expeditions took place in 1963–1964, 1964–1965 (Nemoto and Nasu 1975), and in 1967–1968 (Ivanov 1970). The USSR was the only country involved in the first ten years of the fishery. It was joined in the 1972–1973 season by Japan, who undertook exploratory trawling that season (Nemoto and Nasu 1975), and subsequently in the 1973–1974, 1974–1975, and 1976–1977 seasons. Catches by Japanese ships in these seasons amounted to 59, 656, 2600, 500, and a planned catch of 1000 tons, respectively. Other countries which carried out exploratory fishing in these early years include Chile (1974–1975, 1975–1976), the Federal Republic of Germany (1975–1976, 1977–1978), Poland (1975–1976) and Norway (1976–1977). More recently, the German Democratic Republic, Bulgaria, South Korea and Taiwan have joined these countries.

The fishery was slow to develop although the USSR began marketing “Coral” brand krill-butter and cheese spreads and “Ocean” brand krill paste in 1970. It was not until the 1876–1877 season that the total catch exceeded 100,000 tons.

16.2.2 CATCH STATISTICS

The FAO statistics began reporting krill separately in 1973. Prior to this, the catches in the areas adjacent to Antarctica were reported as “Marine Crustacea unspecified.” The recorded catches over the 1969–1970 to 1974–1975 seasons were 2,000, 2,500, 6,000, 10,000, 5,476 and 8,867, respectively. Commercial krill catching on a larger scale began in the 1976–1977 season when the catch reached 135,000 tons (Figure 16.1), and subsequently, the catches increased rapidly to a peak of 528,000 tons in 1982–1983. Catches declined to a low of 130,875 in the 1984–1985 season, but they recovered to 445,673 tons in the 1986–1987 season. Subsequently, they have remained at around 370,000 tons (Table 16.1).

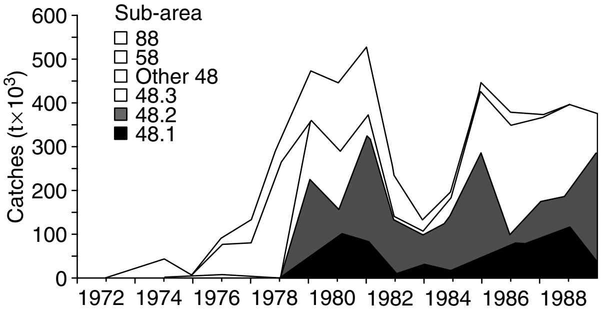


FIGURE 16.1 The total krill catch by Subarea since 1973. (From Redrawn with additions from SC-CCAMLR., *Rep. Ninth Meeting of CCAMLR Hobart, Australia 22–26 October 1990*, CCAMLR, Hobart, 1990. With permission.)

TABLE 16.1
Sizes (kg) of Individual Fish Stocks in the Southern Ocean Prior to Exploitation

Season	Catch(t)	Comments	Source
1961–1962	4	Krill	Budkoviskiy and Yarago (1967)
1963–1964	70	Krill	Stasenko (1967)
1964–1965	306	Krill	Nemoto and Nasu (1975)
1966–1967	?	Krill	Nemoto and Nasu (1975)
1967–1968	> 140	Krill	Ivanov(1970)
1969–1970	100	UMC	FAO (1976)
1970–1971	1,300	UMC	FAO (1976)
1971–1972	2,100	UMC	FAO (1976)
1972–1973	7,459	Krill	FAO (1976) Nemoto and Nasu (1975)

Source: From Kock, K.H., *Antarctic Fish and Fisheries*, Cambridge University Press, Cambridge, 1992. With permission.

16.2.3 PROBLEMS WITH THE EXPLOITATION OF KRILL

There are a number of problems associated with the harvesting and processing of krill. In areas where krill concentrations are found is the main obstacle to fishing operations. Krill concentration determines the length of the fishing season that on average lasts five months, from mid-November to mid-April. However, when weather conditions are favorable, the season may extend to seven months or longer in the northerly areas of the Southern Ocean.

Problems also arise when the catch rate, or quantities of krill per haul, exceed the processing capacity onboard ships. Any surplus can only be used for the production of animal feed because the raw krill spoils easily. This is caused by the very active system of proteolytic enzymes in the krill. Such activity is particularly high in immature krill, due to the intensive metabolism associated with their growth (Mitskevitch and Mosolov 1981). Immediately after death, interrelated biochemical changes take place reducing the quality of krill for processing. These include autolysis, which results in drips and unpleasant odors, as well as changes in color and texture. Bacterial decomposition of the krill's tissues begins after 12–16 h. After 3–4 h of storage at air temperatures, the intensity of changes in taste, odor, and texture reaches such a level that the raw material is no longer fit for processing into food (Andreev et al. 1981). During cold storage, proteolytic activity increases due to the diffusion of enzymes from the intestines to muscle tissue. The shelf life of frozen krill at −18°C is only three months (Bidenko et al. 1981).

Additional processing problems are caused by the phytoplankton upon which krill feed. Intensively feeding "green" krill are unfit for processing into mince-type products (Bykova and Radakova 1981) and produce canned products of inferior quality. Krill processing is also made more difficult by the presence of by-catch species (salps, jellyfish, juvenile fish, and fish larvae), which often constitute over 20% of the catch.

A paper written by Soevik and Braekkan in 1979 on the presence of fluoride in krill considerably impacted the optimistic views on the potential of krill for human consumption and animal feed. High fluoride levels found in whole krill (up to 2440 ppm) led these authors to state, "This [high level] would make krill in any form, even peeled, fail to comply with the requirements for human consumption." Numerous publications have confirmed the high levels of fluoride in krill (e.g., Hempel and Mathey 1981; Boone and Manthey 1983; Adelung et al. 1987; Schneppenheim 1990) compared with other Antarctic animals (Schneppenheim 1980; Oelenschlager and Manthey 1982; Culik 1987). However, it has been found that most of the fluoride in living krill is concentrated in its exoskeleton. It has been shown that the fluoride migrates from the shell to the muscle tissue in frozen krill (Christians and Leinemann 1980; Christians et al. 1980). Lowering the temperature to −40°C stops the migration process. By first separating the body fluids, the migration of fluoride into the muscle tissue during the frozen storage period is reduced. Similarly, boiling the raw material arrests the migration. Techniques have also been developed for the production of meat with reduced shell content. Such procedures can however, result in the production of an acceptable product. The U.S. Food and Drug Administration concluded that the 14 ppm of fluoride contained in krill meat does not constitute a health hazard. However, care will need to be taken to prepare and market krill products which are both acceptable and meet stringent health standards.

16.2.4 CATCHING AND PROCESSING KRILL

A number of recent reviews on the development of krill fishery deal with the catching of krill, the technology of krill utilization, the mechanization of the processing krill, and the problems of krill industry economics and marketing (Grantham 1977; McElroy 1980a, 1980b; Budzinski et al. 1985).

16.2.4.1 Krill Fishing Techniques

As discussed in Chapter 5, krill concentrations are readily located by hydro-acoustic techniques which enable fishermen to distinguish such concentrations from those of other organisms such as salps and jellyfish. Krill fishing techniques are generally similar to those used for pelagic fish. Because krill are characterized by low resistance to mechanical damage, large single trawls are of little value as the raw material is badly crushed when the trawl is brought aboard. Experience has shown that single hauls should not exceed 5–6 tons for the processing to proceed smoothly. Polish factory trawlers have found that 70–89% of krill are caught in the daytime.

16.2.4.2 Daily Catch Rates

Many factors influence catch rates, including type of krill concentrations, size of vessel and type of fishing gear, ice and weather conditions, processing capacity of the vessel, etc. Early publications estimated the daily catch rate on the basis of potentially obtainable catch in tons per hour, leading to over-optimistic estimates of the daily catch rates. The highest catch rate achieved by a Federal Republic of Germany experimental trawling expedition was 35 tons in eight minutes, with an overall catch rate of 8–12 tons h^{-1}. USSR catches have been quoted at 139–272 tons day^{-1}. It has been estimated that daily catch rates of 200–300 tons day^{-1} should be practicable, and that under favorable conditions, 500 tons day^{-1} should be possible.

These optimistic forecasts have not been realized in practice. Results from three Polish factory trawlers over the 1977–1978 season show that the vessels caught 8003 tons of krill in 139 days of fishing at a daily rate of 57.8 tons per vessel (Russek et al. 1981). This is similar to the catch rates reported for a large Japanese factory trawler (104.5 m in length), which in the 1981–1982 and 1982–1983 fishing seasons fished for 115 and 118 days, respectively, with an average catch of 51.5 tons day^{-1}.

16.2.4.3 Krill as a Raw Material

The chemical composition of krill is well balanced in terms of a potential food material. The nitrogenous substances in krill hover around 13% of wet weight, made up of 8% true protein and 2.5% true amino acids (Grantham 1977). The amino acid fraction is characterized by its relatively high content (46%) of essential amino acids. Thus, it is a highly nutritious food for human consumption.

16.2.4.4 Possibilities of Krill Processing

There are a number of products that can be processed from krill. They include:

1. Frozen, boiled-frozen, and dried krill. With the exception of the Asian markets, sale prospects of these products are not promising. In countries where euphausiids are a traditional food (Japan, South Korea, and Taiwan), more attention is being paid to products produced from frozen and dried krill.
2. Coagulated and minced krill. In the USSR, Poland, the Federal Republic of Germany, and South Korea, the interest in krill products is concentrated on coagulated pastes and minces. Coagulated pastes are produced by pressing out protein from krill by means of a screw press, thermal coagulation of the juice, then separating coagulated protein from the liquid, cooling of the paste, freezing and finally, packaging. The biological and nutritive value of the coagulated paste is high and comparable to fish. In the USSR, there is wide experience in marketing coagulated pastes as a variety of canned products, including pastes, shrimp butter, cheese with paste, etc. However, problems of consumer acceptance have not been solved. Krill mince is produced from precooked raw material. It is a dense pink paste which appears to have limited use except as an additive to other food products.
3. Whole tail meat. Tail meat is considered the most valuable krill food product but also the most difficult to obtain satisfactorily (Grantham 1977). Research on the production of whole tail meat in Denmark, Chile, Japan, the Federal Republic of Germany, the United States, and the USSR has resulted in three main methods for its production- roller peeling, attrition of boiled-frozen krill, and flotation of the shells from boiled krill. Tail meat can be used for a variety of products, including casseroles, stews, sausages, pates, krill sticks, and others.

De-proteinized shells of krill contain 30–40% chitin. By deacetylation of chitin, a valuable product, chitosan is obtained. Considerable research has been carried out in the past few years on the production technology and possible industrial application of chitin/chitosan and their derivatives. A present application of chitosan on a commercial scale is waste water treatment, where it acts as a protein coagulant. Chitosan can also be used for the removal of heavy metals, including plutonium and uranium. Promising results have also been obtained using it as a haemostatic agent (Fradet 1985). Chitin and its derivatives are biodegradable and therefore, do not introduce any disturbances into the human body. This makes chitosan an appealing substance for the controlled release of drugs, nutrients, agricultural chemicals, etc. (Muzzarelli 1977).

16.2.5 FUTURE PROSPECTS

The worldwide interest in krill resources during the years 1980–1987 was much lower than during the 1974–1979 period, when many studies published by international, governmental, and private institutions had prophesied that the exploitation of krill resources would reduce the world deficit of animal protein, and make the problem of undernutrition in some countries less severe. While it has been demonstrated that krill can be caught in large quantity and processed into products that are nutritive and acceptable for human consumption, many problems remain to be solved before the krill fishing industry can develop a firm basis.

In the past few years, the expected gradual rise in krill catches has not materialized. This may in part be due to the fact that marketing of krill products is commercially not viable. Budzinski et al. (1985) have carried out a detailed study of the production costs, prices, and demand for krill products. Their study is an advance of earlier studies by authors such as Eddie (1977), McElroy (1980a), and Mitchell and Sandbrook (1980). Budzinski et al. based their estimate of production costs mainly on the actual costs incurred by Polish vessels fishing for export to countries in FAO Major Fishing Areas numbers 48.1 and 48.2 (see Figure 16.2). On this basis, the cost of catching and manufacturing 1 kg of tail meat, delivered in frozen blocks and treated as a semi-finished product by inland processors, would most likely amount to U.S. \$3.60. This might be expected to drop to U.S. \$2.20 as efficiency improved. The unit cost for meal production was estimated at U.S. \$2,035 ton^{-1} for a vessel with a daily catch rate of 55 tons, and \$1,999 with a daily catch rate of 65 tons. These unit costs figures considerably exceeded fish meal prices on the world market and the authors concluded that meal for animal food production from krill would not be viable.

More serious problems, however, are encountered in the marketing of krill products. There is a great need for extensive, systematic, and impartial processing and marketing research. A demand for krill products has yet to be established at a price that would be profitable to the producers. With currently available technology it is possible

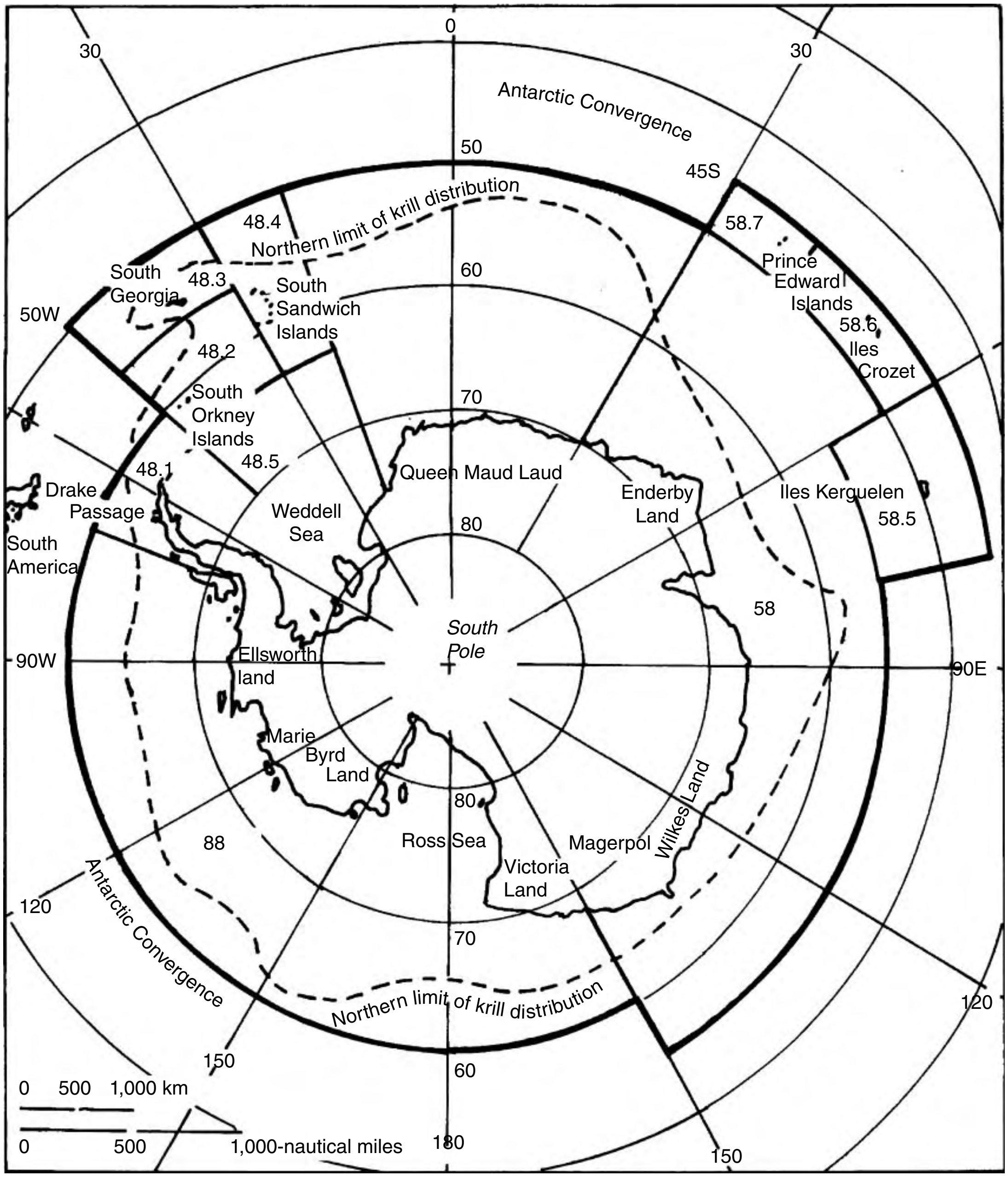


FIGURE 16.2 The boundaries of the *Convention* on the Conservation of Antarctic Marine Living Resources and the FAO southern Ocean Fishing Areas. The numbered areas are the areas established by FAO for the reporting of statistical data on fish catches.

to produce krill on factory trawlers into tail meat, canned, and minced products. It is considered that techniques for the production of tail meat developed in Japan, Poland, and the USSR are best prospects for the profitable exploitation of krill resources. However, two main conditions must be met for this to happen (Budzinski et al. 1985). First, krill tail meat would need to be accepted in the market as an analogue or substitute for small shrimp. In 1984, the average prices for the lowest grade of frozen headless shrimp from India, Pakistan, and Sri Lanka was U.S. \$3.75 to \$4.00 per kg to U.S. ports, and U.S. \$3.30 to \$3.80 to Japanese ports. Grantham (1977) thought it unlikely that the price of krill tail meat could be higher than 70% of the locally prevailing price for small shrimp. On this basis, the anticipated price for krill tail meat would have been U.S. \$2.50 to \$2.90 per kg. A more optimistic view by some experts puts the price of krill on U.S. and Japanese markets at U.S. \$3.00 to \$4.00 per kg. This results in a return to the industry of a minimum of U.S. \$2,500 tonne^{-1} in the first case and U.S. \$3,000 ton^{-1} in the second. However, the profitability threshold for commercial fishing operations could still be higher.

The exploitation model above is based on the assumption that the factory trawler would catch fish and squid in the remaining six months after the krill season, and that the vessels would be based at a close port. When fishing operations start in distant ports in Europe, the United States, and Japan the number of days at sea would increase and output would drop, making the unit cost of production of tail meat much higher. For this reason, Japanese fishing companies have entered into joint fishing agreements with Chilean companies. In addition, any further substantial rise in fuel costs could substantially affect the economic viability.

Thus, it is clear that considerable difficulties still encountered in the utilization of Antarctic krill for human food, animal meal, and other products, are greater than those found in the production and marketing of other products of marine origin. In addition to the processing problems mentioned above, the high fluoride content of the raw material imposes some constraints. Technological solutions can overcome the latter problem, but they will add to the cost of production. The best prospects for the future exploitation of krill appear to lie in high-quality, low-volume products for human consumption. Supplies of frozen, fresh, and boiled krill to some Far East countries could be an exception. There are, however, serious economic constraints to the development of mass production aimed at increasing the supply of highly processed protein products to developing countries. Thus, the original hopes of alleviating problems of protein shortage in developing countries are unlikely to be realized.

Additionally, there is the question as to whether krill exploitation would have an impact on those predators dependent on krill. Specifically, could it prevent the recovery of whale stocks? In relation to total whale stocks, the present level of exploitation is small. However, the potential for overexploitation of localized stocks still exists. Everson and Goss (1991) have analyzed fine scale-catch data reported in recent years on krill fishery in the Atlantic sector. Their analyses indicate that krill fishery is concentrated on the continental shelf or close to it. Seasonal changes in fishery location are in the main associated with the pack-ice northern limit. During the summer months, the fishery is operating in areas where key krill predators are likely to be active. It is therefore likely that krill catches in such areas, although minor in the context of the total krill resource, could deplete the krill available to its predators.

16.3 FISH

16.3.1 INTRODUCTION

As commercial exploitation of Antarctic fish stocks is comparatively recent, detailed information available on their biology, age and growth, stock sizes, stock discreteness, natural mortality, and recruitment is limited in comparison to that available for Northern Hemisphere fish stocks. Only recently has reliable information been collected on aspects such as catch statistics, fishing effort, impact of fishing on the stocks, and catch-per-unit-effort (CPUE). The available information has been summarized by Kock (1975), Everson (1977b, 1978, 1981), Anonymous (1985a, 1985b), Kock et al. (1985), and Kock and Shimadzu (1996).

The Southern Ocean is divided into three major fishing areas (numbers 48, 58, and 88). Each is divided into subzones as proposed by Everson (1977b), and subsequently modified by the 1984 meeting of the Scientific Committee of the Commission on the Conservation of Antarctic Marine Living Resources (see Figure 16.2). Due to the lack of major exploitable pelagic stocks, trawling is primarily directed on demersal (bottom-living) fish of the suborder Notothenoidei at depths down to 500 m. The most important fishing grounds are:

1. In the Atlantic Ocean Sector (FAO Area 48), along the Scotia Arc (Shag Rocks, South Georgia, South Sandwich Islands, South Orkney Islands, Elephant Island, South Shetland Islands, and Joineville Island)
2. In the Indian Ocean Sector (FAO Area 58) (Ob and Lena Seamounts, Crozet Island, Shiff Bank, Kerguelen Islands, Kerguelen-Heard Ridge, and MacDonald Islands).

16.3.2 THE DEVELOPMENT OF THE ANTARCTIC FISHERIES

Attempts to exploit Antarctic fish stocks commercially date back to the beginning of this century. E. Vanhoffen, a biologist from the German *Gauss* expedition, hoped to find commercially utilizable fish in the Southern Ocean. He also proposed to increase the fish harvest from Kerguelen waters by the introduction of new species from the islands of St. Paul and New Amsterdam (Vanhoeffen 1902). His suggestion was not acted upon, but recently, trout and salmon were introduced into the rivers of the Kerguelen Islands. Also, proposals have been advanced for the seeding of Pacific salmon into South Chilean waters, from where they could undertake feeding migrations into Antarctic waters (Joyner et al. 1974).

While Vanhoffen put forward his ideas, whalers discovered large concentrations of marbled Notothenia (*Notothenia rossii*) off of South Georgia. A considerable number of barrels of salted fish were sold to Buenos Aires and the Norwegian biologist, Sorling, raised the possibility of establishing an important fishery off of the island. This suggestion was not followed up due to the abundance of more profitable whales and the distance from the market. Repeated fishing trials by Argentinean, Norwegian, and Japanese companies in the 1930s, 1950s, and 1960s with purse seiners and small bottom trawlers all failed (Olsen 1954).

Of approximately 270 fish species known from the Southern Ocean, 12 (separated into some 30 stocks) are or have been the subject to regular commercial exploitation (Kock 1992). Since 1984, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has regulated this exploitation. However, population (stock) sizes and trends are available only for a number of these stocks.

Exploratory fishing by the Soviet Union in the Scotia Sea, commencing at the beginning of the 1960s, developed into large-scale fishing around South Georgia in the late 1960s. The main target species was the marbled notothenia (*N. rossii*) and catches soon reached a peak of more than 400,000 tons in the 1969–1970 season, followed by rapid decline to a few thousand tons over the next two seasons (Figure 16.3) (Everson 1978). This decline can be attributed to a lower fishing effort (e.g., fewer vessels), and a sharp decline in the CUPE (Everson 1977b). Fishing effort subsequently increased from 1975 to 1976 onwards with the entry of Poland, the German Democratic Republic, and Bulgaria into the fishery, and its extension to the South Orkney Islands in 1977–78 (Sosinski and Kuranty 1979; Sosinski and Sikora 1979). This led to another rapid build up of catches between 150,000 and 200,000 tons. Much of this increase was due to catches of the icefish (*Champsocephalus gunnari*) in 1976–1977 and 1977–1978 (FAO 1981). From 1978 to 1979 onwards, fishing was extended to the South Shetland Islands and Joineville Island (Sosinski and Sikora 1977). In the 1978–79 season, catches declined to 130,000 tons and until 1981–1982, they oscillated around 100,000 tons. The catches consisted mainly of *N. rossii*, and *C. gunnari* and *Notothenia guentheri* in subsequent years. In 1982–1983, catches rose again (mostly *C. gunnari*) to more than 160,000 tons, nearly all by the USSR. The change from early dominance by *N. rossii* to later dominance by *C. gunnari* was probably due to heavy fishing for *N. rossii* in the early years reducing its standing stock, thus, causing the effort to be transferred to other species. The pattern of catches is typical of the situation when a virgin stock is exploited: initial high catches followed by a sharp decline (see Figure 16.2).

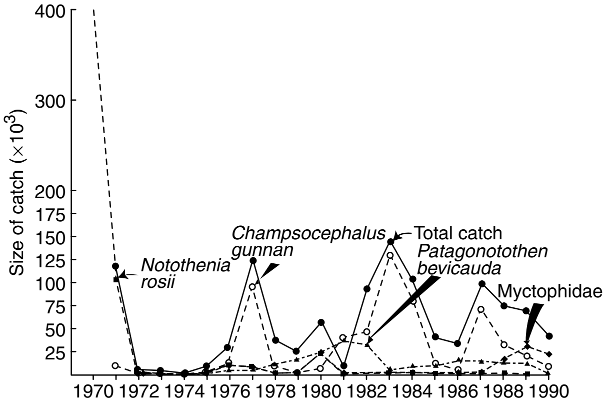


FIGURE 16.3 Catches of various fish species from Subarea 18.3 (South Georgia Subarea) by year. The total catch (●—●) and that of the three major species, *N. rossii* (■---■), *Champsocephalus gunnari* (○---○), and *Patagonotothen brevicaudata* (▲---▲). Other minor species contributing to the total catch include *Chaenocephalus aceratus*, *Pseudochaenichthys georgianus*, *Notothenia squamifrons*, *Dissostichus eleganoides*, and Myctophid species (◆---◆). (From Based on data in SC-CCAMLR, *Rep. Ninth Meeting of the Sci.Comm., Annex 6*, 287 1990. With permission.)

There is evidence that a demersal fish biomass of approximately 750 kt had been present on the shelf around South Georgia (excluding Shag Rocks) prior to the beginning of commercial exploitation in 1979–1970, with *N. rossii* making up to approximately 75% of it (Table 16.3; Figure 16.4). This corresponds to a biomass of approximately 20–22 tons km^{-2}. By 1976–1976, fish biomass was only 40% of the value owing to the removal of most *N. rossii*. It would have been less if two strong year-classes of the mackerel icefish, *C. gunnari*, had not been recruited to the stock. Other fish stocks which declined substantially after only a few years of fishing were the green notothenia, *Gobionotothen gibberifrons*, the Scotia Sea icefish, *Chaenocephalus aceratus*, and the South Georgia icefish, *Pseudochaenichtys georgianus*. At the end of the 1977–1978 fishing season, standing stock biomass of fish around South Georgia was apparently less than 20% of its original size. Since then, it has fluctuated around 20–25%.

Fish biomass on the shelf of the South Orkney Islands should have been of the order of 250 kt prior to exploitation, of which at least 60–70% comprised *C. gunnari*. This would correspond to a biomass of 10–12 tons km^{-2}. By 1979–1980, fish biomass was probably less than 20% of the pristine biomass and has fluctuated around that value since then (Kock 1991).

Kock and Koster (1990) and Kock and Shimadzu (1996) recently analyzed the status of exploited fish stocks in the Atlantic sector (Figure 16.4). Of the exploited stocks, *N. rossii* is the species most adversely affected by the fishery. The present stock size is less than 5% of the amount before the fishery started. Recruitment has fallen since the second half of the 1970s and even if catch levels were zero or less than 1000 tons, an increase in stock size to only about 40,000 tons could be expected at the turn of the century. This is still less than 10% of the unexploited stock size. Kock and Koster (1990) considered that the stocks of *C. gunnari* around South Georgia and the Antarctic Peninsula were

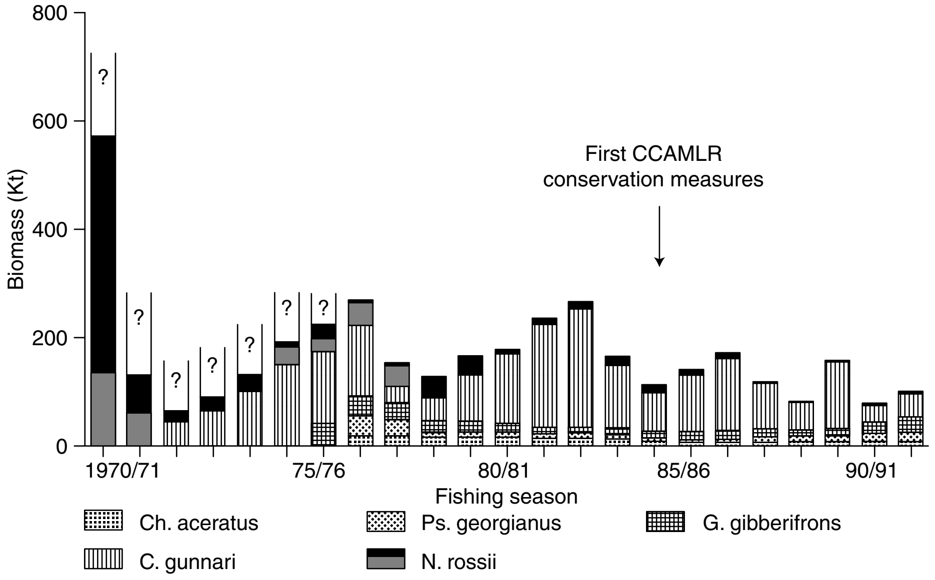


FIGURE 16.4 Trends in biomass of the most abundant fish species around South Georgia. (From Kock, K.-H. Shimadzu, Y., *Southern Ocean Ecology: The BIOMASS Experience*, Cambridge University Press, Cambridge, 289, 1996. With permission.)

urgently in need of conservation measures. Some measures have already been established (CCAMLR 1988). It is hoped that the findings documented by Kock and Koster (1990), as well as those of the CCAMLR Working Group on Fish Stock Assessment, will bring about a change from the purely "reactive management," which CCAMLR adhered to in the first years, to more predictive (i.e., active) management measures in tune with the objectives of Article II of the Convention on the Conservation of Antarctic Marine Living Resources (see the next chapter).

Exploitation of fish in the Indian Ocean Sector began around Kerguelen, after several exploratory cruises by the USSR in 1958–1959 to 1960–1961. Three years of semi-commercial fishing preceded commercial exploitation that started in 1970. The progress of the fishery was similar to that which occurred in the Atlantic Sector—a rapid build up of catches in 1971–1972 to 229,500 tons (about 65% *N. rossii*), followed by low catches of 12,000–13,000 tons in the next two years (Duhamel and Hureau 1990). This was followed by a second and third maximum with 101,000 and 90,000 tones, respectively, in 1974–1975 and 1977–1978, followed by several years of low catches (Figure 16.5). The main target species were the icefish (*C. gunnari*) and the grey notothenia (*N. squamifrons*), which together made up 75–85% of the catches. In 1978, the French Government established a 200-mile EEZ around Kerguelen. Since then, the fishery has been strictly controlled by the French authorities and the Crozet Islands have been closed to fishing. Both the number and allowable catch of the Soviet vessels were limited, and in 1981, three French deep-sea trawlers joined the Soviet vessels (a maximum of seven vessels for the area was set by the French authorities).

Demersal fish biomass on the Kerguelen shelf prior to exploitation in 1970–1971 should have been of the order of 450–550 kt with *N. rossii* and the Grey Notothenia *Lepidonothen squamifrons*, making up to 50 and 25% of the biomass, respectively (Table 16.2). This corresponds to a biomass of 4–5 tons km^{-2}. In the period 1974–1976, the biomass may have been reduced to less than 200 tons, mostly owing to a reduction in the stock of *N. rossii* (Figure 16.5). Since the 1980s, the biomass is unlikely to have been much more than 120 tons, owing to the low stock sizes of *N. rossii* and *L. squamifrons* (Duhamel and Hureau 1990; Kock 1991).

Heard Island waters were fished by Soviet ships during 1977 and 1978, but were terminated when Australia created a

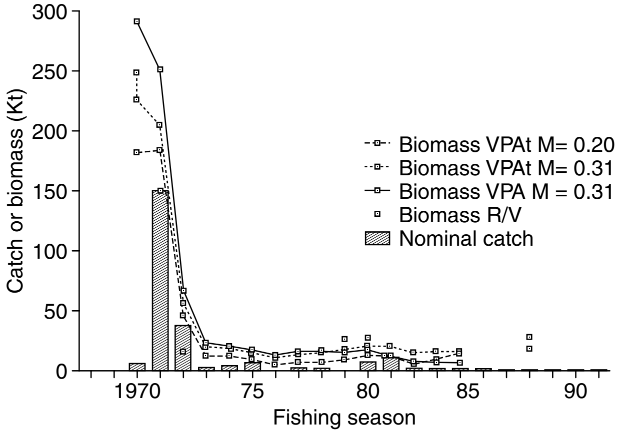


FIGURE 16.5 Nominal catch and trends in biomass of *Notothenia rossii* around the Kerguelen Islands. VPAI: virtual population analysis tuned to indices of biomass estimates; *M*: instantaneous rate of natural mortality; RV: research vessel. (From Kock, K.-H. Shimadzu, Y., *Southern Ocean Ecology: The BIOMASS Experience*, Cambridge University Press, Cambridge, 290, 1992. With permission.)

TABLE 16.2
Estimates of Stock Sizes (in millions) of Ice Seals Present in the Southern Ocean

Species	Original Stock Size	Recent Stock Size Estimate	Date to Which Estimate Applies	Total Catch Since 1920
Blue	150,000	8,000(total)	1965–1978	307,638
Fin	750,000	70,000(total)	1965–1978	664,248
Sci	250,000	15,000(exploitable)	1979	177,811
Right	not known	3,000(total)	1965–1978	Not known
Minke	not known	436,000	1978–1984	106,188
Humpback	90–100,000	40,000(total)	1965–1978	36,504

Source: From Kock, K.-H., Shimadzu, Y., *Southern Ocean Ecology: The BIOMASS Perspective*, Cambridge University Press, Cambridge, 196, 1992. With permission.

200-mile EEZ around the Island. There have been no fisheries established around Macquarie Island or the Antarctic Continent. However, the USSR has reported catches of pelagic *Pleurogramma antarcticum* four times between 1977 and 1983. In addition to catches of Nototheniids and Channichthyids, small catches of Southern Blue Whiting (*Micromedistius australis*) and Patagonian Hake (*Merluccius hubsii*) were made in the Atlantic Sector.

16.3.3 IMPACT OF THE FISHING ON THE STOCKS

"The deficiency of the data on catch-per-unit-effort (CPUE) in the Atlantic Ocean sector, the lack of long-term series of age length keys, and of length-frequency data from the most recent years in the Atlantic Ocean sector, make an assessment of the present status of the exploited Antarctic fish stocks very difficulty and speculative" (Kock et al. 1985). Thus, the hard data are currently unavailable to make predictions of what effects the levels of exploitation have had, and will have in the future, on the stocks. Nevertheless, the indications are that in some areas the impact has been severe.

Standing stock biomass of demersal fish has been estimated at about 500,000 tons for South Georgia (Everson 1977b), and about 130,000 tons for Kerguelen (Hureau 1979). Corresponding values for maximum sustainable yield (MSY) have been estimated at 50,000 and 20,000 tons, respectively, although both projections may be underestimates. Catches have exceeded these MSY estimates by considerable amounts in numerous years.

Due to their relatively high age at first sexual maturity and their low growth rates (at least of mature individuals), Antarctic fish are very vulnerable to overfishing, even at low levels of fishing activity. The green notothenia (*Notothenia gibberifrons*), for example, off South Georgia is a typical by-catch species. Catches rarely exceed 10,000 tons. This species reaches a maximum size of 52 cm when about 20 years old and most become sexually mature at about 32–35 cm (6–8 years old) (Boronin and Frolkina 1976). Length composition of the catches in four successive seasons showed a rapid decline of large (i.e., old) individuals from 1975 to 1976 onwards when the stock was obviously in a quasi virgin state. Mean lengths of the fish declined from 41 cm in 1975–1976 to about 30 cm in 1978–79, which is approximately the length at first sexual maturity. Kock (1981) arrived at similar conclusions about the icefish (*C. gunnari*) off of South Georgia by comparing research vessel data from 1975 to 1976 and 1977 to 1978. Kock et al. (1985) provide additional data on a range of species. For *N. rossii mamorata* off of South Georgia, the mean length and average age in Soviet catches declined from 68.1 cm and 9.3 years in 1969 to 59.1 and 6.8 years in 1973. From 1976–1977 to 1980–1981 the mean length of Polish commercial catches declined year-by-year from 59.1 to 43.0 cm. The average age declined from 6.5 to 5.3 years.

Until recently, the lack of any mesh-size regulations, combined with the availability of both adults and juveniles of several species on the fishing grounds, made the species vulnerable to recruitment over-fishing, i.e., exploitation of part of the stock prior to the onset of sexual maturity. This was indicated by the growing proportion of juveniles in catches of green notothenia. Catches of the Patagonian toothfish (*Dissotichus eleganoides*), for example, consisted of more than 90% juveniles.

The abundance of krill appears to be an important factor governing the distribution of larval and juvenile stages of a number of notothenioids. Rembiszewski et al. (1971), Slosarczyk and Rembiszewski (1982), and Slosarczyk (1983) noted that juvenile icefish were a frequent by-catch of krill fisheries in areas of the Scotia Arc, the Bransfield Strait, and west of the Antarctic Peninsula. Juvenile *C. gunnari* and *C. aceratus* have also been reported to be abundant in krill swarms around South Georgia (Kompowski 1980a, 1980b). Slosarczyk and Rembiszewski (1982) and Slosarczyk (1983) calculated that up to several hundred juvenile notothenioids per 100 kg of krill were present in the krill catches, particularly around South Georgia. Off the Balleney Islands, juvenile *Trematomus bernacchii* in concentrations of several thousands per 100 kg of krill, together with the less abundant *Patagonia brychysoma*, have been observed (Slosarczyk 1983).

Thus, there is ample evidence that intensive krill fishing in FAO Area 48, where notothenioids are abundant in, or close to, krill swarms, could endanger the recruitment of a number of notothenioids, as most species are characterized by low absolute fecundity.

16.3.4 BIOMASS AND PRODUCTION

There is limited data available on the biomass and production of Antarctic fish stocks. At Signy Island, Everson (1970a) estimated that the biomass of *Notothenia neglecta*, the dominant species in shallow water, to be 194 kg ha^{-1}, and the annual production to be 0.34 kg ha^{-1}. Hureau (1979) estimated the standing stock of fish on the shelf area around Kerguelen to be about 120,000 tons, or about 24 kg ha^{-1}. This is probably an underestimate due to the small beam trawl that was used in the sampling.

Estimates of fish production have also been made by summing the estimates of total fish consumption by major predators. The total of $15{,}554 \times 10^3$ tons, or 66 kg ha^{-1}, includes all species of fish. The total production of species of potential commercial importance must be assumed to be less, although by what proportion is not known. Production of sexually mature fish has been estimated at about one third of the total figure, i.e., about 5 million tons (Kock et al. 1985).

Demersal fish are, for the most part, restricted to the continental and island shelf areas that together cover approximately 2.2 million km^{-2} (excluding the ice shelves) (Everson 1978). Thus, the total predator consumption of fish if averaged over the whole shelf area is about 7.75 tons km^{-2}. Extrapolation from Croxall's 1984 figures for predatory fish consumption indicates that the production, at least in the Scotia Sea and around South Georgia, might be higher.

However, it should be noted that the above estimates are subject to considerable error, and the figures should only be taken as an indication that they are in the correct order of magnitude. Bearing this in mind, estimated production for the South Georgia continental shelf area (of approximately 36,000 km^{-2}) would be between 230,000 and 280,000 tons for the entire demersal lifespan. Because only a third of this would be due to sexually mature fish, the production of interest to the fishery would be about 77,000 tons yr^{-1}. The stock that is able to be caught, however, would be lower than this. On the basis of commercial catch statistics, Everson (1977b) estimated that the standing stock around South Georgia prior to exploitation was about 500,000 tons and that the annual production was about 90,000 tons. By erring on the side of caution, and taking the lowest possible estimate, the South Georgia area would appear to have been capable of an MSY of 50,000 tons yr^{-1}. As previously discussed, a number of seasons have exceeded this figure since the fishery commenced in the mid-1970s.

16.3.5 RECOVERY OF EXPLOITED STOCKS

The closure of the *N. rossii* fishery in 1985 was one of the first conservation measures adopted by CCAMLR. Since then, no exploitation on a commercial scale has occurred and a large number of surveys have been conducted around Shag Rocks, South Georgia, and in the Scotia Sea to assess the status of the stocks (information summarized in Kock et al. (2004)). Despite the closure of the fishery almost 20 years ago, none of the surveys have indicated a substantial recovery of *N. rossii*, either at South Georgia or off of Elephant Island.

Kock et al. (2004) point out a number of difficulties in estimating the present stock size of *N. rossii*. First, *N. rossii* is not evenly distributed, with a large proportion of the population tending to aggregate in small areas. Random surveys to assess abundance are based on the assumption that the target species is randomly distributed. Second, while the details of the biology and ecology of *N.rossii* is well established (references in Kock et al. 2004), information on factors influencing the meso- and micro-scale distribution and abundance of *N. rossii* remains sparse. Kock et al. (2004) recommend surveys designed to provide more accurate estimates of stock sizes.

16.4 SEALS

16.4.1 THE HISTORY OF ANTARCTIC SEALING

Seven species of seals are found in the Southern Ocean. Four of them, crabeater seal, *Lobodon cinophagus*, leopard seal, *Hydrurga leptonyx*, Weddell seal, *Leptonychotes weddellii*, and Ross seal, *Ommmartophoca rossii*, are true Antarctic seals who are mostly confined to pack and fast ice zones. The other three species occur abundantly on the Subantarctic islands (Elephant seal, Antarctic fur seal) or are rare vagrants from the north of the Antarctic Convergence (Subantarctic fur seal) (Laws 1984). The Antarctic fur seal was the first of the Southern Ocean's living resources to be exploited When Captain Cook returned from his discovery voyage in 1775, he reported that the beaches of South Georgia were swarming with fur seals. It was not long before fur sealers descended on these beaches to slaughter the seals. By 1822, James Weddell, the Scottish sealer, calculated that no fewer than 1,200,000 skins had been taken from the islands and that the species was virtually extinct there. Another rich stock of seals was discovered on the South Shetland Islands in 1819. By 1822, some 320,000 skins had been taken and the population virtually exterminated. Other populations on the South Orkney Islands, the South Sandwich Islands, and Bouvetova suffered a similar fate, and sealing soon declined due to a lack of seals. There were minor revivals of the industry in the 1950s and 1970s, but the seals were not given a chance to recover. This was largely due to the fact that sealers turned to taking Elephant seals for their blubber, a less profitable operation than skinning fur seals, so that they killed fur seals whenever they came across them. By the beginning of this century, the old fashioned fur sealer virtually disappeared from the Southern Ocean.

The lobodontine Antarctic seals, especially the crabeater seal, constitute a very considerable resource that has been virtually untapped. The only occasions on which any substantial harvest appears to have been taken were in 1882–1983 and 1983–1984, when four Dundee whalers and a Norwegian vessel, prospecting for right whales and failing to find them, took 32,588 skins and a great quantity of blubber in the pack-ice zone. It is not known which species was taken, but the numbers involved make it likely that they were crabeaters. The only other commercial venture was in 1984, when the Norwegian sealer *Polarhay* took 861 crabeater seals in an exploratory cruise between the South Orkneys and Elephant Island.

16.4.2 RECOVERY OF THE ANTARCTIC FUR SEAL STOCKS

Population sizes of the four true Antarctic species in the Southern Ocean are given in Table 16.2. It is noted that the more recent population estimates for crabeater and Ross seals are much lower than previous ones (Laws 1984, 1985). However, there are a number of uncertainties concerning these estimates. Recent (tentative) observations suggest a coupling of periodic fluctuations in crabeater, Weddell, and leopard seal populations with large-scale oceanographic variations related to the El Nino Southern Oscillation (ENSO) (Testa et al. 1987). Strong year-classes of crabeater seals from the Antarctic Peninsula were separated by 4–5 year intervals. Dispersal of juvenile leopard seals and fluctuations in the reproductive rate of Weddell seals occurred at about the same interval.

In recent years, the Antarctic fur seal has undergone one of the most spectacular population increases recorded for any marine mammal (Payne 1977; Laws 1979). The most recent account, based mainly on Payne's (1977, 1978) studies, is that of Bonner (1981). After the early exploitation on South Georgia, the fur seal was thought to be extinct and no seals were seen until 1919, when a young male was shot at the eastern end of the island. In the 1930s, a small breeding population with 12 pups was found on Bird Island at the north-west end of South Georgia. It was not until 1956 that studies were initiated on this population where counts were made between 1956 and 1968 and from 1972 to 1975 (Laws 1973, 1979). In 1958, Bonner visited Bird Island and found a flourishing population with a pup production estimated at 3500 (Bonner 1958). Between 1958 and 1972, the annual rate of increase was shown to be 16.8%, and from 1972 to 1975, 14.5%. The annual pup production in 1975 was carefully assessed by Payne (1977, 1978) at 90,000. Further studies by the British Antarctic Survey indicate that the rate of increase at Bird Island diminished, but satellite colonies on the main island continued to increase rapidly. By 1975–1976, over half the number of pups was born on the mainland beaches and the population has continued to rise since then. However, fur seals are very much concentrated at the northwestern end of the island, and many important former breeding sites have no breeding seals or only negligible numbers.

Small breeding groups, which most certainly derive from South Georgia, have been established at the South Shetland, South Orkney, and South Sandwich Islands. The reported rate of increase on the latter two island groups range from 2 to 6% (Laws 1973, 1981; Bonner 1981). On the other hand, Aguaya (1978) has reported that the seals on the South Shetlands have been increasing at 34% per year, a rate of increase which is impossible unless their numbers were being reinforced by immigration from elsewhere. Bonner (1981) estimated that the total annual pup production of the Antarctic fur seal in 1978 was 135,000, corresponding to a total population of 554,000, and that by 1982 it was estimated that there were probably over 900,000 seals.

While the recovery of a nearly exterminated marine mammal population is generally looked upon as a desirable event, there have nevertheless been some undesirable side effects, especially on Bird Island. Bird Island is some 5.5 km long by 1.5 km wide, with less than 5 km of shoreline accessible to the seals. Some 150,000 fur seals now come ashore annually during the breeding season from November to April, a period that coincides with the growing season of terrestrial plants and the breeding season of a number of ground nesting bird species.

Profound changes have taken place in the vegetation of Bird Island since 1966 (Bonner 1985b). Fur seals destroy tussock grass (*Poa flabellata*), which is the dominant plant cover on Bird Island, by trampling and lying on the tussock's tops. Meadows of one of the two flowering plants (*Deschampia antarctica)*, cryptograms (mosses and lichens), are also destroyed by trampling, leading to local erosion. Destruction of the tussock deprives birds, the endemic pipit (*Anthus antarcticus*), the pintail (*Anus georgica)*, several burrowing petrels, the dove prion (*Pachyptila desolata*), the blue petrel (*Halobaena caerulea*), and the common diving petrel (*Porcelllaria aequinoctialis)* of the breeding habitat and protected nest sites for the first two species, foraging habitat for the pipit, and burrowing sites for the petrels. Trampling can cause burrows to collapse, destroying the nests. The destruction of cover exposes the smaller birds to predation by brown skusa (*Catharacta lonnbergia*) when on the ground. The destruction of the tussock grassland also profoundly alters the habitat of many invertebrates.

A question may be posed as to whether this is a return to the pre-exploitation conditions of the late eighteenth century when the fur seal populations were in a pristine state, or whether it represents a new development. From the accounts of the early sealers and the occurrence of fur seal hairs in peat, it appears that breeding colonies were more widely distributed around South Georgia, and while the population was larger, the high densities now seen at Bird Island were not present. Another piece of evidence strongly suggesting that the conditions at Bird Island are more extreme than in the past is the destruction of the lowest raised beach at Freshwater Inlet, a feature that had persisted throughout the pre-exploitation period, but which was rapidly eroded in the span of 15 years after 1960.

It appears that fur seals are bringing about substantial changes to terrestrial ecosystems by destroying vegetation, and initiating serious consequences for some birds (including two species which are much less abundant than the fur seals). Many examples of local abundances of a protected species causing considerable damage to the environment exist (Jewell and Holt 1982). A common response of conservation management to this damage is interventive management. Bonner (1985) points out that it is possible to devise management policies for the fur seal at South Georgia which would control the environmental damage. This would involve fencing off vulnerable areas, or culling the fur seals, or both.

Elephant seals were quicker to recover than the fur seals because their populations were never reduced to a level as low as the fur seals' levels. By 1910, there was a good stock of Elephant seals at South Georgia and the British administrator of the area permitted licensed exploitation; only adult bulls were allowed to be taken and the island was divided into four sealing divisions, only three of which were worked in any one year. In addition, sealing reserves and closed seasons were instituted, and a quota of no more than 6,000 bull per year was set. Under these control measures, sealing was profitably pursued at South Georgia for three decades.

In the 1940s, the quota was raised and had adverse effects on the stock. R. M. Laws, a British biologist who worked with Elephant seals on Signy Island, was asked to propose a management plan for sealing at South Georgia. The plan resulted in the quota being reduced to where it could be properly sustained and its allocation between the various colonies made in proportion to the stocks present. Law's discovery that the ages of the seals could be determined by the growth increments on their teeth made it possible to monitor the age structure of the catch and adjust it accordingly. The Elephant seal population recovered under this new management scheme and the rate of the catch and oil production per seal increased. It was found that the average age at sexual maturity of the females during exploitation was about two years, compared with more than three years in 1977, when the seals had not been harvested for 13 years. During exploitation, the growth of the females was faster due to less competition for food from the much larger males. The South Georgia sealing industry finally ceased in 1964 due to the collapse of whaling around South Georgia, of which sealing was an adjunct.

Elephant seals have been declining over most of their distributional range (Anonymous 1991). The only population in the Southern Ocean that does not appear to have declined is that on South Georgia. After a decline prior to the 1980s, the stock on the Courbet Peninsula (Kerguelen Islands) appears to have stabilized at about two thirds of its initial size (Jouventin and Weimerskirch 1990). There is no hard evidence concerning the causes of the declines. It is likely that natural fluctuations, in prey abundance and availability for example, and also subtle changes in environmental conditions, about which we know little, have influenced the abundance of Elephant seals.

16.4.3 THE CONVENTION ON THE CONSERVATION OF ANTARCTIC SEALS

When the prospect of resuming Antarctic sealing arose with the Norwegian exploratory cruise for pelagic seals in 1964, the SCAR Working Group on Biology proposed to SCAR measures to control such activities if they materialised (they did not in fact). These proposals were conveyed to the Antarctic Treaty, eventually leading to the 1972 signing of the Convention on the Conservation of Antarctic Seals, in London. This Convention is unique in that it was the first international agreement to make provision for the management and protection of a species *before* an industry to exploit them had actually developed. The Convention came into force in March 1978 after it had been ratified by 10 countries.

The Convention applies to the area south of 60°S, though provision is made for the reporting of catches in the areas of floating sea ice north of 60°S. It recognizes the importance of Antarctic seals as a resource and the need to regulate their harvesting. It covers all six species of seals that occur within the Convention area, and catch limits are set for the crabeater (17,500), the leopard (1,200), and Weddell (5,000) seals. The taking of Ross seals (*Omatophoca rossii*), Elephant seals (*Mirounga* spp.), and fur seals (*Arctocephalus* spp.) is completely banned, and the adult stock of Weddell seals is completely protected in breeding colonies on fast ice. The Southern Ocean is divided into six zones and in the event that sealing takes place, one of these would be closed each year in rotation. Three sealing reserves have been established—around the South Orkney Islands, the southwestern Ross Sea, and Edisto Inlet. Provision is made for special permits, exchange of information, future meeting of the consultative parties, review of operations at regular intervals, and for amendments to the Convention. Scientific advice is provided by the SCAR Group of Specialist on Seals. This group also is responsible for coordinating data on the number of seals killed in the Treaty area for scientific purposes and for dog food (this latter practice is being phased out), as required under the "Agreed Measures for the Conservation of Flora and Fauna." The convention provides adequate means of regulation and monitoring should a sealing industry develop at any time in the future.

16.4.4 POSSIBLE FUTURE EXPLOITATION

While the seals of the Southern Ocean represent a considerable natural resource, Bonner (1985a) considers that it is unlikely their harvesting will ever be commercially viable. Such harvesting would be labour intensive and, when combined with the distance from the market and a product that would likely be inferior to that obtained from seals in the Northern Hemisphere, development would be inhibited. Fur seals would be relatively simple to exploit and could be managed in such a way to not deplete stocks. However, as Bonner points out, there is a major impediment to southern sealing industry redevelopment. For instance, a very considerable body of public opinion opposed to the killing of seals has been fostered under the umbrella of conservation lobbyists. Countries that could mount sealing ventures would probably be reluctant to expose themselves to the opposition that would invariably result, even if the industry conduct could be guaranteed to be irreproachable.

16.5 WHALES

16.5.1 THE HISTORY OF ANTARCTIC WHALING

Seven species of baleen whales and eight species of toothed whales occur south of the Polar Frontal Zone. All baleen whale species have been subjected to extensive whaling. The only toothed whale taken regularly has been the sperm whale (*Physerer macrocephalus*). Killer whales (*Orcinus orca*) and southern bottlenose whales (*Hyperoodon planifrons*) were pursued irregularly and in small numbers (Table 16.3).

The earliest record of European whaling available appears to have been carried out by the Norsemen of northwestern Europe between approximately 800 and 1000 AD. Other nations, especially the Basques, joined the hunt for whales and by the end of the fifteenth century, whaling had become a major commercial operation. Although right whales were initially exploited, the whalers soon turned their attention to the bowhead, as they penetrated toward Arctic waters. The stocks of this species became commercially extinct within 50 years. American whaling commenced shortly after the settlement of North America, and in 1772, a major advance took place when the whalers turned their attention to the sperm whales. While the hunt for this species was slow to develop, it eventually ushered in the era of the great Yankee whalers of New England. These New England whalers, joined later by whalers form other countries, particularly the British, gradually spread their activities southwards into the Atlantic first, and then around Cape Horn (1789) into the Pacific.

Sperm whaling flourished until approximately 1850 and subsequently declined rapidly until it reached a low level by 1860. While sperm whales were the main target species, whalers turned their attention to right whales after finding large numbers in the cooler waters of the Southern Hemisphere. Important fisheries for this species developed, particularly off of New Zealand, Australia, and the Kerguelen Islands, about 1,800–1,850. From 1840 onwards, right whales were found in the cooler waters of the North Pacific. Later still, Bowheads were found in the Bering Sea, and subsequently in the Chukchi and Beaufort Seas. In 1953, Captain Charles Scammon discovered calving grounds of the grey whale in Baja, California. The exploitation of this species, like that of the bowhead, lasted less than 50 years before the population was reduced to a very low level.

TABLE 16.3
Southern Hemisphere Whale Population Estimates, Accumulated Catch, and Estimated Mass of Whales

	1970	1989
Blue whales	8,000	453
Humpback whales	3,000	4,047
Fin whales	100,000	2,096
Sei whales	37,000	1,498
Sperm whales	950,000	3,059

Source: From Kock, K.-H., Shinazdu, Y., *Southern Ocean Ecology: The BIOMASS Perspective*, El-Sayed, S. Z., Ed., Cambridge University Press, Cambridge, 298, 1996. With permission.

Throughout this period, whaling techniques had hardly changed from the early days of European whaling. Whalers still hunted from rowing boats with hand harpoons and processed their whales at sea alongside their ships. This changed when, in 1868, the Norwegian, Svend Foyn, developed the cannon-fired harpoon gun. The harpoon was fitted with hinged barbs that opened while in the whale's body and the tip consisted of a grenade which detonated inside the whale. The steam-powered whale chaser was developed to take advantage of this new weapon, enabling the whalers to catch faster swimming species which had not been possible to catch by earlier methods.

From Norway, this second wave of whaling spread throughout the world, following a similar route as earlier whaling, but expanding more rapidly. This modern whaling operation reached Newfoundland by 1898 and penetrated the Pacific by 1900. The scene was now set for the last great whale gold rush—the exploitation of the Antarctic whale stocks. This dates from 1904, when the Norwegian whaler C. A. Larsen opened a whaling station at Grytviken in Cumberland Bay, South Georgia. The success of this operation encouraged other whalers to move into the Antarctic in hopes of exploiting the large stocks of blue and fin whales found there. Stations were set up not only in South Georgia, where a British company operated at Leith Harbour, but also in the South Orkney, South Shetland, and Deception Islands. The Southern Ocean rapidly became the centre of whaling in the world, and between 1910 and 1925, 50% of the world's annual catch was taken from these waters.

Because all of this early whaling was carried out in the Falklands Island Dependency, it occurred within the territorial waters controlled by the government of the United Kingdom. By 1908, the British had instituted the first practical controls on harvesting. They imposed a licensing system and protection of females with calves. All parts of the whale were to be used, not just the valuable blubber, and a tax was levied on every barrel of whale oil produced. In order to avoid these restrictions, attempts were made to develop a factory ship that could operate at sea. The break-through came in 1925, when the factory ship *Lancing*, fitted with a stern slipway, operated successfully for the first time in Antarctic waters. With this development, whalers were freed from the restriction to areas where they could take their whales ashore. Consequently, whaling in Antarctic waters began to build rapidly: in 1925–1926 there were two floating factory ships at work with nine catchers, while in the 1930–1931 season, 41 factory ships operated with 205 catchers, catching some 37,500 whales. In the 1936–1937 season, catches peaked at 46,000 whales. There was a hiatus during World War II, and the catches never again reached their pre-war levels, although from 1947–1948 to 1964–1965 catches were maintained in the vicinity of 30,000 whales per year. Thereafter, catches fell off very rapidly as a result of both depletion of whale stocks and the adoption of more conservative management measures.

The history of whaling in the Southern Ocean is shown in Figure 16.4. Shore based stations were able to initially take numbers of humpback whales which were close to the land around the island bases. As the numbers of this species were reduced, the catchers tended to go further out, taking the largest whales that they came across, the blue and fin whales. The blue whale grows to the largest size (30-m long and 160-tons total weight), and was the most valuable to the industry. As the catches of this species declined, whalers increasingly turned their attention to the fin whale, originally the most abundant whale in the Southern Ocean. Fin whales formed much the largest part of the catch from the middle 1930s and until the early 1960s, when their numbers collapsed very rapidly.

Sei whales were almost entirely ignored by whalers as long as larger species were available in sufficient numbers. However, as the numbers of the larger whales declined, the industry attempted to maintain its profitability by increasing the amount of meat produced from the carcasses and lessening emphasis on oil production. This revision resulted in the catching of greater numbers of sei whales, and their stocks were reduced rather rapidly when more than 60,000 sei whales were caught in four seasons in the mid-1960s. Since 1972, the catches of sei whales were limited by quotas. The relatively small minke whales were ignored until 1971–1972, but since then have formed numerically, the largest component of the southern baleen whale catch. From about this time on, the catch regulated by quotas remained fairly steady at about 5,000–7,000 whales. Although commercial whaling is forbidden in the Southern Ocean, about 300 minke whales have been taken annually by a Japanese Scientific Whaling Programme since 1986–1987.

While the catch of sperm whales in Antarctic waters has always been of secondary importance to the industry, they have nevertheless formed a significant component of the total operation (Figure 16.6). In the ten seasons before the 1979–1980 season, the catch of sperm whales averaged 3,211. This compares with average annual catches of 4,393 and 4,622 sperm whales in the two preceding decades, respectively. Catches of killer whales in the Antarctic have generally been small. The USSR took 110 in the 1958–1959 season, whereas from 1969 to 1978 the average was 24 per season. However, when the catch of sperm whales was reduced to zero in the 1979–1980 season, the USSR caught 916 killer whales (Figure 16.7).

Table 16.3 gives the original and present estimates of whale stocks in the Southern Ocean. A century ago, the initial numbers of baleen whales feeding in the Antarctic waters during the summer totalled about 1,000,000, with a biomass of about 43 million tons. By the 1930s, the population had been reduced to about 340,000. The current biomass is about one-sixth of the initial stock, about 7 million tons. The average weight of all species of whale caught in 1932 was about 66 tons; in 1936, 56 tons; in 1950, 46 tons; in 1970, 23 tons; and in 1978, about 20 tons. The one inescapable fact that emerges from the above account of whaling is that in every case it has caused a severe decline of the exploited stocks. In the next section we shall explore the attempts that were made to regulate the industry, and

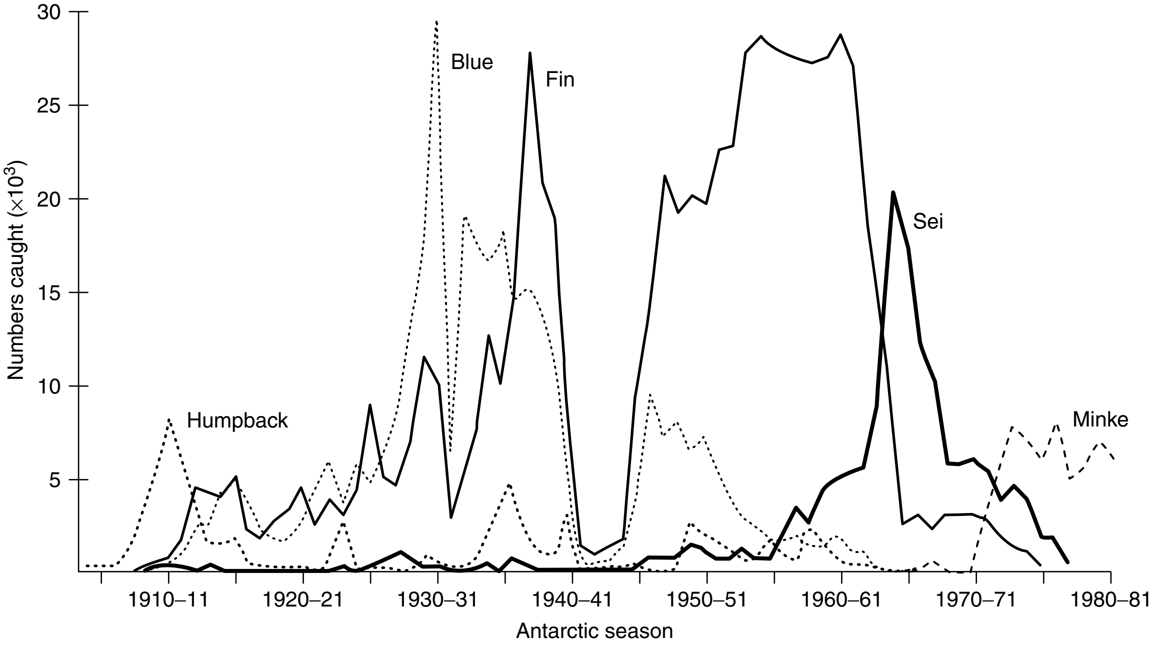


FIGURE 16.6 Catches of whales 1904–1905 to 1980–1981 (including land stations, moored factory ships, and pelagic whaling).

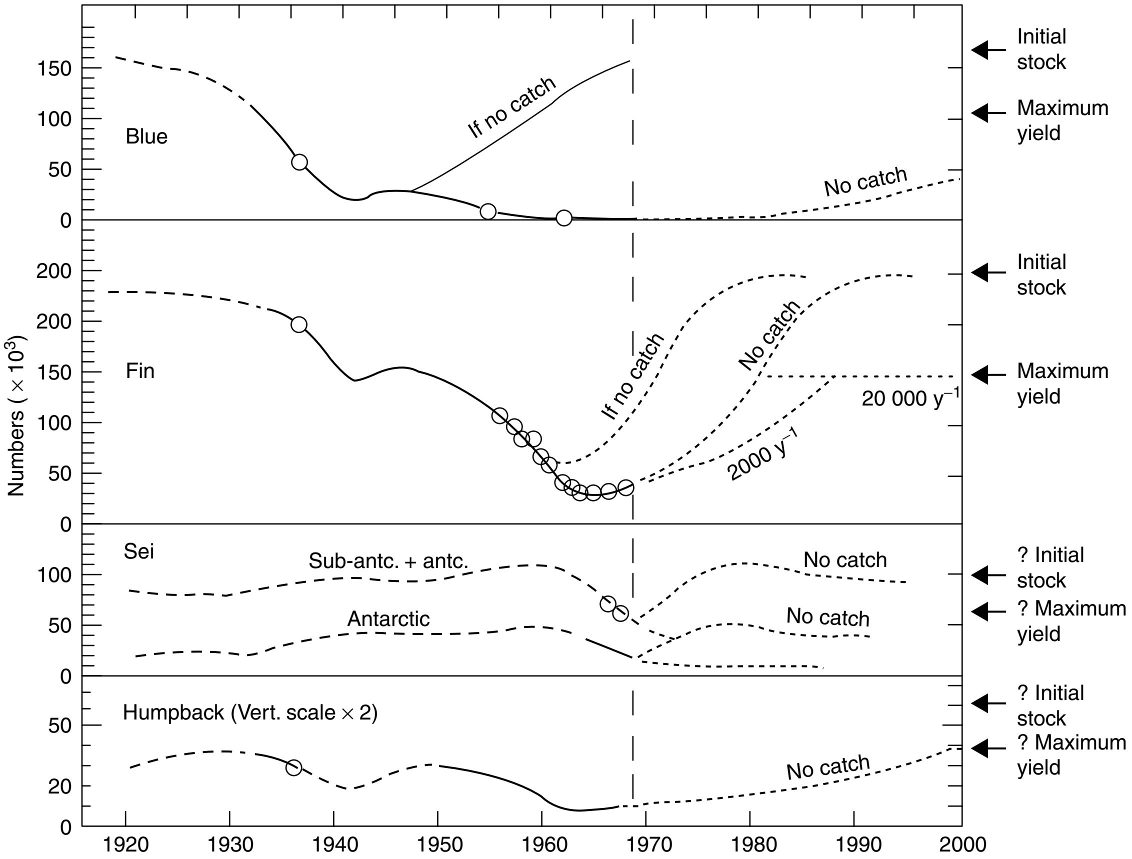


FIGURE 16.7 Estimates of whale stock sizes 1920–1968, with estimates of recovery rates if catching ceased in 1968, or if catching had ceased at an earlier date. (From Based on Mackintosh, N.A., *Antarctic Ecology*, Vol. 1, Holdgate, M., Ed., Academic Press, London, 1, 1970. With permission.)

the reasons for the failure to prevent the over-exploitation of most of the whale stocks.

16.5.2 THE INTERNATIONAL WHALING COMMISSION AND THE REGULATION OF THE ANTARCTIC WHALING INDUSTRY

The reduction which occurred in the blue whale population and the history of whale depletion in the Northern Hemisphere led to serious consideration of conservation methods for Antarctic whales. The First International Convention for the Regulation of Whaling was negotiated in 1931. While the convention provided for the protection of right whales, the protection of females with calves, the licensing of whaling vessels, and for the collection of statistics, it was only partially successful. The next important step was taken in 1937, when the first International Whaling Convention was agreed to by most of the actively involved whaling countries. This added the grey whale to the protected list, established a defined season for whaling in the Southern Hemisphere, and introduced size limits for several species. This convention, which had a life of only one season, was renewed for 1938, and was extended to include the protection of the Southern Hemisphere humpback whales from pelagic, but not from coastal whaling, and the establishment of a so-called sanctuary area in the Pacific sector of the Southern Ocean. Additionally, the whaling industry set up working agreements between most of the countries concerned to limit the number of whales taken and the level of oil production.

After a series of conferences held between 1945 and 1946, the International Convention for the Regulation of Whaling was signed in Washington, USA by 15 countries. The convention recognized in its preamble "the interest the nations of the world in safe-guarding for future generations the great natural resources represented by the whale stocks." It also stated that the purpose of the Convention was to provide for the proper conservation of whale stocks, and thus make possible the orderly development of the whaling industry. The convention set up the International Whaling Commission (IWC) as an executive body to formulate regulatory measures and with the responsibility for their implementation. The commission met for the first time in 1949, and the membership has now expanded to over 40 member governments. A scientific committee was established to advise the commission. The scientific committee has been heavily involved in stock assessment since 1960, a fact reflected by the notable increase in the work of the committee by scientists specializing in population dynamics.

The history of the commission and its problems has been studied by Mackintosh (1965), McHugh (1974), Gulland (1976), and Allen (1980). The commission was unable to prevent the decreases which occurred in the exploited stocks of Antarctic whales in spite of its good intentions. Although an overall limit to the pelagic catch was established, there were three short-comings in the methods used (Gulland 1976): (1) it was expressed as a total quota without separate quotas for the different stocks; (2) the quota was slightly too high and there were no provisions for an easy revision; and (3) no arrangements were made for the allocation of quotas to individual whaling countries. The quota was set in terms of blue whale units (BWUs)—one blue whale being equivalent to two fin whales, six sei whales, and two-and-a-half humpback whales. Thus, the whalers were free to pursue whichever whales were the most profitable regardless of the stocks' state. Whalers which came across one of the few remaining blue whales would pursue and capture it, because blue whales were the most cost-effective species. Thus, while the whalers increased their catch of the smaller and more abundant fin and sei whales, they at the same time continued to inflict further damage on the already depleted stocks of blue whales. As a result, the blue whales were being caught long after the majority of scientists had demanded their protection. In face of declining numbers of blue and humpback whales, the commission took additional measures to protect them, mainly through reducing the length of the open season for these species. Ultimately, both species were so reduced in numbers that they were given complete protection.

The lack of any division of the total quota between countries soon led to economic difficulties. Initially the open season was four months long, but of the various counties, 22 attempted to increase their quotas by increasing their fleets. The quota was reached increasingly earlier, and the open season was reduced to 64 days. This state of affairs could not continue, and in 1961, the whaling countries met outside the auspices of the IWC to divide the spoils. Japan got 33%, Norway 32%, the Soviet Union 20%, Great Britain 9%, and the Netherlands 6%.

In addition to the fatal errors made by the Commission in not adopting both species quotas and national quotas, the commission was deprived of real "teeth" for most of its existence by the provision which enabled any country to enter an objection to proposed conservation amendments within a 90-day period following the annual meeting. The objecting nation was then not bound by the amendment. This built-in veto made it almost impossible to implement any serious conservation measures during the 1950s. As Chapman (1973) has pointed out, the combination of the blue whale quota system, together with the lack of national quotas, and the requirement for unanimous decisions rendered the commission virtually impotent during ten crucial years.

Management of whale stocks, as with most other marine resources, is based on the concept that each stock has a natural rate of increase through births and a natural rate of mortality which balance against each other to reach an equilibrium level. Reduction in the number of whales in a particular stock leads to compensating changes in the recruitment rate through earlier maturity and increased pregnancy rates, so that the stock can rebuild to its previous level. Once the carrying capacity of the habitat niche occupied by the stock is reached, recruitment declines through factors such as food limitation and the stock numbers stabilize once again.

In 1974, the IWC adopted in principle the so-called "new management procedure," which consisted of formalized rules to be applied by the commission on the basis of advice by the scientific committee. It also determined what the catch limits should be for those stocks whose exploitation would be permitted.

These rules divided the stocks into three categories:

1. Initial management stocks, which may be reduced in a controlled manner to the maximum sustainable yield (MSY) level, or some optimum that is determined
2. Sustainable management stocks, which are to be maintained at or near the maximum sustainable
3. Protection stocks, which are below the maximum sustained management level and which should be fully protected.

This strategy was based on the theory of MSY and was not entirely successful for many reasons. First, the scientific knowledge of the stocks had been inadequate and secondly, the models that were developed had been less precise than had proved necessary to operate the policy. The whole approach presupposed that the number of animals in each whale stock was the direct and only cause of changes in their vital parameters; through density-dependent responses to food availability, for example. As will be discussed later, this approach is inadequate due to inter-species interactions, where whales share a common food resource. Other ecosystem variables, such as the responses of other krill consumers (seals, birds, fish, and cephalopods), also play a role. One positive result of the new approach was that more and more stocks were found to be below the theoretical MSY level, and were therefore given total protection.

16.5.3 THE ECONOMICS OF THE WHALING INDUSTRY

The question arises as to why whalers kill the goose that laid the golden egg. Why were they not interested in conserving whale stocks so that a sustainable yield of whales could be maintained into the indefinite future? Figure 16.5 illustrates what might have happened to the stocks if conservation measures had been implemented early enough, and what the sustainable catch might have been. The answers to the above questions are to be found in the economics of whale fisheries and its influence on industry policy, combined with the fact that whalers were exploiting a common resource that no one owned. The demise of pelagic whaling, to some degree, parallels the collapse of other marine resources such as the anchoveta fishery in Peru in the early 1970s.

Fishing, like any other industry, is a function of cost-benefit balance. With a freely competitive and completely unregulated fishery, a balance will eventually be struck between the biological productivity of the fishery and the rate of harvesting. At first when the stocks are abundant and fishermen few, the profits are very high. These high profits attract further fishermen, who deplete the stocks and cause the prices to fall. At the balance, when the stocks are at the so-called bionomic equilibrium, there will be zero profits and no incentive either for further fishermen to join or for greater effort by those already involved. This was the situation that was reached for many of the fisheries of whale stocks.

One of the major reasons why this balance was reached and why whaling nations bitterly resisted demands to cut back on catch quotas or for a monatorium, relates to the high-risk and high-discount rate of the industry. Maintenance costs in the industry are very high and deterioration of equipment in the Antarctic environment is severe. As in any business, whalers' investment decisions would be based on the desire to maximize the present value of their profits. There would be a minimum expected rate of return, usually based on the "opportunity cost," obtained by putting the money into some equally risky alternative investment, discounting any future profit by the expected rate of return. The discount rate takes into account such things as the cost of borrowing money and the likely inflation, as well as the risks of the business. This becomes particularly important in investment decisions to exploit natural resources.

The whaling industry never was, is not, and never will be interested in sustainable-yield exploitation, simply because it makes no economic sense (Figure 16.4). When considering the exploitation of a stock of whales, the industry could choose between milking and mining, between conserving the asset for ever and harvesting only the sustainable yield, or selling off the whole resource for an early profit which could be invested in some other venture. The crucial point is the relationship between the rate of return on whales versus the rate of return on money. If whale multiplied more rapidly than money, milking would be better than mining. Whale stocks, however, reproduce slowly, certainly less than 4% per annum, while monetary investments often grow in excess of 10% per annum. Conservation will not pay as long as this is true.

16.5.4 CURRENT STATUS OF THE ANTARCTIC WHALE STOCKS

Until recently, most assessments of whale population sizes have relied on information obtained from commercial whale fisheries, and in particular, CUPE. However, there have been difficulties in relating changes in CUPE to changes in whale abundance (Gambell 1989), and the situation has been further complicated by the cessation of commercial whaling in Antarctic waters in 1988. Thus, in recent years emphasis has been placed on dedicated sighting surveys. At the 1989 meeting of the IWC, the Scientific Committee presented estimates for various whale stocks. Included was a series of new abundance estimates for large whales in the Antarctic (south of 60°S) from eight years of the International Decade of Cetacean Research sighting cruises. These estimates in comparison with the 1970 estimates were shown in Table 16.3.

These figures were substantially lower than previously thought. In addition, minke whale Antarctic populations (95% confidence limits) have been estimated at being 760,396 (132,220) (International Whaling Commission ICW1990).

From the data listed above, it is clear that populations of humpback, and particularly minke whales, have been increasing at a higher rate than that of other species. Surveys of migrating humpack whales have been conducted off the Australian east coast since 1981 (Paterson and Paterson 1989; Bryden et al. 1990). These whales are from the Area V stock which was formerly heavily exploited. The estimated number of migrating whales from May to August in 1981, 1982, 1986, and 1987 were 356, 396, 778, and 790, respectively, representing an increase of 130–140% over 5 years, or an annual net increase of approximately 14%. The total numbers are underestimated, as recent evidence has shown that the migration continued beyond the period of observation (Paterson and Paterson 1989). Estimates collected by the International Whaling CommissionIWC (1990) for the annual rate of increase of whale stocks that have been protected for at least 20 years, include five for humpback whale stocks that ranged from 4.8 to 13.8%. Bryden et al.'s estimate is at the higher end of this range and it is clear that the area-V population is increasing rapidly.

16.5.5 THE FUTURE OF ANTARCTIC WHALES

Currently there is a monatorium on whaling. The question then arises as to whether at some time in the future whaling could be resumed, and if so what controls would be applied to the fishery. Much will depend on the future of the IWC. Despite all of the criticism that has been levelled at it, the IWC still constitutes the one organization that would be in a position to develop the necessary models and mechanisms for the rational exploitation of whale stocks. The best thing would be for nations which were formerly involved in Antarctic whaling to maintain a strong and indefinite commitment to the Commission or some renegotiated international body, and for all the current non-signatory whaling nations to be brought into the orbit of the commission.

While taken as a whole, the post-war history of whaling conservation in Antarctica has been a failure. Gulland (1976) points out that in spite of the disasters that befell the IWC, it did have some real achievements. While some species did become commercially extinct, the right, blue, and humpback whales have been protected and do appear to be increasing. The fin whale was rescued from commercial extinction and held at a level where a small sustainable harvest was maintained for a period, while sie whale stocks were kept at a level giving a maximum sustainable yield.

With the current monatorium and the possibility of its extension, the whale populations will recover to some extent. However, at present we can only guess as to what level of recovery will be gained, and it is fairly certain that the species ratio will never be the same as it was before exploitation. In addition, if an intensive krill fishery were to develop, the recovery plateau could be much lower than anticipated. The question then arises as to whether the preservationist ideal of totally protected populations for the indefinite future will be realized? Given human history, this is doubtful. The pressures of human population increase, climatic changes, and uncertainties of food crops as a result of such changes, will probably dictate that some form of whaling will occur in the future. One of the problems that would be faced by any regulatory body is the effect that cessation of whaling will have had on the acquisition of data, and in particular of information concerning the manner in which stocks may be changing in comparison under universal protection. The relationship of whale management to that of managing Southern Ocean living resources as a whole will be discussed in Chapter 18.

17 Ecosystem Changes Resulting from Resource Exploitation

CONTENTS

17.1 INTRODUCTION

In the previous chapter, the impact of living resource exploitation on the stocks of krill, fish, seals, and whales was explored. Here, changes in species attributes such as nutritional condition, growth rates, reproductive parameters, and ecosystem dynamics that have resulted from the changed relationships between predators and their prey will be discussed. As discussed in previous chapters, ecosystems are dynamic entities with complex relationships between their component parts. In the Southern Ocean ecosystem krill is a dominant prey species at the base of the food web intimately affecting species groups such as whales, seals, birds, fish, and squid. It is evident that krill are fundamental to the functioning of the Southern Ocean ecosystem from the data discussed previously on krill consumption by predators.

Food webs are dynamic with the various components interacting through competition and predation within the constraints imposed by the physical environment and the processes of primary production and decomposition. It is into this dynamic system that man has entered as a commercial predator (Figure17.1). Before the exploitation of baleen whales, there would have been significant competition between krill-eating species, and one can assume that reduced whale populations would allow greater use of the krill resource by their competitors. This potentially could lead to increased populations of seals, seabirds, squid, and those baleen whale populations that had not been exploited. Evidence for this will be discussed below.

17.2 ECOSYSTEM CHANGES FOLLOWING THE DECLINE IN WHALE AND FISH STOCKS

17.2.1 INTRODUCTION

The current hypotheses concerning the present status of the Antarctic marine ecosystem include three main assumptions:

1. As a result of reduced baleen whale stocks, krill availability increased.
2. Nonexploited krill predators responded functionally and numerically to the increase in krill availability.
3. A new carrying capacity and community composition developed.

Before the advent of man, a balance would have been achieved between the competing species of consumers (and their predators) within the undisturbed ecosystem, such that each population remained at or near its asymptote for the natural environmental pressures and restraints to which it was exposed. In such a situation, the recruitment coefficient (r) would approximate the natural mortality coefficient (M) so that the population fluctuated about a stable level (Anonymous 1985a).

If there were a long-term trend changing the environmental pressures and constraints, those populations that were subject to greater pressures and restraints would be exposed to higher mortality and/or lower recruitment such that $r-M$ being negative would bring about a decline in the population,

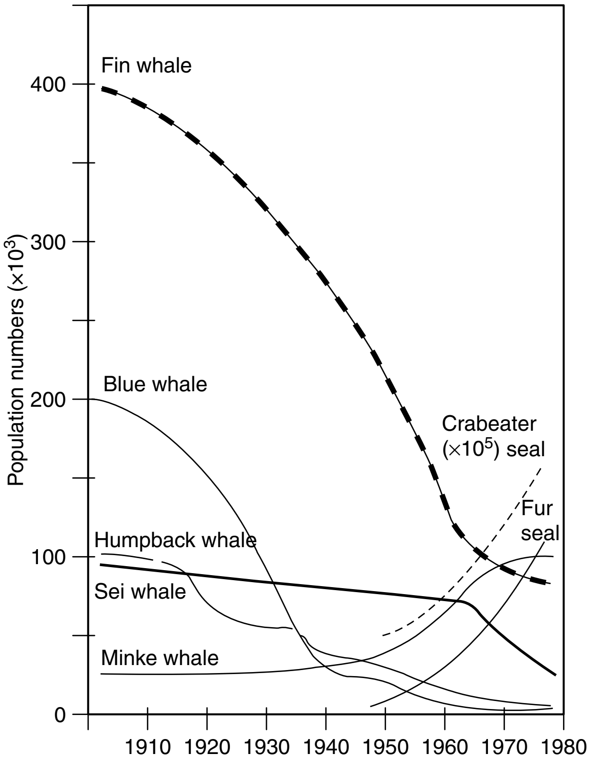


FIGURE 17.1 Changes in whale and seal populations in the Southern Ocean from 1900 to 1980. (Based on information in the Southern Ocean Convention Workshop on the Management of Antarctic Marine Living Organisms, 1980).

while a population under reduced pressure or restraints would have a positive value for $r-M$, resulting in an increase in the population. This would result in adjustments between the competing species such that a fresh balance, possibly in different proportions to that existing previously, would result.

The removal this century of nearly 84% of Antarctic baleen whale biomass (Laws 1977b) may have temporarily reduced competition among krill predators. As the populations of these consumers were reduced, competition for food between the remaining whales and other krill consumers was eased and the resulting improved nutrition would result in faster growth, earlier maturity, higher reproductive rates (Laws 1977b), and the potential for better survival of the young. In such a situation, the difference between recruitment (r) and natural mortality (M) would become positive enabling the population not being hunted to increase exponentially in the form

$$N = Ne^{(r-M)T}.$$

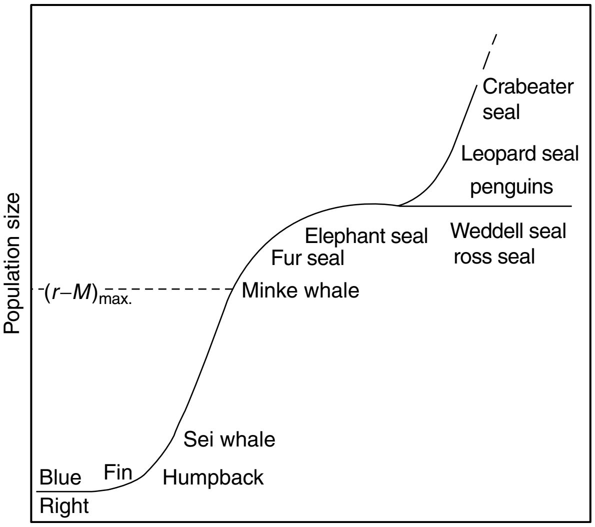


FIGURE 17.2 Present relative positions of major consumers in the Antarctic marine ecosystem on a population growth curve. (From Anon, *Selected Papers Presented to the Scientific Committee oc CCAMLR 1982–1986, Part I*, CCAMLR, Hobart, 227, 1985. With permission.)

An estimate of the current relative position of the major consumers on the sigmoid population growth curve is indicated in Figure 17.2 (Anonymous 1985a). In absolute terms, the vertical scale will be different for each species, but the figure nevertheless illustrates the relative conditions of the populations. Evidence in support of the assumption upon which the figure was based and for increased growth and pregnancy rates will now be considered.

17.2.2 CHANGES IN REPRODUCTIVE PARAMETERS

Food availability is considered to be an important determinant of maturity, i.e., the age at which sexual maturity is attained could decrease as a result of a higher level of nutrition stimulating growth. Mackintosh (1942), Laws (1960a, 1961, 1977a, 1977b), Lockyer (1972, 1974), and Gambell (1973, 1975, 1976) all noted that shifts in growth rates, pregnancy rates and age of sexual maturity in seals and in blue and sei whales have a high correlation with whaling activities in the Southern Ocean. They considered that these changes implied that the whale stocks before exploitation were food-limited and perhaps close to maximum population levels. Under such conditions growth may have slowed down and sexual maturity delayed. With the decline in whale stocks, more krill would presumably have been available to the remaining whales, allowing for faster growth, higher pregnancy rates, and earlier sexual maturity (Figure 17.3).

In fin whales, for example, energy requirements for lactating females are 60–70% higher than for other females (Lockyer 1981a). Increased food supply could also permit mature whales to reduce the time required to recover from a pregnancy and calf-rearing (Sampson 1989), i.e., females might be capable of breeding more rapidly than once in two years (Laws 1961). Thus a number of authors have associated reported changes in reproductive parameters with density-dependent responses to exploitation and a potential release of pressure on prey. However, as Kock and Shimadzu (2004) point out, many of the reported changes do not stand up to critical examination and are inconclusive, primarily due to methodological problems.

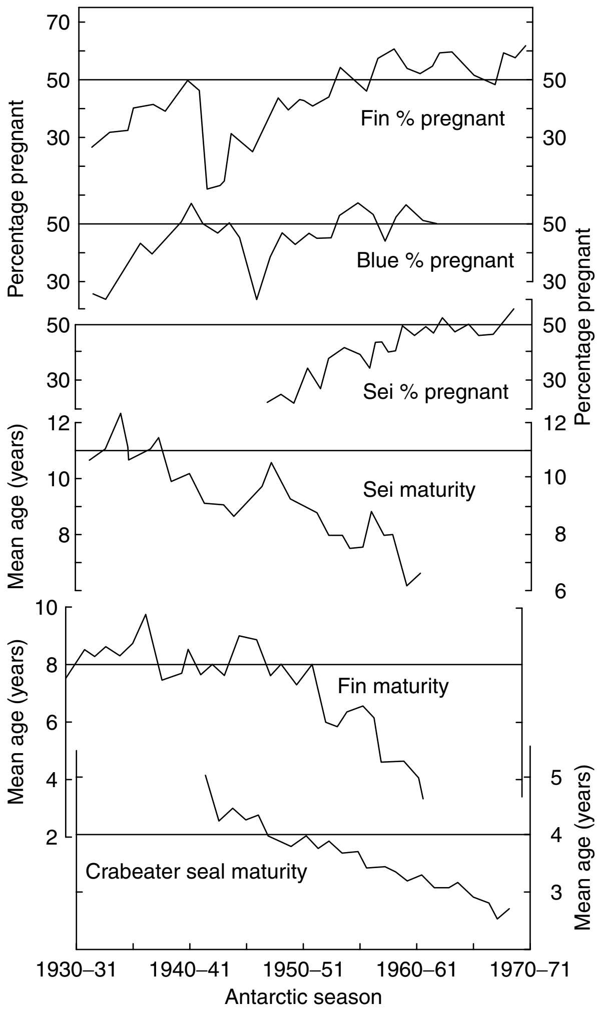


FIGURE 17.3 Collective evidence for changes in pregnancy rates and age at sexual maturity in female Fin, Blue, and Sei Whales and advancing age at sexual maturity in crabeater seals. (From Bengtson, J.L., *Selected Papers Presented to the Scientific Committee of CCAMLR 1983–1984, Part I*, CCAMLR, Hobart, 43, 1985; after Laws, R.M., *Philiosophical Transactions of the Royal Society of London*, *Series B*, 279, 81, 1977a. incorporating data from Lockyer, C., *Journal du Conseil*, *Conseil Permanent International pour l' Exploration de la Mer*, 34, 276–294, 1972; Lockyer, C., *Journal du Conseil*, *Conseil Permanent International pour l' Exploration de la Mer*, 36, 71–81, 1974; Gambell, R., *Journal of Reproduction and Fertility* (*Supplement*), 19, 531–551, 1973; Laws, R.M., *In Adaptions within Antartic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 411–438, 1977b. With permission).

17.2.3 Pregnancy Rates in Baleen Whales

Mackintosh (1942) was the first to suggest that pregnancy rates of female baleen whales in the Southern Hemisphere were increasing. His figures showed that pregnancy rates in Blue Whales increased from about 48% in the period 1935 to 31 to about 66% during the 1932–1941 period. He also observed an increase in Fin Whale pregnancy rates from 65% to 80% in the same period. Similar percentages were given by Laws (1961) who calculated that the Fin Whale pregnancy rates rose from 46% to 76% between the years 1925 and 1930. Later analyses by Gambell (1973, 1975, 1976) confirmed these results and gave data for other species (Figure 17.3).

However, Mizroch (1980, 1981a, 1981b) has argued that the data may be suspect because of the high natural variability of pregnancy rates and the pooling of data across months. Mizroch and York (1984) found a very high interseasonal and interannual variability in the data but no apparent trend to assert an increase in pregnancy rates or a shortened breeding cycle during the course of exploitation. In contrast, Sampson (1989) observed that females of a given length were more frequently pregnant in recent catches (Figure 17.3) by including length of pregnant females more rigorously in his statistical models. A further complication is that some of the data, especially the recording of biological data, in the earlier years of exploitation, was carried out by nonqualified personnel.

17.2.4 Recruitment Rates in Fin Whales

Measurements of recruitment rates have shown no evidence of any compensatory rise accompanying the decline in whale stocks. Recruitment rates fell rather than rose during the 1930s. However, the method used (cohort analysis) appears to be unsuitable for estimating recruitment rates in baleen whales as it is critically dependent on a number of assumptions, such as stable growth rates and the absence of size selection during exploitation which are unlikely to be met. An increase in growth rate, for example, would lead to an erroneous decline in year-class strength.

17.2.5 Age at Sexual Maturity

Age at the attainment of sexual maturity is another indicator parameter that scientists have examined in the baleen whales of the Southern Ocean. On the basis of several analyses, including the transition phase in the ear plugs, counts of *corpora albicanta*, and percent of mature individuals within age classes, a decline in the age at sexual maturity has been suggested for several baleen whale species (Lockyer 1972, 1974; Laws 1977a, 1977b; Masaki 1977). Both Gambell (1973) and Masaki (1977) found evidence of decreases in the age of sexual maturity in sei whales from about 12 years to 6 years over the period from 1930–1931 to 1960–1961. Direct study of the reproductive status of fin whales compiled in the mid-1960s indicated an age of sexual maturity of six to seven years for both sexes (Ohsumi 1972). Kato (1983) evaluated trends in the age at sexual maturity of minke whales using all three methods. He found a similar decrease in the age of sexual maturity, which he attributed to reduced competition with harvested whales and a higher availability of krill (Figure 17.4). Again, like the pregnancy rate increase, scientists have questioned these results. Cooke and de la

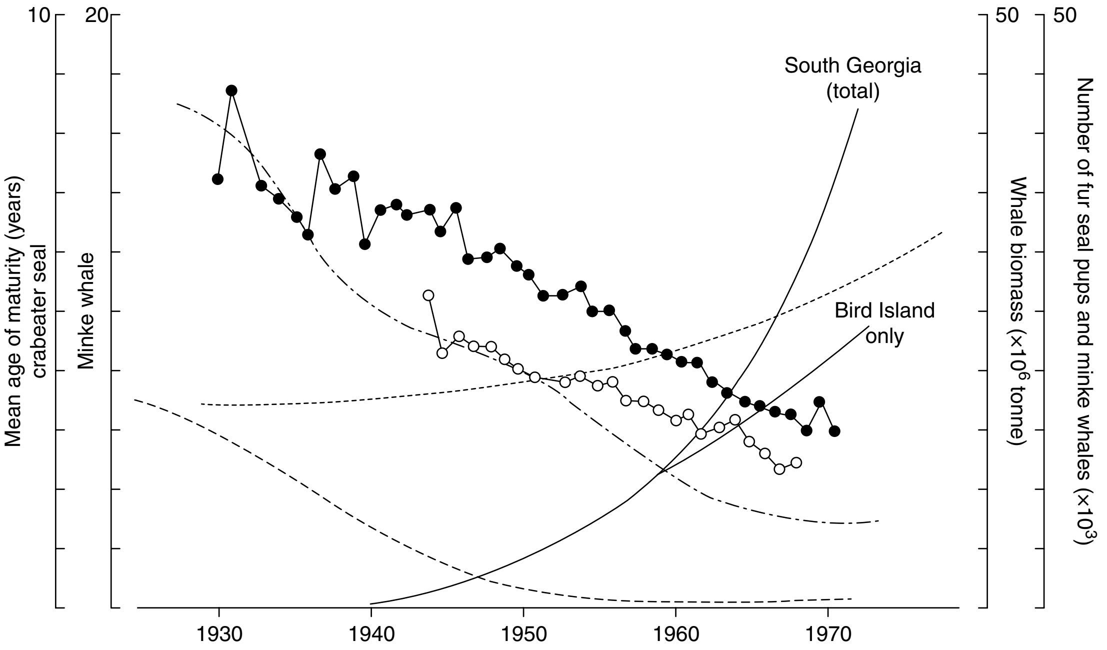


FIGURE 17.4 Interspecific correlations between krill feeding animals and baleen whale biomass in the Antarctic marine ecosystem. Mean age of minke whale sexual maturity (Kato 1983); mean age crabeater seal sexual maturity (Laws 1977a); total baleen whale biomass (Gambell 1975); Minke whale biomass (Gambell 1975); Blue Whale biomass (Gambell 1975); number of fur seal pups (Laws 1977a). (From Bengtson, J.L., *Selected Papers Presented to the Scientific Committee of CCAMLR 1983–1984, Part I*, CCAMLR, Hobart, 43, 1985; After Kato, H., *International Whaling Committee Reports*, 33, 393–399, 1983. With permission.)

Mare (1983) have suggested that the trends observed may have been artifacts from the data due to errors in age determination and under-representation of the most recent cohorts in the samples. However, subsequent studies (Sakuramoto et al. 1985; Kato 1997) confirmed that the observed decline in age at sexual maturity of Minke Whales from 12 to 13 years in the mid-1930s to 10 years in 1955 and a further decline to seven to eight years in the early 1970s was real (Figure 17.4). This controversy as to whether the observed trends reflect true population conditions or artifacts of sampling, analysis and interpretation is as yet unresolved, although the weight of evidence would appear to support the hypothesis that the changes are real.

Such dramatic increases in growth rates must involve considerably increased feeding following the depletion of blue and fin whale stocks. This illustrates a density dependent response by the remaining whales. Surprisingly, in spite of the evidence for an increase in pregnancy rates and a decline in the age of sexual maturity, the expected corresponding direct estimates have not confirmed an increase in recruitment rates. In fact, some analyses suggest a decline in recruitment (Clarke 1983). Nevertheless, normal population theory would suggest that the density dependent responses discussed above would occur because any random decline in its numbers would drive a species very quickly to extinction. However in the case of the southern Minke Whales, there has been an increase in abundance prior to the onset of its exploitation. Evidence from the age distribution of the initial stocks reinforces this thought, which suggests enhanced recruitment rates substantially exceeding the estimated natural mortality (International Whaling Commission 1979). Researchers estimate that the minke whale population which lay between 172 and 225 thousand in 1960 rose to about 323,000 in 1976 (Brown and Lockyer 1984). On the other hand, although the Australian populations of the sperm whale were reduced to such an extent that complete protection was imposed, there is little direct evidence of any changes having occurred in their reproductive characteristics compared to those found in baleen whales (Gambell 1985).

Mitchell (1975) speculated that following the reduction of southern right whales in southern waters, sei whales extended their range to utilize food resources previously unavailable to them due to competition from right whales. There is also evidence that minke whales have also extended their range.

17.3 CHANGES IN SEAL POPULATION DYNAMICS

Seals that utilize krill may have also responded to declining whale stocks (see Figure 17.5). The rapid growth in the populations of Antarctic fur seals discussed in Chapter 8 may have been due in part to an increased availability of krill (Laws 1977a, 1977b; Payne 1977; Croxall and Prince 1979). However, it is difficult to separate the effects of potentially increased krill availability from the recovery of

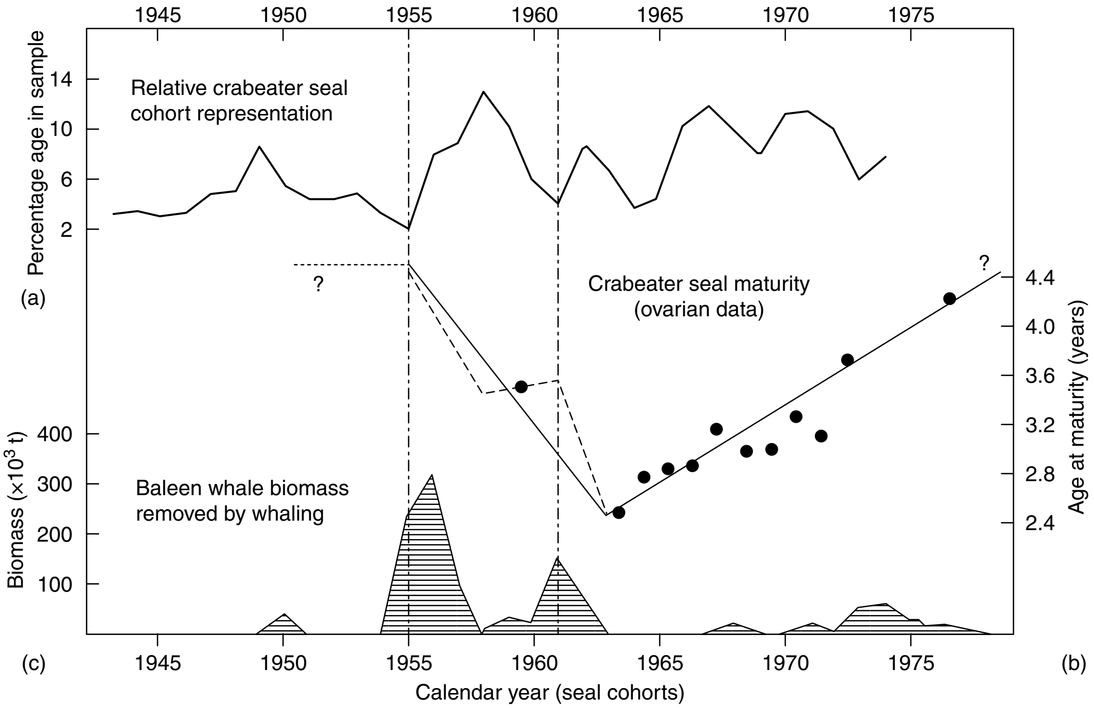


FIGURE 17.5 (a) Relative representation of seal cohorts. The percent age distribution of 7–21 year olds plotted for each collection year. Means of these values were calculated for each calendar year, yielding the curve shown. (b) Age at maturity as estimated from ovarian material. Mean values for 2–7-year olds from each collection year plotted by mean cohort year (4.5 years prior to collection year). Dotted line shows presumed trend of maturity, and dashed line shows alternative trend of decline. (c) Baleen whale biomass removed from area I annually. The following average body size (metric tons) is assumed: blue, 88; fin, 50; humpback, 27; sei, 18.5; and minke, 7. (From Bengtson, J.L., *Selected Papers Presented to the Scientific Committee of CCAMLR 1983–1984, Part I*, CCAMLR, Hobart, 43, 1985. After Bengston, J.L., Laws, R.M., *Selected Papers Presented to the Scientific Committee of CCAMIR 1982–1984. Part II*, Commission for the Conservation of Antartic Marine Living Resources, Hobart, 341, 1984. With permission.)

the fur seal populations from over-exploitation in the early 1800s. On the other hand, increases in the populations of Crabeater and Leopard Seals may be directly related to the decline in whale populations. Based on Law's (1977a) data on crabeater seal survival and pregnancy rates Beddington and Grenfell (1980) modeled crabeater seal populations and concluded that the average annual increase between 1947 and 1979 was about 3% per annum. On the basis of the larger data set then available, they concluded that both the pregnancy rate and the annual survival rate were both higher than originally assumed and considered that a maximum annual rate of increase in recent years of 7.5% was not unlikely. Figure 17.4 suggests that the crabeater seal population was approximately 5 million up to 1950, with maximal rates of increase in the 1970s and deceleration in the 1980s, which would result in a population of approximately 50 million by the end of the century. The fur seal, which has increased at a rate of 15–17%, is projected to reach a level of 4 million. Laws (1984a) assumes a similar rate of increase (7.5%) for the leopard seal as for the crabeater. Projected backward and forward from 1972, this suggests that the total population may have been about 60,000 up to 1955, 440,000 in 1982, and would reach about 600,000 by the year 2000.

Laws (1977b) used tooth back-calculation (back-calculating age at maturity evidenced by the transition in rates of cementum deposition) in crabeater seals to demonstrate a decrease in the age at sexual maturity from approximately 4.5 years in 1945 to 2.5 years in the late 1960s (Figure 17.5). However, Bengtson and Siniff (1981) who examined a small sample of seals taken in 1977 near the South Shetland Islands, could find no clear evidence of a decrease in the age of sexual maturity. Bengtson and Laws (1984) further examined larger samples of crabeater seals of both sexes and all age classes collected in 13 seasons from 1964 to 1982, to test the hypothesis that the presumed increase in seal, fish, and seabird populations in the early 1970s that followed the decline in whale stocks, should have resulted in a reversal of the declining age of sexual maturity. They demonstrated that the tooth back-calculation technique used in earlier studies produced trends that were artifacts of sampling. However, direct evaluation of ovarian *corpora* showed an increasing trend in the age of sexual maturity as predicted (Bengtson and Laws 1984). Crabeater seal age at sexual maturity was found to have increased steadily from about 2.5 years in 1962 to over 4 years in 1976. Therefore, it appears that the age of sexual maturity in crabeater seals fell and rose in response to the presumed availability of krill.

17.4 CHANGES IN BREEDING SUCCESS IN BIRDS

Evidence of increases in bird populations in response to changes in krill availability is somewhat inconclusive. While Prévost (1981) doubts that seabird populations have increased in response to the reduction in whale numbers Conroy and White (1973) and Conroy (1975) presented information that suggested that populations of king, macaroni, Adélie, chinstrap, and gentoo penguins have increased in the Scotia Arc area during the period of commercial whaling. Data on more recent population counts and breeding success of birds on South Georgia, Signey, and Bird Islands indicate increases in king, emperor, macaroni, Adélie, chinstrap, and gentoo penguins in the Scotia Arc region (Croxall 1984) indicating that the trend noted in the early 1970s has continued.

Changes in food availability and competition have presumably led to a new balance in the biomass composition of the community. Chapter 5 gives estimates of the consumption of krill by the major consumers. Although the data for whales, seals, and birds is reasonably good, no reliable estimates for fish consumption are available, nor is data available for squid consumption, which is probably large. What is certain is that shifts in krill consumption and in the biomass composition of krill consumers have occurred. As some populations have increased there is evidence that in some areas a reversal in the declining age at sexual maturity is taking place, for example, in the Crabeater Seals (Bengtson and Laws 1984) and that in these areas the populations are stabilizing at a new level. Increases in the populations of competing species (seal and birds, and perhaps some fish and squid populations) may inhibit the recovery of the protected whale stocks (Tranter 1982). What is clear is that the present community composition of the Southern Ocean marine ecosystem is substantially different from that prior to sealing and whaling. What is less clear is whether this situation can be reversed.

17.5 THE "WHALE REDUCTION-KRILL SURPLUS" HYPOTHESIS

Most of the top-level predators forage in different zones of the Southern Ocean at different stages of their life cycle. In addition, during the breeding season in particular they are often segregated feeding in different areas. In spite of this ecological separation of many species, there exists a potential of competition for food. In the more northern areas sei whales and southern right whales are likely competitors for copepods over most of their distributional range. The depletion of right whales from the early to mid-nineteenth century onward may have led to an increase in the sei whale population(s).

Simultaneously with the decline of the great baleen whale stocks, considerable changes have been observed in the population sizes and reproductive characteristics of krill and non-krill predators. Although reservations have been expressed, numerous authors have suggested that such changes have been brought about by the availability of food released by the reduced number of whales. However, during the same time period, climatic changes in temperature, precipitation, snow cover, and ice cover have been observed regionally. For example, there appears to have been a cold period during 1925–1935 in the Southern Scotia Arc region followed by a warming which amounted to an increase of 2°C by 1940. This could have had a considerable impact on feeding and/or breeding success.

Changes in reproductive characteristics have frequently been cited "as a consequence of a density-dependent response to the decline of the great baleen whales." However, as discussed above, many of these changes have been demonstrated to be artifacts from data rather than showing real trends, or have been found to be inconclusive. For sei whales, for example, which were unlikely to compete for food with other baleen whales in the Southern Ocean, comparable responses in reproductive parameters were observed even before stocks of that species were significantly exploited in the1960s (Gambell 1973).

The example that is most frequently quoted as an illustration of the "whale reduction-krill surplus" hypothesis has been the correlation of increases in the stock size of minke whales, crabeater seals and chinstrap and Adélie penguins with the decline in the great baleen whales. Blue whales, minke whales, crabeater seals, chinstrap penguins, and Adélie penguins are potential competitors for krill in the Marginal Ice Zone in spring and early summer. Possible benefits from the reduction in blue whale stocks were likely to occur to in similar-sized predators with the broadest niche overlap, which would probably be minke whales rather than seals or penguins (Murphy et al. 1988). The number of minke whales has increased while the age at sexual maturity has apparently declined from 12 to 13 years in the 1940s to 7 years in the 1970s.

Agonistic trends in age at sexual maturity and the population sizes of crabeater seals and minke whales appear to be either largely biased (Bengtson and Laws 1985) or still awaiting confirmation. Increases in the populations of chinstrap penguins in the South Shetland Island and Adélie penguins in the Ross Sea are likely to be associated with the gradual decrease in cold winters with extensive ice cover rather than on an increased availability of krill as a food resource (Taylor, Wilson, Thomas 1990; Fraser et al. 1992).

The recovery of Antarctic fur seals could be another example of a species that might have benefited from the reduction of competitive predators. Recovery rates, at least from 1958 to 1972 were faster than expected from other marine mammal populations recovering from overhunting (Laws 1977a). Fur seals at South Georgia remained at very low levels from about 1870 to the early 1950s, when very little sealing occurred (Bonner 1984). Their increase only began with the severe reduction of baleen whales around the island.

It is clear that many populations of Antarctic top-level predators have undergone remarkable changes in their biological parameters, in the last decades. The direct and indirect effects of harvesting had resulted in declines in populations of the great baleen whales, sperm whales, fur seals, king penguins, some albatross species, small petrels on the Subantarctic Islands and a number of fish stocks. Although these declines were associated with the deletion of the great baleen whales, there appears to be much less direct evidence to support the "whale reduction-krill surplus" hypothesis. Trends in environmental conditions offer equally or even more likely explanations for the observed trends in abundance or biological parameters.

17.6 POTENTIAL ECOSYSTEM CHANGES THAT MIGHT RESULT FROM FUTURE RESOURCE EXPLOITATION

For the purposes of considering potential impacts and conservation strategies, Edwards and Heap (1981) believe that it is useful to think of the living resources of the Southern Ocean in terms of three broad levels of population:

1. Species in the *low trophic levels*, which form the food base for species in the higher trophic levels (e.g., zooplankton, particularly krill)
2. Species at *intermediate trophic levels*, which prey on low trophic levels but are themselves subject to significant predation by the top trophic level (e.g., squid and fish)
3. Species at the *top trophic level*, which prey on levels 1 and 2, but are not themselves subject to significant natural predation (e.g., whales, seals, and birds).

Research suggests that the effect of harvesting species that make up the final stages of the food chain (level 3) and are not themselves preyed upon (e.g., whales) is to increase the productivity of other species at the same trophic level (e.g., seals and birds). But the effect on the ecosystem of harvesting species on which predators depend (e.g., krill, level 1, and, possibly to a lesser extent, level 2) is increased competition between the predators for a reduced quantity of prey.

With the current state of knowledge, it is difficult to predict with any certainty the impact that a substantial krill harvest would have on the Southern Ocean ecosystem. It could result in (1) increases in the abundance of competing species, i.e., a shift in trophic relationships from a phytoplankton-krill-marine mammal food chain to a phytoplankton-copepod-fish food chain; (2) interference with the recovery of depleted whale stocks; (3) depletion of dependent populations of seals, birds, fish, and squid; and (4) depletion of krill populations.

In the Southern Ocean ecosystem, krill occupy a role identified by Paine (1966) as that of a "keystone predator" (one that has a dominant influence in structuring the community). Dayton (1972) coined the term "foundation species" for nonpredators, those species at low levels in the food web that contribute in a major way to community structure and function. Species such as krill, through which a significant proportion of the energy and nutrients of an ecosystem flow, represent such a fundamental unit of the system. If they are stressed, the effects on the ecosystem can be more dramatic than when species at higher levels are stressed.

It is unclear as to what level of commercial krill harvesting would significantly affect krill and other species. One possibility is that competition for food among zooplankton would be reduced. However, as detailed in Chapter 5, krill consume only a small proportion of the total phytoplankton production and it would appear that the zooplankton is not food limited. On the other hand, current data are insufficient to judge whether, or at what level, vital parameters of krill, such as recruitment, survival or growth would be affected by an overall reduction in their biomass caused by commercial harvesting. In addition, our lack of understanding of the discreteness of krill stocks (see Chapter 5) does not enable predictions to be made as to how different fishing strategies might affect the stocks. Everson (1981) postulated that significant differences in the potential impacts of commercial fisheries depending on whether krill stocks are continuous or discrete (Table 17.1).

However it is clear that a substantial reduction in krill biomass is likely to have a direct effect of krill predators. A large-scale commercial harvest of krill would result in a reduction of krill availability and an increase in competition between the various krill consumers. This has occurred in other large-scale commercial pelagic fisheries (e.g., the Californian sardine, *Sardinops sagux*, the Peruvian anchovy, *Engraulis ringeus*, and the South African pilchard *Sardinops ocellatus* fisheries). Reduced krill availability would probably result in lower growth rates and reproductive rates, and consequently recruitment of the krill consumers. In a simple model of the joint exploitation of krill and whales, Horwood (1981) demonstrated that harvesting of krill decreased whale abundance. Ultimately, significantly lowered krill biomass would result in steady, or even declining, populations of whales, seals, seabird, and other groups.

The degree to which the various krill consumers would be affected by krill fishing would depend upon the species and its ecology (Bengtson 1985a, 1985b). For example, Gulland (1983a, 1983b) noted that while all Antarctic baleen whales consume krill, the proportion of krill in the diet of each species varies considerably. Consequently, the degree to which krill availability will affect each species will also vary. Krill predominate in the diet of blue and minke whales; for example, whereas copepods are the principal food of sei whales. Sei whales, therefore, could be expected to benefit from a change to copepod dominance in the pelagic food chain.

Commercial fisheries also have the potential to change the behavior and distribution, as well as the density of krill. Gulland (1983a) has raised the question as to whether dispersion of krill swarms by commercial harvesting might affect the availability of krill to predators to a greater or lesser extent than change in the absolute abundance of krill itself. Longhurst (1981) discussed the important role of

TABLE 17.1
Postulated Effects of an Intensive Krill Fishery in One Limited Area

	Krill Stock	
	One Continuous	**Several Discrete**
On krill (stock parameters)		
(a) Growth	Small	Probably small
(b) Mortality	No change (male)	May change (male) Small (female) Large(female)
(c) Biomass	Small	Significant reduction after start of fishing
On natural consumers		
Species linked closely to fishing area (e.g. breeding birds)		
(i) Intensive fishing prior to critical predator period each season	Significant in fishing area elsewhere minimal	Significant: increasing with time to level off eventually
(ii) Intensive fishing during and after critical predator period	Small	Significant in subsequent years
Species not tied to fishing area (e.g. whales)		
Intensive fishing before predator normally present in fishing area	Small overall	Reduced density (i.e. feeding elsewhere)
Intensive fishing before and after predator present in fishing area	None or slight reduction in density	Slight reduction in short term reduction in long term

Source: From Everson, I., *Biological Investigations of Marine Antarctic Systems and Stocks*, El-Sayed, S.Z., Ed., Scott Polar Research Institute, Cambridge, 31, 1981. With permission.

patchy distribution of plankton within marine ecosystems. Lasker (1975, 1980b) demonstrated the inability of larval fish to survive if they cannot locate phytoplankton above a certain threshold density. If euphausiids were dispersed rather than concentrated in layers or swarms, the energetic costs to baleen whales searching for food would be higher than the calorific value of the prey themselves. Nemoto and Harrison (1981) have stressed the importance of dense swarms of euphausiids for baleen whales, noting that although *Euphausia tricantha* is distributed in high latitudes throughout the Southern Ocean, it is not found in the stomachs of baleen whales presumably because it not accessible to whales in the energy efficient form of dense swarms (Baker 1959). Similarly although the copepod *Calanoides acutus* is abundant in Antarctic waters, it is not a prey species for many of the large predators presumably due to it lack of swarming behavior (Andrews 1966). However, the likelihood of krill swarms being dispersed, or their behavior being affected by fishing activity, and the consequent effect on predators is not known.

Probably the most important potential impact of krill harvests would be the shifts that might occur in the ecosystem species composition and the abundance of the predominant species. Investigators have examined the impact of removing species from the food web. For example, Pimm (1984) outlined the effects of removing predators from benthic and littoral systems. Well-known documented examples of previous shifts in dominant species include: the collapse of the sardine stocks off the Californian coasts in the 1930s and their replacement by anchovies (Gulland 1983a, 1993b); the crash of anchovetta stocks off Peru in 1972 to be replaced by sardines (Idyll 1973; Murphy 1977); declines in herring and mackerel stocks in the North Sea leading to increase in cod, haddock, and plaice (Holden 1978); and the ecological replacement of depleted herring and mackerel stocks in the eastern north Atlantic by the sand lance (*Ammodytes* sp.) (Sherman et al. 1981). As we have seen the perturbation induced by commercial whaling has resulted in a change in the composition of the dominant mammal species. However, the degree to which it may again be approaching a steady state is not known.

Krill predators have commonly been ranked in the following order according to their importance as krill consumers.

Prior to Whale Exploitation	**Currently**
Baleen whales	Seals
Fish	Seabirds
Cephalopods	Cephalopods
Seabirds	Fish
Seals	Baleen whales

This reversal of ranking reflects the removal of approximately 1.5 million whales between 1904 and 1986 and refined estimates of krill consumption of the major predator groups. However, both rankings are still speculative and estimates of prey consumption are still subject to great uncertainties. In particular, the role of cephalopods as krill consumers is as yet not known with any certainty.

18 Management of Living Resources

CONTENTS

18.1 INTRODUCTION

The history of the exploitation of the living resources of the Southern Ocean has led to the severe depletion of the stocks of fur seals, many of the whale species, and some of the fish stocks. Although the stocks of the fur seals have made a remarkable recovery, the extent to which the exploited whale and fish stocks will recover is uncertain. It is unlikely that the seal stocks will be exploited in the foreseeable future and currently a moratorium is in effect on the further harvesting of whales. However, exploitation of both fish and krill continue. The fish resources are not large and their exploitation will need to be strictly controlled and limited. Although the krill catches have exceeded 500,000 tons on only one occasion, the potential for considerable expansion could have serious consequences for the Southern Ocean marine ecosystem as a whole.

Traditionally the management of marine living resources has been conducted with reference to the harvested species alone, being built around the concept of "unit stock" (Edwards and Hennemuth 1975). However, it is clear that this single-species approach is not adequate for the ecosystem protection envisaged under the Convention for the Conservation of Antarctic Marine Living Resources. This protection must take into account interrelations of the biotic components as well as their physical environment. The type of integrated comprehensive plan that makes provision for rationally controlled harvesting of the component species cannot be achieved by the conventional single-species maximum sustainable yield (MSY) approach (Laevastu and Larkins 1981). The succeeding sections in this chapter shall consider what is involved in the ecosystem approach to the management of the living resources of the Southern Ocean.

18.2 THE CONVENTION ON THE CONSERVATION OF ANTARCTIC MARINE LIVING RESOURCES (CCAMLR)

The expansion of the krill fishery in the early 1980s followed the progressive overfishing of fin fish stocks in the Southern Ocean (Kock 1992). This raised serious concerns about the sustainability of Antarctic marine living resource in general and of krill in particular given its key position in the Antarctic food web (Mitchell and Sandbrook 1980). Consequently, the Antarctic Treaty Consultative parties initiated negotiations to provide management, conservation, and sustainable utilization of the marine living resources found south of the Antarctic Polar Front (Edwards and Heap 1981). The fisheries Convention on the Conservation of Antarctic Marine Living Resources, which was enforced on April 7, 1982, was in many ways the outcome of the work of the SCAR Group of Specialists on the Living Resources of the Southern Ocean and the BIOMASS Programme (Knox 1984). As is usual in such international fisheries agreements the convention established two main institutions: a commission charged with carrying out its objectives and a scientific committee charged with providing advice to the Commission.

The convention is unique in that the preamble to the convention recognizes "the importance of safeguarding… the integrity of the ecosystem and the seas surrounding Antarctica." It not only strove to guarantee the conservation and rational use of Antarctic marine living resources, but also aimed to ensure that irreversible and negative impacts of harvesting did not affect both harvested species and those dependent on them as a source of food or in some other ecologically related way. These provisions laid the foundation for what has since been termed the "ecosystem approach" and clearly indicated that caution should be used to minimize the risk of irreversible changes within the convention area arising from the harvesting and associated activities (Nicol 1991). These objectives recognize the need to ensure the continued health of individual species of Antarctic marine organisms and define the rational use of living resources as actions that will not disturb the ecosystem's balance. In simple and practical terms, these objectives require that:

1. Harvested populations should be assessed and monitored
2. Ecological interactions between harvested and other species, either dependent on or related to them, should be defined and quantified
3. Levels of depletion should be estimated to effectively monitor the restoration of depleted species.

The area covered by the convention is shown in Figure 16.3; it covers approximately 8% of the world ocean and the northern boundary is the approximate position of the Antarctic convergence. The structure of the convention and its subsidiary bodies is depicted in Figure 18.1. Due to limited available data on the status of Antarctic stocks and species interactions, the scientific committee initially set out to develop a programme of commercial fisheries data collection and analysis, as well as directed ecological research, to obtain the necessary information. A number of working groups were established:

- Informal Group on the Long-term Programme of the Work of the Scientific Committee
- Working Group on Fish Stock Assessment
- Working Group on Krill
- Working Group on the CCAMLR Ecosystem Monitoring and Management

In 1994, the Working Group on Krill and the Working Group on CCAMLR Ecosystem Monitoring and Management were amalgamated into the Working Group on Ecosystem Monitoring and Management.

The Working Group on Fish Stock Assessment advises the scientific committee on potential catch levels for harvested species other than krill (Agnew 1997). It regularly reviews the catch and effort statistics and the size and age composition of commercial and research catches. One major problem they have encountered has been that attempts to provide such advice "were being regularly and substantially undermined by the failure to provide data in a timely manner" (SC-CCAMLR 1990b). In many instances the commission has acted on the recommendations of the scientific committee, but in others it has not acted on them or delayed their implementation. This is partly due to the fact that the commission's decisions are arrived at by consensus and not by a majority decision. The third meeting of the commission in 1984 provided the first conservation measures for the depleted stocks of finfish. The fourth meeting in 1985 followed initial mesh-regulation measures for aiding the recovery of fish stocks with the adoption of more stringent regulations prohibiting all directed fishing for the bottom-living species of Antarctic cod, *Notothenia rossii*, in the waters of South Georgia, the South Orkneys, and the Antarctic Peninsula. The fifth meeting in 1986 adopted conservation measures prohibiting fishing for the severely depleted Antarctic cod, and permitting the commission to set catch limitations as a management technique. The sixth meeting in 1987 established new conservation measures to address the serious depletion of fish stocks. Three measures of significance were taken for the first time: an overall total allowable catch for each species (TACs that have been set annually since then), a reporting system, and a closed season. Later fishing for *N. rossii* in the South Georgia region was prohibited.

The CCAMLR represents a significant milestone in the evolution of a more holistic approach to the conservation and management of marine living resources (Sherman and Ryan 1988; Constable 2004). It is a young convention still in the process of coming to grips with this task, but the indications are that it has been operating more smoothly and efficiently each year. The conservation measures instituted so far prove that it is able to reach important and difficult decisions. Clearly the difficulties involved in implementing the ecosystem approach will require more and new research. In light of the history of marine living resource depletion in most seas CCAMLR represents a new approach to management that will be followed with great interest.

18.3 ECOSYSTEM APPROACH TO THE MANAGEMENT OF THE LIVING RESOURCES OF THE SOUTHERN OCEAN

Figure 18.1 presents a scheme of the principal processes and interactions of the marine ecosystem that need to be considered in the context of an ecosystem-based management system. The development of an ecosystem-based management procedure is the primary task of the CCAMLR Working Group on Ecosystem Monitoring and Management. Accounts of the evolution of this working group are presented by Everson (2002) and Miller (2003). Since the late 1980s, CCAMLR has developed the precautionary approach, which incorporates the principles of how scientific evidence could be used in the decision-making

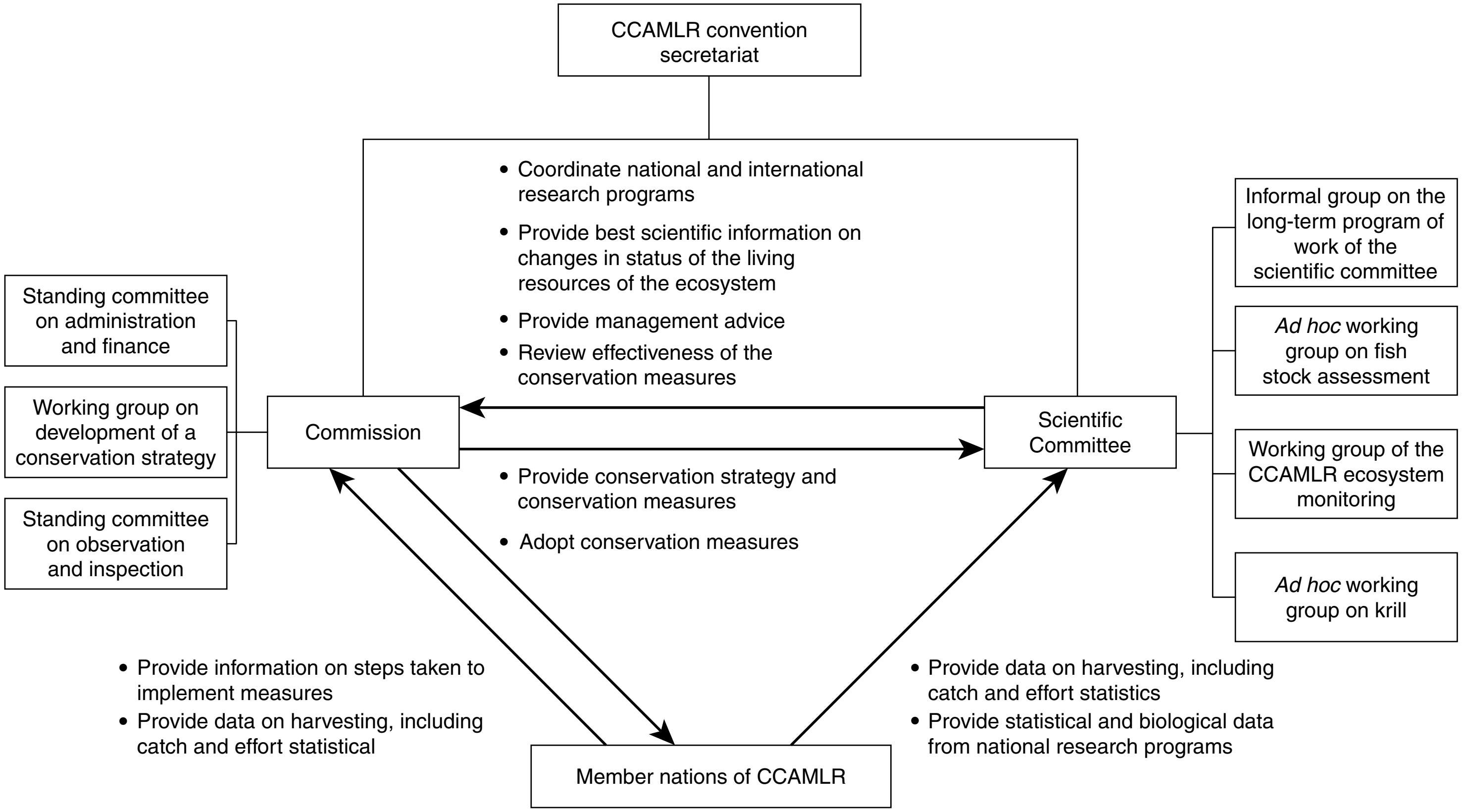


FIGURE 18.1 Organizational structure of the convention on the conservation of antarctic marine living resources. (From Sherman, K., Ryan, A.F., *Oceanus*, 31, 59, 1988. With permission.)

process (CCAMLR 2003; Constable et al. 2004). While this approach is based on the management of a single species (Antarctic krill, or *Euphausia superba*) it takes into account the needs of predators in determining catch limits. Its application is based on a management procedure with prearranged decisions that specify how harvest controls (catch limits) will be adjusted given the scientific assessment available (de la Mare 1996, 1998). Figure 18.2 illustrates the ecosystem approach to managing the effects of fishing on dependent and related species.

Although the single species approach can have some validity for species in the top trophic level, such as whales and seals, even then there are several risks and problems associated with such an approach (Edwards and Hennemuth 1975). These have been listed in The Southern Ocean Convention Workshop on the Management of Antarctic Marine Living Resources (1980).

1. Often the data is noisy, inadequate, or simply not available.
2. As the harvested population changes to new densities, its various life-history parameters change, and consequently its ability to recover from environmental disturbance also changes.
3. The interplay between the dynamic behavior of the population and the level of harvesting will depend on the details of the population's recruitment curve, which in turn depends on the lifehistory strategy of the species. Seal recruitment curves vary widely and are, for example, very different from those for whales and krill. Furthermore the recruitment curve for krill is as yet little understood.
4. Compounding these problems is the fact that many populations (such as krill swarms) are patchily distributed, so that it cannot be assumed that yields are simply linearly proportional to fishing effort and stock density. Studies of herring population's harvesting curves that incorporate the effects of patchiness are likely to generate systems with more than one equilibrium point well as exhibiting the potential for sudden collapse under harvesting.
5. The recruitment of new cohorts into adult, sexually mature populations involves substantial lag times, which add an extra complication to population dynamics.

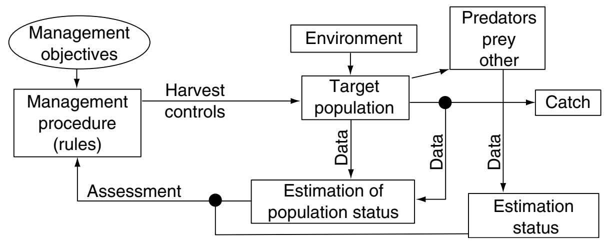


FIGURE 18.2 An illustration of the ecosystem-based approach to managing the effects of fishing on dependent and related species (after de la Mare 1996). The management procedure is a set of decision rules used to adjust harvest controls in response to assessments such that the operational objectives will be highly likely to be met. The physical world (shaded boxes) represents the actual state of the system which is observed through the monitoring program. Assessments take account of uncertainty concerning how the physical world would function and the relationships between the monitoring program and the physical world. (From Constable, A.J., *CCAMLR*, 9, 236, 2002. With permission.)

All the difficulties and problems outlined above also apply to multispecies/multitrophic-level fisheries, but in addition the system interactions introduce further complications (Dickie 1975, 1979).

There are several problems in dealing with static concepts such as MSY when several species are involved. MSY for top-trophic-level species is typically attained by not harvesting the lower levels; MSY for the lower levels is typically achieved by minimizing their natural death rate by eliminating all their predators. Therefore it is not possible to simultaneously exploit both top and bottom levels for MSY.

There are also considerable problems associated with the trajectories or the change in numbers against time that the system components are likely to take towards any specified equilibrium point. Predator-prey systems are well known for their cyclical behavior, especially when the prey populations change on a slower time scale than the predator populations (as is the case with krill).

In addition, many multispecies systems possess several equilibrium or stable states. As a consequence, a disturbed or harvested system can move irreversibly to a new equilibrium state. There are many instances of this in the literature.

The essential features of the ecosystem approach to be adopted by CCAMLR as detailed in Article II of the convention are:

1. The ecosystem is to be managed in a manner that maintains the ecological relationships between harvested, dependent, and competing populations.
2. Management will include the restoration of *depleted populations* (to a level defined in 3).
3. Management will prevent any harvested populations from falling below a level close to the greatest net annual increment.
4. Management will take into account *the indirect impact of harvesting* and prevent (or minimize the risk of) changes in the marine ecosystem that are not potentially reversible over one or two decades.

As Gulland (1986) points out, the direct implementation of the objectives detailed above will not be easy. For example (3) involves management for stable recruitment, but as we know more about fish populations it is clear that stable recruitment is comparatively rare in nature. Data on recruitment range from the apparently random (or at least with little discernable patterns) year-to-year fluctuations over some three orders of magnitude in the North Sea haddock, to the long-term (over many decades) changes between periods of high and low abundance in many clupeoid stocks (Scandinavian herring, Californian sardine). Gulland (1986) points out that the history of some clupeoid stocks also shows that changes can occur, sometimes possibly triggered by overexploitation, but sometimes due to solely to natural events that are not reversible in “two or three decades,” and that it would be surprising if some elements of the Southern Ocean marine ecosystem did not exhibit similar instability and changes that are, in the short term, irreversible.

Gulland (1986) further points out that the objectives, as expressed in the convention, are not intended to be an exposition of the scientific realities and complexities of the Southern Ocean ecosystem, but are largely the result of the difficult negotiations leading up to the agreement on the text of the convention when there were very different views regarding approaches to managing and conserving the Southern Ocean ecosystem, both within and between countries. Consequently there are a number of problems facing the Scientific Committee and the Commission of CCAMLR in interpreting the precise scientific meaning of portions of the text of the convention.

An ability to manage rationally, and to take into account the indirect impacts of harvesting, implies an ability to predict the effect of perturbing the system. Inevitably this implies *quantitative* prediction. Such quantitative predictions require the construction of a model in which “species–species,” as well as “man–species” interactions are taken into account explicitly rather than implicitly (i.e., a multispecies model). Such a model depends upon adequate information for parameters such as the population sizes of the interacting species and the manner in which these sizes have changed and are now changing over time.

The ecosystem approach outlined above requires:

1. An adequate information base
2. The development of multispecies models
3. Directed ecological studies
4. Ecological monitoring

Each of these requirements will be considered in turn.

18.3.1 Information Needs

At its 1985 meeting, the Scientific Committee of CCAMLR decided on a long-term programme for the committee. It identified a major task as that of providing information and management advice about a complex ecosystem. To accomplish this task the committee must oversee the collection, analysis, and reporting of a broad spectrum of data that would include “fisheries statistics, biological attributes and status of target and nontarget species, characteristics of the physical environment, and ecological relations among living resources and their environment” (CCAMLR 1988).

18.3.2 Fisheries Assessment

A major problem that has faced the scientific committee has been the deficiencies of access to and reporting of data on the activities of commercial fishing. Modern fisheries assessment techniques require detailed data on fishing activities and catch characteristics, including data on fishing methods (e.g., trawl characteristics and mesh sizes), fishing locations, catch level, by-catch composition, age and length composition of the catches, etc. For many species and areas of the Southern Ocean such comprehensive data is not available and much of the effort of the scientific committee at its early meetings has gone into the drafting of better procedures for obtaining such information. In particular the lack of information on net selectivity for all Antarctic fish species was emphasized and research on this topic was recommended for high priority.

Another critical area addressed by the scientific committee was the relationships between krill density and catch per unit effort (CPUE). Recommendations have been made for detailed reporting on krill fishing to include data on the type of vessel, gear used (with detailed information on items such as the effective mouth opening of the trawl, mesh sizes, etc.), tow information (duration, depth, towing speed etc.), and detailed catch records (total catch, approximate species composition, average sizes, etc.).

One of the tasks facing the Working Group on Krill was to develop methods to estimate appropriate levels of krill harvesting (i.e., yield). The Working group concentrated on developing calculations of long-term yield based on the approaches of Beddington and Cooke (1983), as initially modified by Butterworth, Punt, and Basson (1991), Butterworth et al. (1994). This resulted in the development of the Krill Yield Model (KYM).

18.3.3 Ecosystem Dynamics

The convention requires that the fisheries in the convention area be conducted so as to maintain the ecological relationships between harvested, dependent, and related populations of the Antarctic marine fauna; take into account the indirect impacts of harvesting; ensure that depleted populations are restored to a level close to that which ensures the greatest annual increment; and prevent changes, or minimize the risk of changes in the marine ecosystem that are not potentially reversible over two or three decades. This presupposes a good understanding of the dynamics of the Southern Ocean ecosystem.

One of the key questions that needs to be addressed is whether the rate of recovery of the whale stocks, or the level that would be reached by such recovery, would be affected by different levels of krill harvesting. To provide answers to the above, two sets of questions need to be addressed (Gulland 1986).

First, researchers must know which parameters (age at sexual maturity, percentage of pregnant females, juvenile mortality, etc.) of whale stocks are affected by changes in krill stocks (abundance, density at particular times and in particular areas), and whether changes are simple (e.g., linear with krill density) or occur at critical levels. Evidence from some of the more realistic models of the dynamics of large mammal populations (Fowler and Smith 1981) suggests that the relations between parameter values and population density may be nonlinear and that the onset of density-dependent factors may be abrupt at high populations densities and may lead to a substantial and sustained drop in carrying capacity. We also need to know whether such changes in whale parameters are the same as those caused by changes in whale abundance, for example, social dependent factors within the whale stocks that are not, or only partly, associated with krill availability.

Second, researchers must be able to measure changes in abundance and any other characteristics of the krill stocks that are important for the population dynamics of whales, and to determine the extent to which these changes are due to fishing for krill, and to predict the impact of such characteristics on the future development or modifications of that fishery. Given the current deficiencies in the database (for example, the wide range of variance in krill abundance estimates, the unresolved questions of krill longevity and fecundity, and the need for improvement in CPUE data), this is a very tall order.

A second key question that needs to be addressed is the degree of stability and reversibility of the Southern Ocean ecosystem. There is a large volume of literature on the stability of ecosystems as a function of the number and abundances of the component species and their interrelationships (see Cushing 1981 for a review). From this information it is clear that there can be more than one stable equilibrium position. Thus if the exploitation of krill, whales, or other species components displaces the ecosystem across the boundary between the areas of attraction of two stable points, the system may not return to its original position even if all exploitation ceased.

Researchers not know whether there is a real danger of nonreversible changes in the Southern Ocean ecosystem, and in particular whether the larger baleen whales will ever recover to their former population levels. The drastic reduction in the fur seal population has been reversed and the population is approaching its pre-exploitation level, although the breeding distribution is not the same as it used to be. It may well be that following the depletion of the large whales, the smaller "r-selected" species would have, by virtue of their reproductive strategy, expanded more rapidly; however, it might also be expected that in the long-run (and the long-run may be very long indeed) the larger "k-selected" species would have, by virtue of their reproductive strategy, the competitive advantage and would recover to their initial level, provided that they have maintained a foothold in the system (Gulland 1986). Information is therefore needed on both past changes in the system and on the changes that are currently taking place.

18.3.4 Directed Ecological Studies

It is clear that an understanding of the structure and function of the Southern Ocean marine ecosystem is fundamental to the management of the living resources. Such an understanding can only come from extensive ecological studies directed at both system-wide studies as well as ones that address specific data needs targeted by management questions.

18.4 THE ROLE OF MODELLING STUDIES

The ecosystem approach to management as required under Article II of the convention necessitates the availability of an acceptable multispecies model of the Southern Ocean ecosystem. In Chapter 15, modelling the ecosystem and its subsystems was discussed. Such models were concerned with the dynamics of the ecosystem, especially directed at quantifying energy flow and the circulation of materials through the system, and were not specifically developed to answer management questions. In the final section of this chapter we will discuss the reasons why an acceptable multispecies model with predictive capacity is not possible at this point in time. However, more simplified theoretical models can play a useful role in interpreting the likely behavior of the system under different types and levels of perturbation (Beddington, Beverton, and Lavigne 1985).

In a series of papers (for example, May et al. 1979; Beddington and May 1980, Beddington and Cooke 1983; 1982; Yamanaka 1983; Beddington and de la Mare 1984; Shimadzu 1984b; Sissenwine 1985) various authors have discussed simple models of the components of the Southern Ocean ecosystem. It is not possible to review these here and readers can refer to the original works for details. Beddington and de la Mare (1985) point out that the text of the Convention on the Conservation of Antarctic Marine Living Resources raises a variety of complex problems that can only be illuminated by the use of models. One whole set of problems is concerned with the interpretation of the behavior of the system under different types of perturbation, for instance, the different levels of krill harvest.

Most of the simple models that elucidate the behavior of the system employ simple predator-prey models (e.g., May et al. 1979; Beddington and May 1980, 1982; Beddington and Cooke 1981; Yamanaka 1983; Shimadzu 1984b) framed in differential equations based on density dependent processes and assume that the unexploited system is in equilibrium. Most of the models use the Maximum Sustainable Yield (MSY) concept, not because it is likely to be a practically achievable objective but, because of its familiarity, it is a useful concept around which to develop discussion. In addition, for all practical purposes the MSY level can be equated with the level of maximum net productivity referred to in the convention. Beddington and de la Mare (1984) discuss the implications of models of krill–whales, krill–whales–seals, and krill–cephalopods–sperm whales. Generally, the predictions derived from the krill–whales and krill–whale–seals models have been realized.

The models developed to date are relatively simple models that consider at most three interacting species. However, to provide general management guidance, and especially to assess the effects of exploitation in a complex ecosystem, holistic ecosystem models that emphasize the role of exploited species need to be developed. The models described in Chapter 15 started with trophodynamics computations at the base of the food web, for example, basic organic production. Such models do not always lead to reliable quantitative results because the pathways of basic organic production to secondary and tertiary production are very variable in space and time, and not fully known quantitatively.

Smith (1978) and Cushing (1981) have discussed the scales of temporal variability in marine ecosystems. Long-term series for phytoplankton, zooplankton, and fish production are available for the North Atlantic, the North Sea, and off California. These all show considerable fluctuations in abundance and there is strong evidence of cyclical periodicity. It has been shown that such are linked with climatic events; for example, the periodicity of the Norwegian herring has been correlated with the amount of ice cover north of Iceland (Beverton and Lee 1965), and fluctuations in zooplankton and fish stocks (sardines, anchovies, hake, mackerel, and saury) off California with upwelling (Soutar and Isaacs 1974). These studies have show that primary production is variable in response to oceanographic conditions. Recent research in the Southern Ocean demonstrates that production varies both spatially and from year to year (see Chapters 2, 5, 13, and 15). However, evidence for cyclic phenomena requires long-term series of data on the order of several decades. For the Southern Ocean long-term series are not available.

Various authors (for example, Beddington and de La Mare 1984; Sissenwine 1985; Butterworth 1986) have recognized that to achieve the objectives of CCAMLR Article II it will be necessary to develop a suite of multi-species models for the Southern Ocean marine ecosystem as a whole (or at least for some geographically isolated parts of the system). Miller (1986b) points out that to date such models have appeared to have been used less, or have been less useful, in decision-making about managing renewable fish resources. So far, models developed for the Southern Ocean are inadequate to address the range of problems that face managers in interpreting Article II of the convention. Managers are primarily concerned with demersal fin fisheries and the krill system with its important predators (including whales, seals, penguins, and various seabird species). Article II requires the managers to guarantee that fishing activity is reasonably stable over a long period of time, while at the same time ensuring the restoration of depleted species.

Levin, Marin, and Powell (1988) have listed the important questions being addressed in scientific studies of the living marine resources in the Southern Ocean:

1. How important are physical processes, such as the movement of fronts and sea-surface contiguous zones, in determining the distribution and dynamics of krill and fish?
2. How important are biological factors such as predation and food availability?
3. What is the interaction between spatial patterns and fishing behavior?
4. How can theoretical approaches to stock assessment and prediction facilitate the estimation of the size of the resource, and aid in the development of optimal harvesting strategies?

Physical and biological factors interact to produce patterns of multiple spatial and temporal scales, and the development of predictive models must involve an examination of such scales (Denham and Powell 1984; Levin, Marin, and Powell 1988). Spectral analysis and other statistical procedures allow comparisons of observed distributions of physical factors, primary producers, and consumers (e.g., Weber 1984; Weber, El-Sayed, and Hampton 1986); mechanistic investigations provide complimentary information on natural time and space scales for biological and physical processes underlying patterns. The modelling approach used by Levin, Marin, and Powell (1988) assumes that phytoplankton abundance is determined by physical processes. On the other hand Weber, El-Sayed, and Hampton (1986) believe that grazing is an important factor in the small-scale distribution of phytoplankton.

Miller (1986b) recommends that a suite of models with different model outputs will be required to meet the objectives of Article II. Eight attributes (purpose, description, variables, driving forces, time horizons, time steps, constraints, and data) were identified as the essential elements in the development of suitable simulations of important Antarctic marine system interactions, and to facilitate the formation of a suitable decision-making protocol for management purposes. The *purpose* of a model refers to the specific reason for the model's use. The *description* encompasses the type of model (for example, speculative simulation model or predictive model) being used. The outputs of the model are the quantitative or qualitative changes in values of dependent *variables* in response to *driving forces* that are the independent variable or parameters that force the behavior of the modeled system. The *time horizon* is the period in which the behavior of the variables is assessed, and the *time step* is the incremental period within the model. The *constraints* are the bounds imposed on the behavior or interpretation of the model (for instance, limitations of data), and the *data* are the items of information upon which the model is structured.

Table 18.1 provides an example of the kinds of models that need to be developed. Such a model might be used when exploring decisions in the contest of predators (for example, crabeater seals) and their prey (i.e., krill). The model would explore causal factors, determining the relative abundance of predators within the system. Such a multispecies model would be directly relevant to the performance of the joint exploitation of several coexisting predators (such as seals and whales), the abundance of which may be influenced directly by exploitation or by competition for resources which are themselves harvested (for example, krill).

Laevastu and Favorite (1981) have outlined modelling developments that lead to a holistic ecosystem simulation directed towards management needs. In particular they describe a biomass-based (DYNUMES) model with spatial

TABLE 18.1
An Example of the Attributes Required for a Model Exploring Management Decisions in the Context of Predators

Purpose	To explore possible mechanisms influencing the abundance of predators in the system
Description	Speculative multi-species predator simulation model
Variables	Predator biomass
Driving forces	Prey biomass and harvesting
Time horizon	5 years
Time steps	1 year unless there is a seasonal influence on the population
Constraints	Data limited
Data	Predator population sizes and dynamics, consumption rates, diet analysis

Source: From Miller, D.G.M., *Selected Scientific Papers CCAMLR, 1986*, 295, 1986b. With permission.

resolution that was developed for the eastern Bering Sea (Laevastu and Larkin 1981). Figure 18.3 presents a simplified view of the principal processes emphasized in the DYMUMES simulation. In the simulation a complex series of computations are carried out at each point on a grid covering the area of study for each time step (for example, monthly). The numerous species-specific coefficients (such as growth coefficients, food requirements, and fishing mortality coefficients) are influenced by a number of factors at each grid point and at each time step. Growth of biomass, fishery yields, mortalities, consumptions (predation), and migrations are also computed in each time step. The simulations also include most of the pronounced environment-biota interactions (such as, depth, temperature, nature of the bottom, currents, etc.). The DYMUMES model is a bulk biomass model that is heavily dependent on reliable estimates of the quantitative composition of the food of species and/or ecological groups. While such information is available for some species in the Southern Ocean there are large gaps that make it difficult at this time to develop a model similar to that of Laevastu and Favorite.

The DYNUMES model run over several year spans shows that marine ecosystems are unstable and sensitive to changes in growth rates, relative distributions, abundance of predators/prey, and changes in the composition of food. Due to the multiple interactions in the ecosystem, the abundance and distribution of most species show quasicyclical variations (Laevastu and Favorite 1981).

One outcome of the new ecosystem approach to fisheries is the realization of the shortcomings of the single species approaches that lack trophodynamic interactions among species. Another is the realization of the necessity to deal with age/size dependent mortalities, and to ascertain predation mortalities as well as spawning stress mortalities in ecosystem models.

Quantitative numerical ecosystem simulation models can reveal processes and resultant changes in the ecosystem that have not been easily observed in the past, and they permit ecological experiments that would be impossible to conduct in nature. Such simulations with emphasis on exploited populations can provide new powerful tools for fisheries management. They not only allow the determination of the magnitude of the resources and their distributions, but also the simulation of variable space and time responses to any desired/or any prescribed fishery that indirectly influences other species via inter-species interactions. Such simulations have shown how important it is to determine the magnitudes and periods of largescale "natural fluctuations" in the marine ecosystem that can occur without the influence of the fishery.

Gulland (1983b) stressed the importance of understanding species interactions, changes in behavior, and fluctuations in vital rates due to density dependent factors. Changes in any of these parameters may be nonlinear. For example, how does the abundance of blue or minke whales affect the population dynamics of sei whales? Is the total abundance of krill or the abundance of dense krill swarms more critical to predators? To what extent might the dispersion of krill swarms by commercial harvesting affect prey accessibility for various predators? These and other questions regarding interactions in the Southern Ocean ecosystem stress the need for the development of multispecies ecosystem models that incorporate the species interactions outlined above.

Models of the Antarctic marine ecosystem mostly comprise statistical models of the distribution and abundance of marine species, particularly as they relate to krill (see Constable et al. 2000 for review); population models of krill (Constable et al. 2000); and estimates of consumption of krill by predators (for example, Croxall, Ricketts, and Wood 1990; Croll and Tershy 1998). Few models take account of the spatial and temporal dynamics of the system (but see Croxall, Prince, and Ricketts 1985, for a spatial and seasonal analysis of krill consumption by seals and seabirds, and Mangel and Switzer 1998, for spatial and temporal variation in the foraging success of Adélie penguins), or of the uncertainties surrounding the structure of the models or the estimates of parameters.

For the purposes of developing an ecosystem-based management system, plausible models that capture the dynamics of major species are needed (Beddington and de la Mare 1985; Butterworth 1986; de la Mar 1986). Green (1977) represents an early attempt at dynamic modelling for the Antarctic marine ecosystem. Theoretical approaches to the effects of exploitation of Southern Ocean living resources

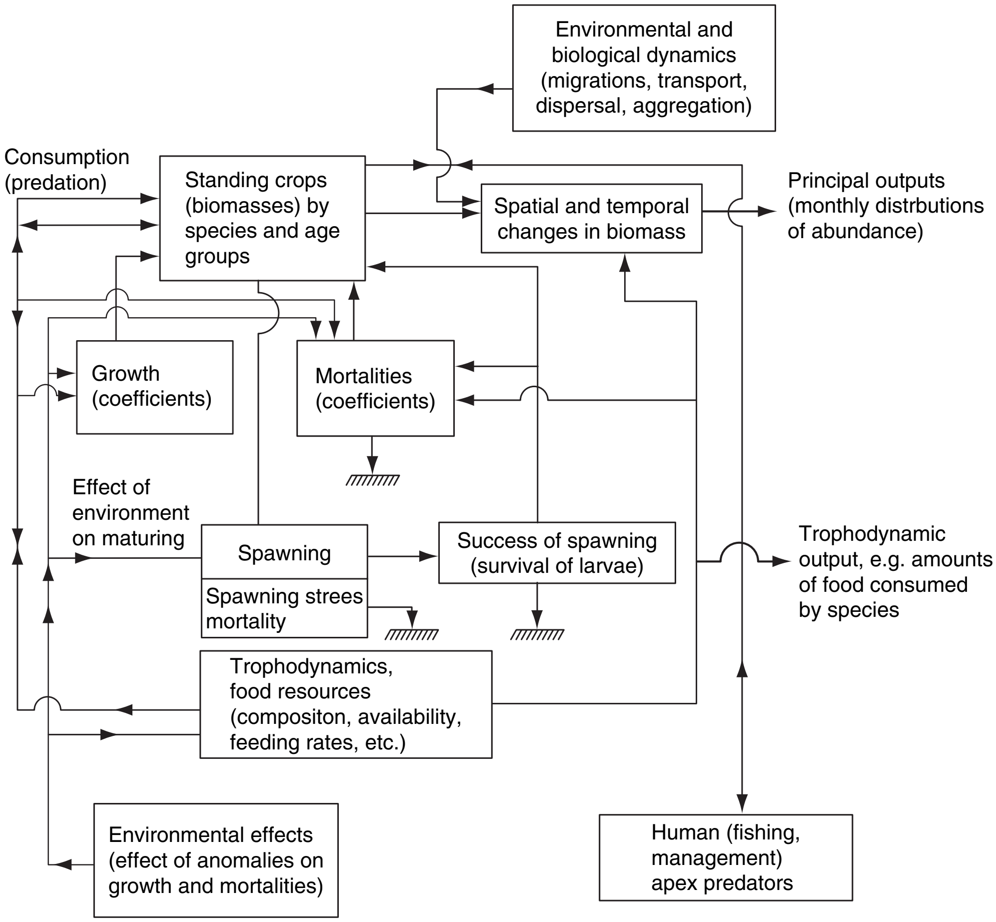


FIGURE 18.3 Scheme of principal and processes and interactions in the marine ecosystem. (From Laevastu, T., Favoutite, F., *Analysis of Marine Ecosystems*, Longhurst, A. R., Ed., Academic Press, London and New York, 701, 1981. With permission.)

were explored by May et al. (1979), and Beddington and May (1982).

The most important task will be to develop models with sufficient complexity to capture the dynamics of the major species and how they might respond to changes in the ecosystem, noting that these models will not capture all interactions amongst all species and the physical dynamics of the system (Butterworth 1986; de la Mare 1998). The aim is to develop these kinds of models, taking care to adequately encapsulate important indirect effects on the major species.

Although it is recognized that there are deficiencies in the data base as far as the Southern Ocean is concerned, there is an urgent need for work to commence on the development of models of the type outlined above to help resolve some of the issues in resource management currently facing the Commission on the Conservation of Antarctic Marine Living Resources. Although it is impossible to develop such a model for the Southern Ocean as a whole, models could be developed on a regional basis. In the first instance a model of the South Georgia–Antarctic Peninsula area would be feasible as the database is more complete for this region than for other parts of the Southern Ocean.

18.5 MONITORING INDICATORS OF POSSIBLE ECOLOGICAL CHANGES IN THE ANTARCTIC MARINE ECOSYSTEM

One of the central problems in the management of the Southern Ocean "ecosystem" is the assessment of actual and potential impacts on the system by various harvest regimes (species and quantities to be harvested). This question can be approached in three different ways:

1. Assessment of target species directly
2. Evaluating target competitors and by-catch species
3. Monitoring predators

At its third annual meeting, held in Hobart in September 1984, the Scientific Committee of CCAMLR established an ad hoc working group to formulate and recommend actions for planning, implementing, and coordinating multinational research programs necessary to effectively assess and monitor key components of the Southern Ocean marine ecosystem. This group first met in Seattle, Washington in May 1985 and, following consideration of its report at the September 1985 meeting of the scientific committee, a formal working group was constituted for the CCAMLR Ecosystem Monitoring Programme (Figure 18.4). This working group met in July 1986 to develop definitive proposals for a monitoring program, and in 1988 (CCAMLR 1988) published a handbook on standard methods for monitoring parameters. The management of the krill fishery and the Ecosystem Monitoring Programme have been reviewed by Constable (2002), Everson (2002), and Miller (2003).

Andrew (1997) has provided a concise background of the development of the CCAMLR Ecosystem Monitoring Programme. This was established in 1985 with the following objectives:

> To detect and record significant changes in critical components of the ecosystem to serve as a basis for the conservation of Antarctic marine living resources. The monitoring system should be designed to distinguish between changes due to the harvesting of commercial species and changes due to environmental variability, both physical and biological.

18.5.1 TARGET SPECIES

As we have seen there are considerable problems in simulating the stocks of krill in particular and in evaluating population changes that might be due to harvesting. Gulland (1983) has pointed out that the patchy distribution of krill swarms, plus the uncertainty of how much krill is present outside the swarms, makes it difficult to interpret the relationship between catch and effort data. Furthermore, the fishery statistics for krill may reflect processing capacity and temporary abundance of krill at fishing sites rather than regional population densities.

Krill biomass is likely to be a function of the time of the year and it may be sensitive to large recruitment fluctuations typical of many relatively short-lived marine species. A large variance is likely in any index of the size of krill populations (see Chapter 5). In addition krill behavior markedly affects catchability (the ratio of catch-per-unit-effort (CPUE) to biomass), and therefore affects indices of catch rate. The Scientific Committee of CCAMLR has set up an Ad Hoc Workshop on Krill CPUE.

18.5.2 TARGET COMPETITORS AND BYCATCH SPECIES

Competitors of krill include other herbivorous zooplankton such as salps, copepods, and juvenile fish. If the abundance of krill was affected by harvesting then these competitors might be expected to manifest compensatory responses resulting from altered competition. However, research has shown that the populations of such competitors are subject to the same spatial and seasonal variation as those of the krill (Longhurst 1981). Salp populations are well-known for their cyclical population fluctuations. By-catch species include some of the competitors, especially larval fishes. While the monitoring of by-catch species would help in evaluating whether nontarget zooplankton and juvenile fishes manifest responses to krill fishing pressure (for example, competitive displacement), it is unlikely to provide any reliable quantitative measures.

18.5.3 PREDATORS

Fluctuations in food availability as discussed in Chapter 5 may be reflected in the responses of the primary and secondary predators of krill. Many species variables such as growth, reproduction, and behavior are flexible parameters that change in response to factors such as prey availability. A number of recent papers (such as Eberhart 1977; Eberhart and Siniff 1977; Fowler 1980; Hanks 1981) have explored

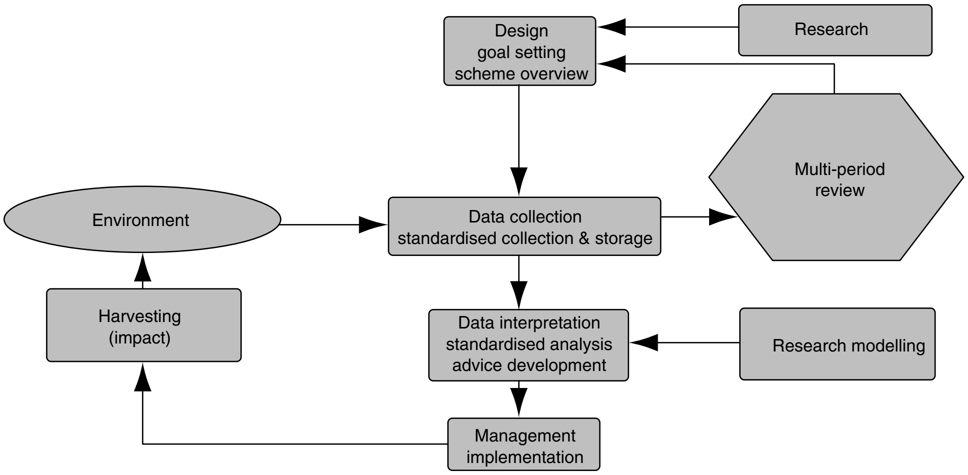


FIGURE 18.4 Schematic representation of the CCAMLR Ecosystem Monitoring Program (CEMP) (after Agnew 1997). The centre three items, along with application of krill precautionary catch limits (management implementation) represent the major areas addressed during the first ten years of the program (1985–1995). Key activities occupy the centre of the diagram and these are complemented by research activities and associated deliberations on the right. The environment is affected by both harvesting and natural variation. Obviously, management events control harvesting, thereby forming a feedback loop within CEMP. (From Miller, D.G.M., *CCAMLR Sci.*, 9, 203, 2003. With permission.)

the use of various indices to assess the status of large mammal populations, while Green-Hammond et al. (1983) and Bengston (1985b) have discussed the general principles of indicator species monitoring and the criteria for their selection.

The choice of predatory species has been based on criteria whose definition has evolved over several years. These have been summarized by Croxall, Davis, and O'Connell (1988b) as:

1. Important components (in terms of prey consumption of the Southern Ocean system)
2. Specialist predators on harvestable prey, especially krill
3. Having broad geographical breeding ranges, including sites near and far from areas likely to be subject to intensive fishing
4. Having ready accessibility to breeding sites and toleration of human presence and activity

A number of species of penguins and seals have been designated as CEMP species and several locations have been selected as CEMP Network Sites for monitoring programmes.

According to Croxall (1989) the possible aims of the CEMP might include any or all of the following:

1. To detect changes in indices of the status in either demographic or physiological (such as condition) aspects and/or reproductive performance of seabirds and seals
2. To relate these changes to indices of prey (at present krill) abundance and availability to the predators
3. To use predator indices, on the basis of the relationships between predators and prey developed above, as a measure of prey availability to predators and prey stock abundance
4. To use the predator indices to detect changes in food availability that result from commercial harvesting as distinct from changes due to natural fluctuations in the biological and physical environment

The dependent species that have been identified for the CCAMLR Ecosystem Monitoring Programme are: Adélie (*Pygoscelis adeliae*), chinstrap (*P. antarctica*), gentoo (*P. papua*) and macaroni (*Eudyptes chrysolophus*) penguins, black-browed albatross (*Diomedea melanophrys*), Antarctic (*Thalasspica antarctica*) and cape (*Daption capensis*) petrels, Antarctic fur seal (*Arctocephalus gazella*), and crabeater (*Lobodon carcinophagus*) seal. The CEMP parameters for dependent species along with the time and space scales of their dependence on krill are set out in Table 18.1. A full description of the CCAMLR standard sampling protocols for each of the parameters is given in CCAMLR (2003).

The parameters currently recommended for penguin monitoring studies are: breeding population size, breeding success, incubation shift duration, chick fledging weight, adult arrival weight, and demographic parameters (SC-CCAMLR 1988). Trivelpiece et al. (1990) have examined data based on these parameters from studies carried out over several years in Admiralty Bay, King George Island on Adélie and chinstrap penguins. The parameters showed considerable variability. However, interpretation of the variability was greatly enhanced when several parameters were considered simultaneously.

The questions addressed in this monitoring programme are (Everson 2002):

1. Is the availability of krill changing?
2. Are populations of dependent species in decline?
3. How much krill is required by the dependent species?
4. Is the availability of krill changing?
5. Are populations of dependent species in decline?
6. How much krill is required by the dependent species?
7. What is the extent of overlap between krill fishing and foraging by dependent species?

One of the major problems involved in these ecosystem monitoring studies is to distinguish natural fluctuations in population density and breeding success from those due to reduced food supply caused by commercial harvesting. Some of the short-term and long-term variability in the Southern Ocean marine system have been discussed in Chapter 15. Variability in Antarctic seabird population densities and breeding success are well documented; see, for example, Whitehead, Johnstone, and Burton (1990) for Adélie penguins, southern fulmars and Antarctic petrels in Prydz Bay; Ainley and LeReserche (1973), and Wilson (1990) for Adélie penguins on Ross Island; Taylor, Wilson, and Thomas (1990) for Adélie penguins in the Ross Sea Region; and Lishman (1985) for Adélie penguins at Signey Island. Reduced breeding success and decline in population numbers in nearly all of these studies have been attributed either to the increased energetic costs of travelling over sea ice in years of persistent ice and/or the scarcity of food resources. Taylor, Wilson, and Thomas (1990) in their surveys of Adélie penguins in the Ross Sea Region where there are thirty-eight rookeries with a total of 1,082,000 breeding pairs—about half the world population—have shown that nearly all the rookeries have increased in size over the last ten-twenty years. Possible reasons for the increase and annual fluctuations in numbers include seasonal variations in sea ice and weather conditions, and longer-term climatic change. It is of interest that the diets of the southernmost rookeries at Cape Bird and Cape Crozier are different from those of the more northerly rookeries. Krill, which does not figure in the diets of the southern rookeries, is the predominant food item for the birds in the more northern rookeries. These results stress the need for caution when using trends in bird populations to detect the impact of man-induced changes such as those brought about by krill harvesting.

It is clear that the influence of naturally varying environmental parameters is of sufficient magnitude to obscure the effects of man-induced changes over the short term. This suggests the need for long-term integrated studies of avian population parameters, prey distribution and abundance, weather conditions, and fluctuations in oceanographic conditions.

18.6 EXPERIMENTAL FISHING AS A MANAGEMENT TOOL

In 1984 Australia presented as a basis for discussion a proposal to undertake a coordinated fishing and research experiment at selected sites in the Southern Ocean (Anon 1985b). A number of sites were proposed, including areas adjacent to the Scotia Arc, around South Georgia, and regions of the South Indian Ocean. For the Prydz Bay Gyre (55–110°E) an experiment was proposed in two phases of five years each. During the first phase the level and type of fishing effort would be held constant while the ecology of the site would be documented, population levels and trends of target and key consumer species would be assessed, and complementary research would be undertaken to further refine a conceptual and quantitative ecological model of the experimental site. In the second phase of the experiment the system would be manipulated through planned variations in the level and type of fishing effort and, possibly, by the co-harvesting of selected consumer species. The effects of this manipulation would be studied and the results used to develop a plan for the management of the Prydz Bay subsystem.

The aim of this experimental approach would be to enable management guidelines for Southern Ocean fisheries to be based on the best possible scientific advice derived from experience and the results of scientific research. In discussing the ways in which the development of a multispecies model for the Southern Ocean ecosystem could be facilitated, Butterworth (1985) considered that without carefully regulated experimental programs to reduce certain predator populations in a few selected areas, the dynamic parameters required for workable multispecies models could be determined only with great difficulty and after considerable time.

18.7 ALTERNATIVE MANAGEMENT STRATEGIES

It is abundantly clear that traditional fisheries management programs are inappropriate for the management of the living resources of the Southern Ocean and that the management issues are complex. Consequently new management approaches are necessary. In discussing the limitations of the mean sustainable yield (MSY) approach to the management of fish resources Holt (1978) lists a series of principles that should be used as the basis for the reformulation of management objectives:

1. Ecosystems should be maintained in such a state that both their consumptive and nonconsumptive values to humanity can be realized on a continuing basis.
2. Options for different uses by present and succeeding human generations should be ensured.
3. Risk of irreversible changes or long-term adverse effects of exploitation should be minimized.
4. Decisions should include a safety factor to allow for limitations of knowledge and the inevitable imperfections of management institutions.
5. Measures to conserve one resource should not be wasted to another.
6. Survey or monitoring, analysis, and assessment should precede planned use and accompany actual use of a resource, and the results should be made available promptly for critical public review.

These are the principles that should underpin the management of the living resources of the Southern Ocean.

Throughout this chapter reference has frequently been made to Article II of the Convention on the Conservation of Antarctic Marine Living Resources. The two key objectives enunciated in this article are "accounting for the indirect impacts of harvesting" and "the restoration of depleted populations." Butterworth (1985) has discussed the practical implications of these objectives and these are set out in Figure 18.5. The requirements for the construction of multispecies models and the difficulties in developing an acceptable multispecies model at this time have been outlined in this chapter.

There are two possible approaches for achieving the second objective, the restoration of depleted populations. The "passive" approach would be to curtail all harvesting (of any species) on the assumption that, after a time (and probably a long time, on the order of centuries, rather than decades) the various species would return to a new population equilibrium, hopefully approaching that of the pre-exploitation levels. An alternative hypothesis would be that more than one stable state exists for the unexploited system, and that the system would not necessarily return to its original unexploited state if undisturbed in the future. The other possible approach then is an "active" one in which other species (in some cases competitors of the exploited species) are harvested to reduce their size and prevent further growth. Again this implies the availability of a multispecies model to predict quantitatively the effect on some species of changing the stock sizes of others. Butterworth (1985b) discusses how the situation might be improved so as to allow the production of such a model. He considers that three lines of investigation are needed:

1. Selection of the major components of the system to be incorporated in the model
2. Assessing the size and growth rates of the component populations more adequately
3. Conducting carefully regulated perturbation experiments

However, in the absence of an acceptable multispecies model, "active" predator harvesting is not a viable option for the Southern Ocean ecosystem *as a whole* at this stage.

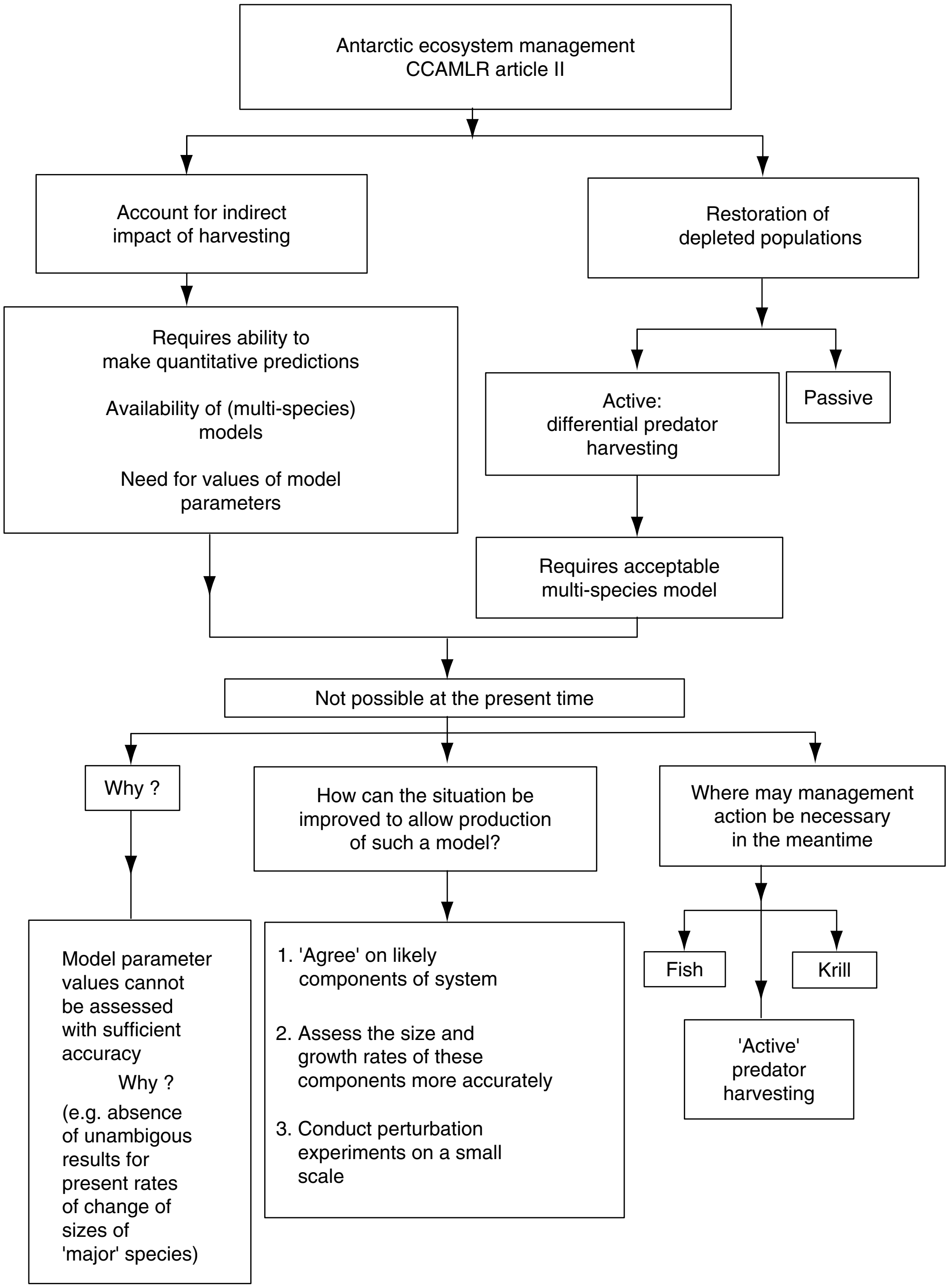


FIGURE 18.5 Plan of antarctic ecosystem management. (From Butterworth, D.S., *Selected Papers Presented to the Scientific Committee of CCAMLR 1982–1984, Part II*, 15, 1985. With permission.)

Nevertheless this could be an option if positive evidence for the existence of more than one stable state for the system were forthcoming.

Since it is clear that many species in the Southern Ocean are predominantly dependent (directly or indirectly) on krill as a food source, it can reasonably be concluded that any substantial depletion of the krill standing stock would have widespread deleterious effects upon at least some of the predator species. In the light of this, avoidance of any substantial reduction in the krill stock should be a particular priority. Butterworth (1985) suggests that the primary objective of krill management should be "the standing stock of krill in each management area must not be permitted to fall to less than an agreed proportion of its current level."

There are, however, a number of problems associated with the above objective. Firstly, there is no definitive evidence for the existence of separate genetic stocks of krill (see Section 5.5.6). In spite of this, "management areas" could be provisionally based on available biological and oceanographic information, together with historic whaling and other records (e.g., Mackintosh 1972). Secondly, as we have seen, there are considerable problems in estimating the biomass and distribution of krill. Thirdly, if krill predator stocks are still increasing in response to the depletion of baleen whale populations, then the krill standing stock could be expected to decrease from its present level.

An important aspect in the management of short-lived species subject to recruitment fluctuations (as appears to be likely in the case of krill) is the requirement to quickly detect and react to poor recruitment periods by decreasing the TAC (total allowable catch) for each management area (or any other major limitation to the catch effort may also be adopted). There is a need therefore to place a ceiling on the rate at which fishing effort (or corresponding TACs) is allowed to increase in the early stages of the development of the fishery to prevent the over-capitalization that has been involved in the decline of many fisheries. In the first instance a conservative empirical ceiling should be set.

Fish stocks have already been heavily exploited in some areas, with past catches representing mainly the depletion of accumulated stocks rather than the harvesting of surplus production (Gulland 1983a, 1983b; Kock, Duhamel, and Hureau 1985). Urgent management measures are necessary to prevent further depletion of the stock. Butterfield (1985) has suggested that as an interim operational objective for the exploited (or potentially exploitable) fish stocks, "the stock-size of the species concerned must not be permitted to fall below, or must be allowed to recover to, an agreed fraction of its estimated pre-exploitation level in each designated management area. He suggests that because surplus production to biomass ratios for Antarctic demersal stocks are low (Gulland 1983a, 1983b), "pulse fishing" may prove to be the only economically viable long-term harvesting strategy (that is, rather than fishing every year, fishing should be carried out intensively over a short period once every number of years). The pulse fishing strategy assumes that the population can always increase after harvesting. Therefore, it is important that the stock-size be not allowed to fall below the agreed level, especially when there is insufficient data to enable surplus production to be accurately estimated.

As Holt (1978) points out, it will not be easy to put the principles outlined in this chapter into operation, and herein lies the challenge to CCAMLR. The scientific committee is composed of dedicated scientists, the majority of whom are, or have been, active an Antarctic marine research. With the cooperation of the SCAR scientific community, I am confident that sound scientific advice based on the best available data will be provided. In the past, this kind of advice has not always been heeded by fisheries commissions as the history of the International Whaling Commission testifies. Some of the early experiences in the operation of the CCAMLR Commission have not been encouraging. It will be up to the members of the commission to resist political and other pressures and to heed and act upon the scientists' recommendations.

19 Ultraviolet Radiation

CONTENTS

19.1 INTRODUCTION

Human activities that have led to the emission of chloroflourocarbons (CFCs), in particular, have reduced the concentration of stratospheric O_3. The most dramatic loss of O_3 has been observed over Antarctica during the austral spring where a 50% reduction in O_3 the widely discussed “ozone hole”—has been documented. The ozone has been depleted by a catalytic cycle involving Cl and ClO

$$\mathrm{Cl} + \mathrm{O_3} \rightarrow \mathrm{ClO} + \mathrm{O_2}$$

$$\mathrm{ClO} + \mathrm{O_3} \rightarrow \mathrm{Cl} + \mathrm{O_2}$$

$$\text{net } \mathrm{O} + \mathrm{O_3} \rightarrow 2\mathrm{O_2}$$

where Cl and ClO are the eventual breakdown products of the CFCs after they have reached the region of strong ultraviolet radiation in the middle and upper atmosphere. Many predict further reductions in average global stratospheric O_3 at all latitudes over the next century. The greatest depletion of O_3 occurs over Antarctica due to a combination of unique chemical and physical features of the springtime austral atmosphere that promote the depletion process (Solomon 1999). Spring ozone values (October mean values) at Halley Station (lat 75°S) has shown evidence of decline from the 1970s onwards (Stachelin et al. 2001). Values were about 300 Dobson Units (DU) in the early 1970s, dropping to about 200 DU by the early 1980s and 125 DU in the 1990s. Meanwhile, biological UV doses have increased by a factor of two over the period 1979–1999 at Halley Bay (Figure 19.1) (Dahlback 2002).

Atmospheric O_3 is a strong selective absorber of ultraviolet radiation. The shortest and most damaging UV wavelengths, UV-C (200–280 nm), are absorbed strongly by the atmosphere, so only negligible amounts reach the earth’s surface. UV-B is also extremely injurious to organisms, and it is this radiation that increases most significantly when atmospheric O_3 is reduced. The longest wavelengths of ultraviolet radiation (UV-A, 320–400 nm) are known to produce both photodamage and photoreactivation in living cells, and this radiation is relatively unaffected by variations in stratospheric O_3 concentrations. Photosynthetically available radiation (PAR, 400–700 nm) like UV-A is largely independent of O_3 concentration. As a consequence,

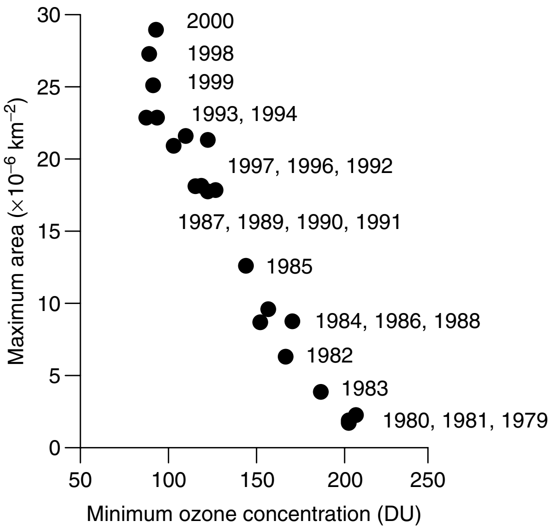


FIGURE 19.1 Relationship between minimum annual ozone concentration over Antarctica and the maximum area enclosed by the 200 DU isolume (data identified by years). Note the greater areas of depletion accompanying lower minima. (From Karentz, D., *Antarctic Biology in a Global Context*, Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backhuys Publishers, Leiden, The Netherlands, 47, 2003. With permission.)

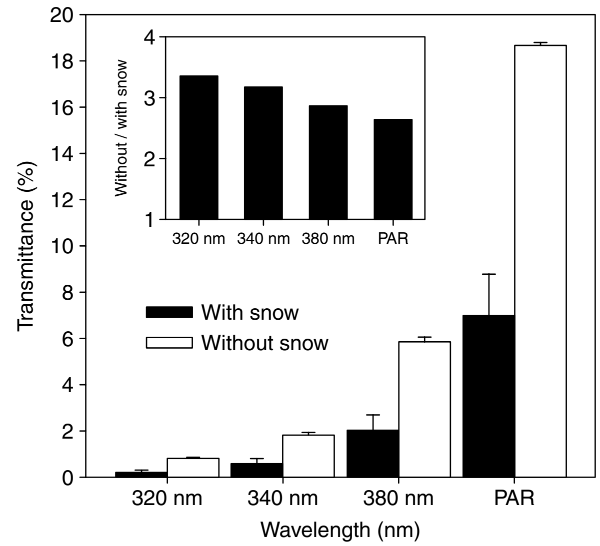


FIGURE 19.2 Transmittance through 0.7 m-thick sea ice with and without the natural 2-cm snow cover, Hudson Bay 16 August 1999. (From Vincent, W.F., Belzile, C., *Antarctic Biology in a Global Context*, Huskies, A.H L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backhuys Publishers, Leiden, The Netherlands, 171, 2003. With permission.)

stratospheric O_3 depletion leads to a dramatic increase in damaging UV-B irradiance Q_{UVB}, whereas the corresponding irradiance in the UV-A (Q_{UVA}) and in the PAR (Q_{PAR}) remain relatively constant. Marchant and Davidson (1991), Pyle et al. (1992), Karentz (2003), Weller and Penhale (1994), Marchant (1997) and Vincent and Belzile (2003) have reviewed ultraviolet radiation in Antarctic marine systems.

There are a number of factors that can mitigate the amount of UV radiation to which organisms in Antarctic marine ecosystems are exposed:

1. *Albedo*. Albedo, the ratio of upwelling (E_u) to downwelling (E_d) irradiance, is the combined result of the surface (specular) reflectance and volume relectance. Given the highly diffusive nature of UVR, the albedo of a water body is relatively insensitive to SZA (solar zenith angle) and waves and varies by 5–8% (Jerome and Bukata 1998). Snow and sea-ice cover have a major impact on albedo and near-surface transmission, and thus the amount of downwelling UV entering the water column. Snow UV albedo is generally greater than 80%. Cold sea-ice albedo is also high but decreases to 50–60% for bare melting ice.
2. *Attenuation by snow and ice*. Figure 19.2 illustrates the impact of snow and sea ice on the transmission of ultraviolet radiation (UVR). The removal of surface snow caused a 3–16-fold increase in under-ice UVR. Even a layer of snow only 2-cm thick reduced UVR by a factor of 3.
3. *Water column transparency*. Colored dissolved organic (CDOM) matter plays a part in biological UV exposure because of its strong UV-absorbing properties. Higher values are found in the Arctic due to the much greater terrestrial input of CDOM. However, in Antarctica high concentration of seston can reduce UV exposure. Arrigo et al. (1998a) found very high particulate absorption in the UV-B region for phytoplankton blooms in the southwestern Ross Sea in the UV-B region.

19.2 BIOLOGICAL HAZARDS OF ULTRAVIOLET RADIATION

Although the decline of the ozone layer modifies only the narrow 40-nm band of the incident UV-B, even low-level exposure to these wavelengths can be lethal for some organisms. Even the exclusion of UV-B radiation under a "normal" ozone column (350–400 DU) can result in increased growth and reproduction in natural communities. Phytoplankton species have been reported to respond negatively to as little as 0.01% of incident UV (Jitts et al. 1976).

The mutagenic and lethal effects of UV-B radiation on aquatic organisms is well documented (see, e.g., Vincent and Ray (1993)). DNA is the primary lethal target, but there are many other UV sensitive biological molecules. Secondary effects of UV exposure involve absorption by RNA, proteins (enzymes, histones, hormones, membrane components, etc.), some pigments, and other molecules.

UV also catalyses photochemical reactions inside cells in their external environment, one notable example being seawater. Radicals produced by such reactions can have toxic effects and cause oxidative stress (Mopper and Zhou 1990). All of the factors listed above contribute to impairment and inactivation of metabolic pathways such as photosynthesis, membrane transport, and nutrient uptake. Subsequent effects can include inhibition of growth reproduction, and ultimately death.

19.3 UV TOLERANCE MECHANISMS

The degree to which an organism is sensitive to UV can be gleaned from analyzing the number and efficiency of repair systems as well as the existence of avoidance strategies like behaviour strategies or the production of sun screens. In response to pressure exerted by UV radiation, cells have developed a variety of mechanisms for minimizing and correcting UV-induced damage. These include: (1) reduction of UV exposure by physical barriers or UV absorbing compounds; (2) physiological mechanisms that can recognize and repair UV-induced damage (Mitchell and Karantz 1993); and (3) the production of antioxidants that can neutralize effects produced by UV phorochemical reactions. Over time, organisms have developed an array of defences to minimize UV exposure and a variety of repair mechanisms to deal with UV-induced damage. As a consequence, one observes a range of tolerance mechanisms for UV radiation across many different taxa (Mitchell and Karantz 1993).

1. *Physical barriers and UV absorbing compounds*. The most obvious way to avoid UV-induced damage is to eliminate or reduce exposure to UV radiation (UVR). This can be accomplished by a variety of behavioural patterns or habitat preferences and by certain morphological and structural features, such as size, shape, and an outer exoskeleton which acts as a barrier.

   The presence of UV-absorbing mycosporine-like amino acid compounds (MAAs) is well documented for many marine organisms including corals, starfish, ascidians, zoanthids, mussels, fish, dinoflagellates and red algae (Karentz 1991). Organisms often contain several MMAs with different absorbing maxima. Thus large regions of the UV spectrum can be absorbed when a complement of several MMAs is present. Table 19.1 lists the presence or absence of eight MMAs in invertebrate and algal groups.
2. *Repair mechanisms*. Direct mutagenic and lethal effects of UV exposure are caused by damage to DNA (see Mitchell and Karentz 1993). DNA damage is potentially debilitating, mutational, or lethal, and must be corrected if the organism is to survive. Three cellular repair mechanisms have been

TABLE 19.1
Presence or Absence of Specific MAA's in Antarctic Marine Groups

	PI	PR	SH	MG	MV	PE	AS	PL
				Invertebrate Phyla				
Protozoa	−	−	−	−	−	−	−	−
Porifera	+	+	+	+	+	+	+	+
Coelerterata	+	+	+	+	+	−	−	−
Ctenophora	−	−	−	−	−	−	−	−
Platyhelminthes	+	+	+	+	+	−	+	+
Nemertinea	+	+	+	+	+	−	−	−
Annelida	+	+	+	+	+	+	+	+
Mollusca	+	+	+	+	+	+	+	−
Arthropoda	+	+	+	+	+	+	+	+
Bryozoa	+	+	+	+	+	−	−	−
Echinodermata	+	+	+	+	+	−	+	−
Chaetognatha	−	−	−	−	−	−	−	−
				Algal Divisions				
Rhodophyta	+	+	+	+	−	+	+	+
Phaeophyta	+	+	−	+	−	−	−	−
Chlorophyta	+	+	+	+	−	−	+	−
Chrysophyta	+	+	+	−	−	−	−	−

Abbreviations are as follows: PI, palythin; PR, porphyra-33; SH, shinorine; MG, mycosporine–glycine; MV, mycosporine–glycine:valine; PE, palythene; AS, asterine-330; and PL, polythinol. Plus signs indicate presence; Minus signs indicate absence.

Source: From Karentz, D., *Ant. Res. Ser.*, 62, 10, 1994. With permission.

identified to correct damage to DNA molecules (Friedberg 1985):

a. *Photoreactivation.* Photoreactivation is a single-enzyme system that is a major repair pathway in prokaryotic cells and is also present in many eukaryotic organisms.
b. *Excision repair (dark repair)* that involves a series of enzymes that recognizes DNA damage, removes the damaged part of the molecule, and resynthesizes that segment of the DNA as a complement of the undamaged segment. It occurs in all types of prokaryote and eukaryote organisms.
c. *Postreplication (recombination) repair*, which is a complex process that occurs after DNA replication and corrects the DNA defect on the basis of information contained in the undamaged strand.

19.4 IMPACTS OF ULTRAVIOLET RADIATION ON ANTARCTIC MARINE BIOTA

19.4.1 Bacteria

Whereas much has been written about phytoplankton, very little has been published on the effects of UV radiation on bacteria. Karentz et al. (1991) tested the ability of six clones of marine bacteria isolated from sea ice to repair UV-damaged DNA by photoactivation and excision repair. The cells were exposed to a gradient of artificial UV-C light. All of the clones had higher viability with post-radiation white light treatment than with dark treatment (Figure 19.3).

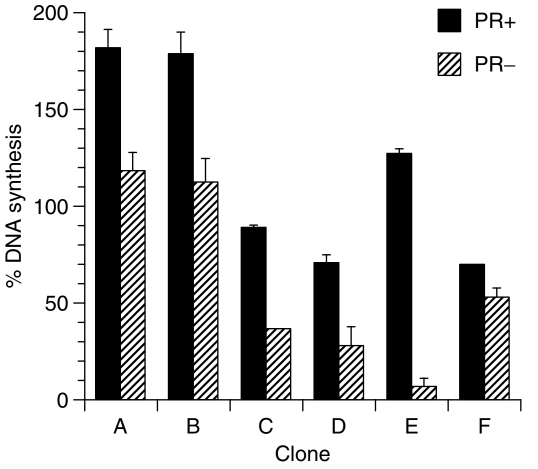


FIGURE 19.3 Percentage of DNA synthesis relative to control values in six clones of sea ice bacteriaexposed to 100 J m^{-2} of UVR. PR+, white-light treatment (supports excision repair); PR-, dark treatment (supports excision repair alone). (From Karentz, D., *Radiation in Antarctica: Measurements and Biological Effects*, Weller, C.S., Penhale, P.A., Eds., American Geophysical Union, Washington, DC, 98, 1994. With permission.)

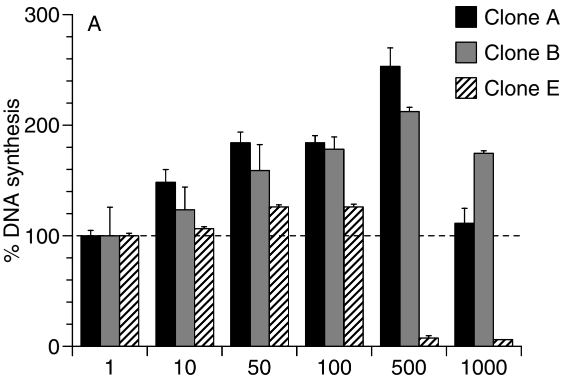


FIGURE 19.4 Enhancement of DNA synthesis in bacteria. (From Karentz, D., *Radiation in Antarctica: Measurements and Biological Effects*, Weller, C.S., Penhale, P.A., Eds., American Geophysical Union, Washington, DC, 103, 1994. With permission.)

Such evidence points to the conclusion that photoreactivation existed as a repair mechanism for UV-damaged DNA in Antarctic marine bacteria. Three clones (A, B, and E) showed large increases in DNA synthesis (Figure 19.4).

Davidson and Marchant (1994) incubated three strains of Antarctic bacteria in an artificial UV-B illumination gradient approximately equivalent to 50–600% of surface midsummer UV-B irradiance measured at lat. 69°S. The viability of these strains was reduced by about 30% following a 30-min exposure at 12°C (their optimum growth temperature at 1.0 W m^{-2}). They concluded that Antarctic bacteria may be under stress from ambient UV-B exposure.

19.4.2 Phytoplankton

Because of their role as primary producers, marine phytoplankton have been the principal focus of research on the impact of UV-radiation in Antarctic marine ecosystems. A major concern is how the phytoplankton growing in the Southern Ocean and in the Marginal Sea-Ice Zone (MIZ) in particular would respond to increased UV radiation (Karentz et al. 1991; Smith et al. 1992; Lubin et al. 1992; Neale et al. 1994). There is considerable evidence that UV exposure affects phytoplankton, specifically inhibition of primary production (e.g., Smith et al. 1992), growth and reproduction (Davidson and Marchant 1994), nitrogen metabolism (Dohler 1998), and motility and phototactic orientation (Hader and Worrest 1991). Subsequent to the pioneering studies of Holm-Hansen et al. (1993) and El-Sayed et al. (1990a, 1990b) numerous studies have investigated the underwater radiation climate and the impacts and responses of Antarctic marine phytoplankton to UV exposure (see Bidigare 1989; Karentz 1991, 1994, 2003; Voytek 1990; Smith et al. 1992; Marchant and Davidson 1991; Marchant 1997; Weller and Penhale 1994).

Two questions that have been investigated are: (1) “Will underwater radiation result in a decline in primary production?” and (2) “Will it result in a change in species composition?”

Investigators have found evidence for a wide range of sensitivity to UV exposure in Antarctic phytoplankton. This sensitivity is species specific with flagellates being the most sensitive and diatoms the least sensitive (Helbling et al. 1994; Villafane et al. 1995). These studies have shown that Antarctic species have the same means of protection from UV radiation as those found in similar species from other latitudes. These include the presence of UV-absorbing molecules (mycosporine-like amino acid compounds) and the existence of DNA repair pathways (photoreactivation and excision repair).

Data on possible decrease in primary production due to UV radiation impact have led to conflicting results. A number of species of Antarctic diatoms have been investigated to determine their sensitivity to UV exposure (Karentz et al. 1991; Arrigo 1994; Davidson and Marchant 1994; Davidson et al. 1994; Neale et al. 1994; Bracher et al. 2000; Marchant, 1997; Bracher and Wiencke 2000). This work has demonstrated that there are distinct differences in cell survival relative to conditions that promote photoreactivation and/or excision repair and has indicated that there is a large variation in species tolerance to UVR based on cell survival data from laboratory exposure experiments (Figure 19.5). Several diatom species showed consistent, distinct increases in cell numbers over control cells when exposed to low UV-B fluorescence (up to 100 J m^{-2}). This demonstrates that UV-B may have a stimulating effect on DNA synthesis and/or cell division (Figure 19.6).

In an investigation of a natural phytoplankton community near Palmer Station, Boucher and Prézelin (1996) found that daily exposure to ambient levels of UVR resulted in a 34% reduction in averaged carbon fixation. The UV-B portion of the solar spectrum inhibited daily primary production rates by 15%, whereas UV-A was responsible for an 18% reduction in daily averaged rates of carbon fixation. From these data they concluded that the springtime diatom-dominated community was just as, or more sensitive, to UV-B to photoinhibitation as the prymesiophyte-dominated communities studied by Smith et al. (1992).

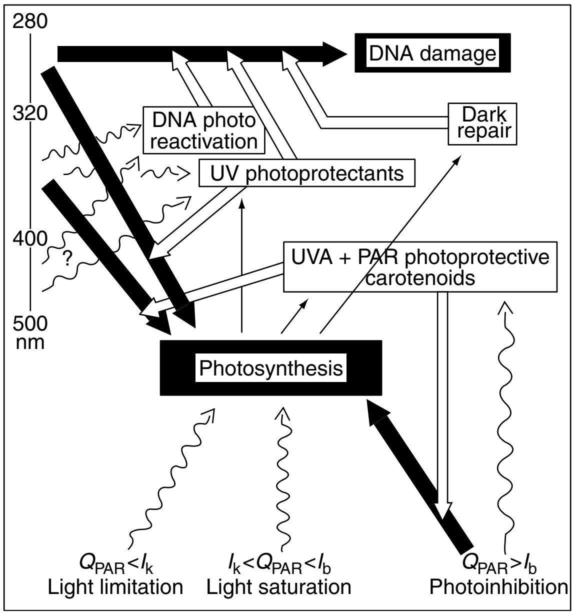


FIGURE 19.6 A working model of photoregulatory interaction of Q_{UVB}, Q_{UVA}, and Q_{PAR} productivity and DNA integrity for phytoplankton communities in the Antarctic Marginal Ice Zone. I_k is the saturation parameter for photosynthesis, and I_b is the photoinhibition onset parameter. Shaded arrow, known direct photoinhibitory effects on phytoplankton viability. Open arrow, known processes that diminish the photoinhibitory effects of Q_{UVB}, Q_{UVA} and Q_{PAR}. Wavy arrow: known light-mediated processes that regulate biosynthetic rates. Straight arrow: known biosynthetic processes that regulate photoprotective processes. Question mark: hypothesized pathways of photoregulation consistent with the database of the cruise in the Bellinghausen Sea in the austral spring of 1990. (Reprinted by permission from Smith, R.C., Prézelin, B.B., Baker, K.S., Bidigare, R.R., Boucher, N.P., Coley, T., Karentz, D., Macintyre, S., Matlick, H.A., Menzies, D., Ondrusek, M., Wan, Z., Waters, K. J., *Science*, 255, 964, 1992. With permission.)

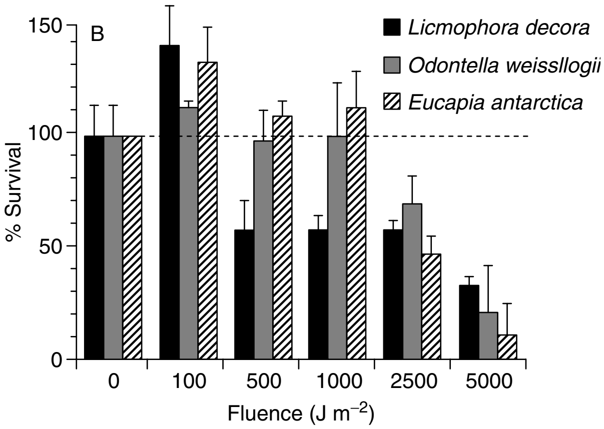


FIGURE 19.5 Increase in cell division (represented by percent survival) of phytoplankton after UV radiation. (From Karentz, D., *Radiation in Antarctica: Measurements and Biological Effects*, Weller, C.S., Penhale, P.A., Eds., American Geophysical Union, Washington, DC, 98, 1994. With permission.)

Smith et al. (1992) depict a working model of the effects of Q_{UVB}, Q_{UVA}, and Q_{PAR} on primary production and DNA integrity for phytoplankton communities in the MIZ (Figure 19.6). In this model Q_{UVB}, Q_{UVA} and Q_{PAR} act differentially to damage DNA integrity and photosynthetic processes. The rate of cell damage by these light-dependent processes may be offset by the rate of UV-A+PAR-dependent photoreactivation, UV absorption by photoreactivation, UV absorption by photoprotective MAAs, high irradiance PAR induction of photoprotective carotenoids, and light-independent ("dark") DNA repair processes. In this model, the differing UV-B exposure-to-response curve for surface and subsurface samples is consistent with the hypothesis that the remediation of UV-B damage to cell vitality is initiated through UV-A, but not UV-B, photoreceptors. The model is consistent with the hypothesis that the ratio of Q_{UVB}:Q_{UVA}, that of Q_{UVB}:Q_{PAR}, or both are critical determinants of the susceptibility of Antarctic phytoplankton to O_3 depletion.

The high-light and high-nutrient waters of the MIZ support between 15 and 75% of the phytoplankton production in the Southern Ocean (Smith and Nelson 1986). Mixed depths during MIZ blooms may be 20 m or less. UV-B may penetrate to depths in excess of 50 m in Antarctic waters (Karentz and Lutz 1990; Smith et al. 1992) and are reported to reduce survival in the upper 10 m (Karentz 1989) and photosynthesis in the upper 10–15 m (Holm-Hansen et al. 1989). Smith et al. (1992) found that ozone depletion resulted in inhibition of integrated water column photosynthesis by at least 6–12%. Thus the elevated UV-B irradiances resulting from the springtime ozone depletion and the subsequent breakup of the polar vortex coincide with the phytoplankton blooms in the ice and MIZ zone.

Other estimates of inhibition of primary production by near-surface UV-B irradiance range from 15 to 30%, while UV-A could result in a further decline of around 50% (Holm-Hansen et al. 1989; Hebling et al. 1995; Davidson and Marchant 1994). These estimates contrast with those of Holm-Hansen et al. (1992) and Hebling et al. (1992). In an investigation off Anvers Island, Hebling et al. (1995) found that under normal ozone column concentrations of 300–350 DU phytoplankton photosynthesis in the upper 20 m decreased by as much as 8.2% due to UV-B radiation (280–232 nm) while the shorter wavelengths (320–360 nm) of UV-A radiation decreased carbon uptake by 10.3%. Under an extreme ozone hole (150 DU), an additional 6.4% carbon loss in the upper 20 m would be expected because of enhanced UV-B radiation. However, if one takes into account the magnitude of ozone depletion, losses in primary production due to enhanced UV-B radiation over the whole Southern Ocean were estimated to be less than 0.15% for the entire year.

Holm-Hansen et al. (1997) investigated the impact of ultraviolet radiation on primary production at Palmer Station. They found considerable variability in the biological response at any specific UV-B irradiance. This was thought to be primarily due to (1) changes in the species composition of the phytoplankton assemblages, which showed large changes in relative numbers of diatoms, small flagellates and cryptophytes during the three-month study; and (2) variability in the photoadaptional state of phytoplankton. UV-A radiation was responsible for approximately twice as much inhibition of photosynthesis as that resulting from UV-B radiation. No inhibition by either UV-B or UV-A could be detected below 10–12 m in a water column where the euphotic zone extended to approximately 50 m. These studies conducted under the deepest ozone hole lend support to the views previously expressed (Holm-Hansen et al. 1993) that the enhanced UV-B radiation resulting from seasonal ozone depletion will not have dramatic impacts on seasonal primary production of the Southern Ocean ecosystem.

Arrigo (1994) developed a numerical model to assess the impact of decreased O_3 concentrations over the Southern Ocean on phytoplankton production. The model included components describing: (1) atmospheric spectral radiation (280–700 nm) as a function of time and latitude; (2) in water bioptics: and (3) primary production as determined by the depth-dependent spectral distribution of ambient irradiance and the action spectrum for photosynthesis. Model results showed that in early spring a 50% reduction in stratospheric O_3 enhanced the integrated production within the euphotic zone by approximately 9% at lat. 75°S and 0.5% at lat. 50°S due to increased transmission of photosynthetically usable radiation, PUR (400–700 nm). Later, as solar angles decreased, UV inhibition overcame PUR-induced enhancement, and integrated phytoplankton production was inhibited by less than 1.0%. By integrating the effect of increasing UV radiation throughout the light cycle and down to the base of the euphotic zone, one finds that the computed deleterious effect of added UV-B is reduced to less than 1.0%. It was concluded that increased transmission of UV-B beneath the ozone hole would result in only a slight incremental increase in UV inhibition of depth-integrated phytoplankton production over what naturally occurs.

Estimates of primary production declines due to UV radiation impacts should be viewed in the context of an estimated interannual variation of around 25% in primary production in the MIZ (Smith et al. 1992).

19.4.2.1 Importance of Vertical Mixing

A number of studies have addressed the role of vertical mixing in the susceptability of Antarctic phytoplankton to UV radiation (Smith and Baker 1982; Cullen and Lesser 1991; Helbling et al. 1994; Neale et al. 1998; Bracher and Wiencke 2000). Helbling et al. (1994) found that the typical characteristics of the upper water column play an important role in explaining the variability of Antarctic primary production attributable to UVR. Cullen and Lesser (1991) have demonstrated that for equal doses of UV-B, short exposures to high irradiance are more damaging than longer exposures to lower irradiance. Consequently, in a rapidly mixing water column, UVR damage to phytoplankton that are approaching the surface may be particularly acute. In their investigations Heibling et al. (1994) found that under some conditions, photosynthetic rates of Antarctic phytoplankton are not significantly affected by solar radiation. In a shallow and stable upper mixed layer (UML), phytoplankton apparently have the capacity to acclimate to changed light conditions by MAA synthesis and repair cycles. When there is very weak stratification, which is often the case in Antarctic waters (Mitchell et al. 1991), phytoplankton will generally be mixed vertically to sufficient depths so that the mean irradiance experienced by the cells is relatively low. The latter may severely limit the extent to which they can adapt. Under such conditions, it can be expected that phytoplankton will not be able to maximize their resistance to UVR and hence will remain vulnerable to high fluorescences of solar radiation should they be returned to surface waters.

19.4.2.2 Changes in Species Composition

There has been considerable interest and also controversy as to whether UVR could result in a change in the species composition of the phytoplankton community. Different phytoplankton species vary widely in their tolerance to UV radiation. For example, the colonial species *Phaeocystis antarctica* has high concentrations of UV-B absorbing compounds while in the motile stage of this alga, many Antarctic diatoms and flagellates either lack or have low levels of UV-B absorbing compounds (Cullen and Lesser 1991; Karentz et al. 1991; Marchant and Davidson 1991; Helbling et al. 1992; 1994; Davidson and Marchnat 1994; Holm-Hansen et al. 1997; Marchant 1997; Karentz 2003). It is therefore possible that this differential susceptibility could lead to a change in species composition of the phytoplankton community.

Vernet et al. (1994) consider that taxonomic composition appears to be one of the most important factors in controlling UV absorption in Antarctic phytoplankton and, ultimately, in influencing photosynthetic inhibition by UV radiation. They compared the capacity for UV radiation absorption in *Phaeocystis*, diatoms and cryptomonads. Cryptomonads had a high alloxanthin content associated with low UV-specific absorption. This suggests that they synthesize less UV-absorbing compounds than prymesiophytes. The authors considered that their apparent inability to synthesize or accumulate UV-absorbing compounds and/or their small size could make this group highly sensitive to UV radiation. Cryptomonads have a widespread distribution in Antarctic waters in late spring and early summer (Jacques and Panouse 1991; Buma et al. 1992). The hypothesis was advanced that cryptomonads' increased susceptibility to UV photodamage-could have consequences for ecosystem structure (species diversity), phytoplankton succession and trophodynamics (Worrest et al. 1981).

Marchant and Davidson (1991) advanced the hypothesis that because of their ability to manufacture UV-absorbing compounds and repair DNA damage, diatoms could be favoured and could dominate phytoplankton assemblages. However, they also stated, "The consequent changes in phytoplankton species composition may be sufficiently slow or slight that they are indiscernible from spatial and interannual variability." In subsequent publications (Davidson and Marchant 1994; Davidson et al. 1994), they suggested that there was little direct evidence of changes in phytoplankton species composition in the Southern Ocean and that changes as a result of UV-B induced mortality are unlikely.

McMinn et al. (1997) examined high-resolution, unbioturbated sediments from the fjords of the Vestfold Hills in East Antarctica. Diatom assemblages from these sediments reflect the diatom component of the phytoplankton and the sea-ice microalgae assemblages at the time of deposition. Twenty-year records from these sequences show no consistent record of changes in species composition, diversity or species richness. Six-hundred-year records from the same area show changes in species abundance greater than those shown in the last 20 years. McMinn et al. concluded that recent changes in diatom abundance generally fall within the limits of natural variability and that there is little evidence of recent changes that might be associated with UV-B-induced change.

19.4.3 SEA-ICE MICROALGAE

Sea-ice microalgae are important primary producers in the sea-ice zone. It has been estimated that they contribute 12% of the total annual primary production in the Southern Ocean (Garrison et al. 1987). They also are an important source of algae to "seed" the phytoplankton blooms of the Marginal Ice Zone.

The transmission of solar radiation through sea ice has been extensively studied, although the scope of most of these studies has been to observations about photosynthetically available radiation (PAR) (e.g., Palmisano et al. 1987; Buckley and Trodahl 1990). Buckley and Trodahl (1990) reported that sea ice is most transparent in early spring. The transmission decreases as summer comes due to absorption by the algae and the development of brine pockets and other inclusions as the sea ice warms. They give ice transmissions at 630 nm where algal absorption is weak so that the transmission here shows the effects of brine inclusions and other defects, and at 300 nm, where the algal absorption is strong. The transmission at 630 nm has a value of about 2% in late October, falling to 1% by mid-November, and thereafter more rapidly. Transmissions of up to 5% at 350 nm have been observed, and transmissions of up to 10% have been observed early in the 1990 season. Because of the continuing decline in the ice transmission throughout the summer, bottom ice microalgae have always experienced their greatest radiation in the spring.

There have been a limited number of investigations of the impact of UV radiation on sea-ice microalgae (El Sayed et al. 1989; Ryan and Beaglehole 1994). The sea ice diffuses the radiation falling onto the ice surface so that the sea-ice microalgae, especially those in the bottom ice, are not subjected to the level of radiation that phytoplankton in the surface layers of the open ocean are. Observations by Ryan and Beaglehole (1994) indicated that the intensity of the UV-B radiation reaching the sea-ice surface during the Antarctic spring was roughly doubled as a result of the ozone hole in the spring of 1990. The maximum spring transmission occurred in the early spring, reaching 10% on clear ice, but by November it was more typically a few tenths of 1%. As can be seen from Figure 19.6, there was no linear relationship between increasing UV-A radiation and photosynthetic response; a significant regression could not be fitted to the data. Ryan and Beaglehole's laboratory and field investigations collectively suggested that the present levels of elevated UV-B due to springtime ozone depletion will have little effect on the bottom sea-ice microalgae, particularly when taken in conjunction with the reducing seasonal variations in the sea-ice transmission.

To date, there have been no reported investigations of the impact of UV radiation on the other components of the sea-ice microbial community—namely, bacteria, protozoa, and invertebrates.

19.4.4 MACROALGAE

In the last decade in particular some detailed investigations have been carried out of Antarctic macroalgae in relation to UV radiation, especially by Hoyer and her coworkers (Bischof et al. 1998; Karsten et al. 1998; Hoyer et al. 2001, 2002, 2003; Hoyer 2003). It was commonly known that algae possessed UV-absorbing compounds (MMAs), mycosporine-like amino acids. However, it is only recently that investigations on their occurrence in Antarctic macroalgae have been carried out. To date seven MMAs (palythine, Porphyra-334, shinorine, mycosporine-glycine, palythene, asterina-330, and palythinol) have been identified in Antarctic macroalgae (Karentz et al. 1991, 1994; Hoyer et al. 2003). All of these MMAs had previously been reported from marine organisms in temperate and tropical latitudes. In Antarctic macroalgae, as elsewhere, MMAs are most abundant in red algae (Rhodophyta). Shinorine is the dominant MMA compound identified from Antarctic red algae. Some species (e.g., *Palmeria decipiens*) possess the full complement of seven MMAs. Red algae with fleshy thalli have a minimum of five MMAs. The crustose calcareous red algae, e.g., *Lithothamnion* sp., had only two MMAs and the lowest total concentration. Absorption spectra of two red algae, *Plocamium* sp. and *Plumariopsis peninularis*, have distinct UV-absorbing features (Figure 19.7). Both species contain shinotine and porphyra-334. *P. peninularis* has a unique spectrophotometric signature in the UV-B region. MMAs are not commonly reported from green algae (Chlorophyta). However, mycosporine-glycine has been found in the subtidal siphonaceous chlorophyte *Lambia antarctica*. Intertidal blue-green algal mats of *Ulothrix* sp. and *Urospora* sp. contain four MMAs but in low concentrations. Two brown algal species (Phaeophyta), *Desmarestia menziesii* and *Adenocystis utricularis* contain small amounts of MMAs.

19.4.4.1 Induction of MMAs in Antarctic Macroalgae

Hoyer et al. (2002) investigated the formation of MMAs in 18 species of Antarctic red algae. Although 8 out of the 18 species showed an induction of MMA formation and accumulation, the remaining 10, mainly deep water species, did not exhibit any traces of MMAs. The eight species that formed MMAs varied considerably in their response to different radiation treatments, indicating that induction, formation and accumulation were the main functions of a very flexible and species-specific mechanism.

19.4.4.2 Temperature and Radiation

Hoyer et al. (2003) investigated the combined effects of temperature and radiation on the macroalgal species *Iridaea cordata, P. decipiens, Prasiola crispa*, *P. antarctica* and *Palmaria palmata*. They found that temperature (5 and 10°C) alone had no effect on MMA occurrence. However, the interaction between temperature and different radiation treatments resulted in significantly higher MMA concentrations at 5°C than at 10°C in both Antarctic red algal species. The authors concluded, "Taking into consideration that UVR affects the depth distribution of algae (Bischof et al. 1998), red algal species tested here will probably survive if global change phenomena become worse, mainly by inhabiting deeper areas where the UVR is more attenuated."

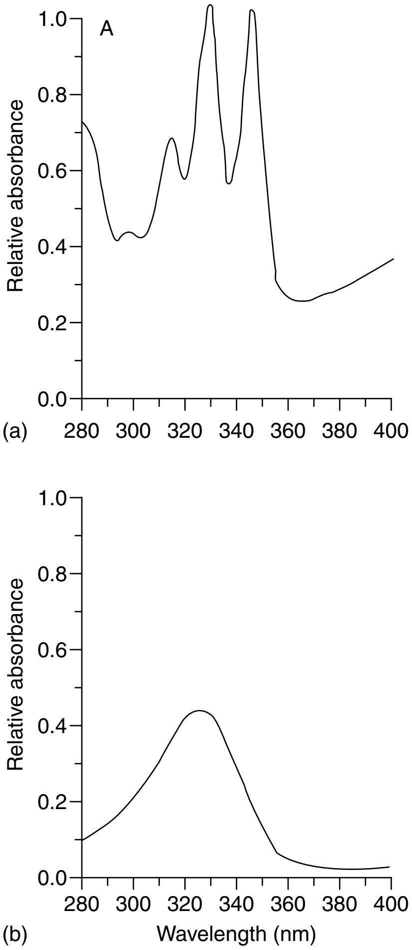


FIGURE 19.7 Spectrophotometric scans of UV wavelengths for methanol extracts of (a) *Plumariopsis peninularis* and (b) *Plocamium* sp. (From Karentz, D., *Radiation in Antarctica: Measurements and Biological Effects*, Weller, C.S., Penhale, P.A., Eds., American Geophysical Union, Washington, DC, 103, 1994. With permission.)

19.4.4.3 Depth Distribution

A number of studies (Karsten et al. 1998, 1999; Hoyer et al. 2001; Hoyer 2003) have shown that a decrease in MAA concentrations and contents of UV-absorbing compounds is coupled with increasing algal depth. This has been shown in transplant experiments in which algal samples were transferred from deep to shallow water and exposed to different solar radiation conditions. Changes in the concentrations of MMAs with changing depth is illustrated in Figure 19.8 for the algal species *I. cordata* and *P. decipiens*.

19.4.5 INVERTEBRATES

Over 50 species of Antarctic marine invertebrates have been surveyed for the presence of MMAs (Karentz et al. 1991; McClintock and Karentz 1997). Nearly 90% contained MMAs and eight specific MMA compounds have been identified (Table 19.1). Seven of these are identical to those found in Antarctic macroalgae (platythine, porphyra-334, shinorine, mycosporine-glycine, playthene, asterina-330 and palythinol) and are common in marine organisms in other parts of the world. An eighth MMA, mycosporine–glycine–valine, was found in the majority of the organisms examined. This MMA has not been reported in organisms from other latitudes and has not been detected in Antarctic macroalgae. Different concentrations of MMAs are found in different tissues such as skin, digestive glands, ovaries and spawn of sea urchins and molluscs (Karentz et al. 1991, 1992). In the Antarctic limpet *Nacella concinna* two MMAs, shinorine and porphyra-334, were found; consistent differences were noted in the various tissues. Additionally, a trend of decreasing MMA concentrations with depth has been found. Animals exposed to higher fluorescences of UV radiation in shallow intertidal areas had higher concentrations of MMAs than organisms collected from deeper areas.

Heterotrophic organisms cannot manufacture MMAs, so they must take up the MMAs in their diet, either as MMA enriched algae or particles (Newman et al. 2000). Newman et al. (2000) demonstrated that Antarctic krill (*Euphausia superba*) obtained a MMA from the phytoplankton that it consumed. How the reabsorption from the diet and the inclusion of individual MMAs in epiderma tissues actually function is the subject of further investigation (Shick et al. 2000).

Some have speculated that enhanced UV radiation may have an impact on krill stocks (Molloy et al. 1997). Newman et al. (1999) investigated the susceptibility of krill (*E. superba*) to UV radiation. Levels of PAR 3–5 times below surface irradiance caused krill to die within a week, while animals kept in the dark survived (Figure 19.8). The addition of UV-B typical of depths up to 15 m were found to significantly accelerate mortality and led to a drop in activity in all experiments (Figure 19.9). Further research is needed to determine whether increased UV radiation will lead to a decline in krill populations. Jarman et al. (1999) determined the base composition percentage of guanine–cytosine base pairs (GC%) of total DNA from *E. superba* to be 32% ?? 0.5%. This is the lowest GC% recorded for a metazoan. Low GC% DNA has high concentrations of thymine (T) residues and consequently a greater abundance of adjacent T residues [T(*n*)] arrays. Ultraviolet B (280–320 nm, UV-B) radiation damages DNA primarily at T(*n*) arrays. It is suggested that krill DNA may be more susceptible to damage from increased levels of UV-B radiation over the Southern Ocean than other Antarctic organisms. Molloy et al. (1997) investigated DNA repair mechanisms in *E. superba*. *E. superba* was found to have a higher activity for a specific DNA repair mechanism than four fish species from the same environment.

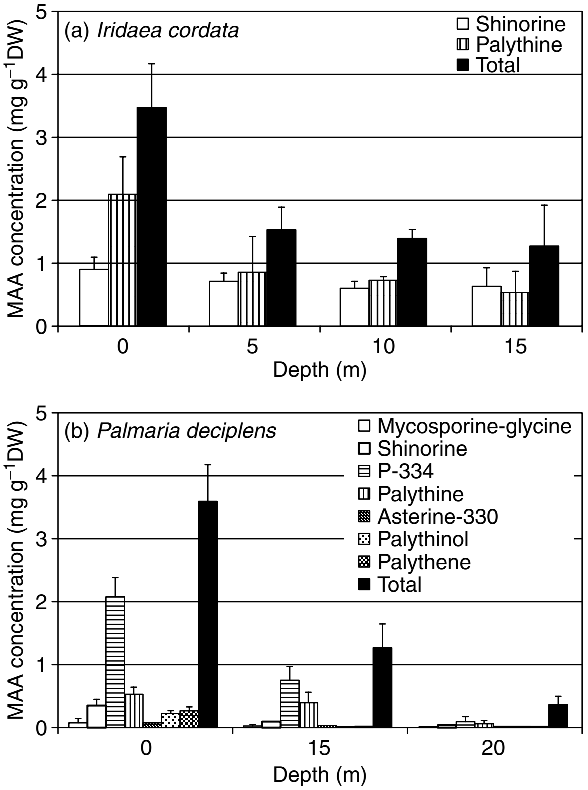


FIGURE 19.8 (a) *Iridaea cordata*. (b) *Palmaria decipiens*. Effect of increasing collection depth on concentrations of individual MAAs. Means ± SD ($n = 3$). (From Hoyer, V., Karsten, U., Sewell, T., Wiencke, C., *Marine Ecology Progress Series*, 211, 124, 2001. With permission.)

Obermüller et al. (2003) investigated the effects of UV radiation on oxidative stress parameters in the Antarctic gammarid amphipods *Gondogeneia antarctica* and *Djerboa furcipes*, and the role of UV-absorbing mycosporine-like amino acids (MMAs) in their diet. The animals were exposed to artificial UV-B light for up to four weeks. Mortality increased to roughly 10% of exposed amphipods under moderate UV-B dose (42–54% of the shallow water in situ dose), i.e., 21–27% of natural atmospheric dose over exposure time, and to a maximum of 28% under high UV-B exposure (50–93% increase of shallow water in situ dose), i.e., 75–97% of natural atmospheric dose over the exposure time. No significant difference between fed and unfed animals could be detected. Batch uptake of MMAs from algal food was not increased under experimental high dose UV-B exposure.

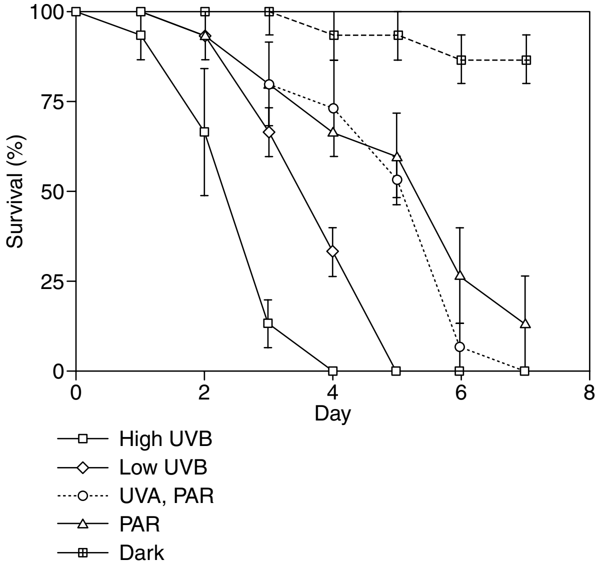


FIGURE 19.9 Mean % survival (±standard error) of krill under different light treatments. (From Newman, S. J., Nicol, S., Ritz, D., Marchant, H., *Polar Biology*, 22(1), 53, 1999. With permission.)

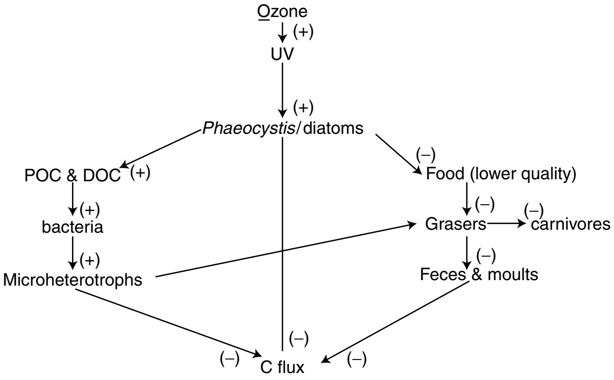


FIGURE 19.10 Potential impact of ozone depletion on the Ross Sea region marine pelagic ecosystem. The signs + or −, on arrows indicate the direction of possible changes. (Reprinted from Marchant, H.T. and Davidson, A.T., in *Proceedings of the International Conference on the Role of Polar Regions in Global Climate Change*, Weller, G., Wilson, C.L., and Severin, B.A.B., Eds., Geophysical Research Institute, Fairbanks, 397, 1991. With permission.)

19.4.6 BENTHIC COMMUNITIES

Little research has been carried out on the impact of UV radiation on benthic communities. Recent research at Palmer Station (Karentz et al. 2004) found that sea urchin embryos suffered DNA damage when exposed to UV radiation and developed abnormally. It is therefore likely that the impact of UV radiation on benthic animals could be greater than was previously thought.

19.4.7 FISH

Many fish species inhabiting the shallow photic zone have UV-absorbing substances like MMAs in their ocular tissues, substances that block transmission of wavelengths less than 400 nm (Shick et al. 2002). They may also acquire MMAs from their diet and tend to accumulate only palythine and asterina-330 via a specific transport mechanism located in their eyes.

19.4.8 MAMMALS

Like birds, seals, and whales are well protected by their outer covering of fur or pigmented skin. Direct UV-B effects on these organisms have not been investigated.

19.5 CONCLUSIONS

Karentz (1994) has considered both the problems involved in assessing the impact of UV radiation and the needs for future research. The following summarizes her conclusions. Although UV radiation as outlined above can have a considerable impact on the survival of many Antarctic species, the effect of ozone depletion on Antarctic ecosystem dynamics is not known at this point in time. What is needed is information on interspecies interactions. Karentz (1994) declares, "At this time the net effect of ozone depletion-related changes on natural populations and communities relative to the balance of the ecosystem cannot be assessed because of insufficient data and lack of appropriate methods." For example, krill productivity estimates have error margins of more than 2 orders of magnitude (Ross and Quentin 1986). This amount of error may be much larger than the potential UV effects.

In addition to the lack of baseline data, there is little information available about the actual UV exposures experienced by Antarctic species (especially the effects of UV exposures on vertically transient organisms or those living under the ice layer). Furthermore, there is essentially no information on the threshold level for tolerance to ambient UV fluorescences. Moreover, neither the range of abilities for UV photoadaptation nor the time course for adaptation has been addressed. The existence of UV tolerance mechanisms in Antarctic species has been addressed, but it remains to be determined how effective they are under the current UV-B levels that are regulated by ozone depletion.

Due to differential susceptibility to damage from UV radiation, it is possible for the species composition of the phytoplankton to change. For example, an increase in the alga *P. antarctica* that contains high concentrations of ultraviolet-radiation-absorbing compounds at the expense of diatoms would have consequent impacts on the trophodynamics of krill and other grazers (Marchant and Davidson 1991) (Figure 19.10). Because the Southern Ocean food web is driven by the annual phytoplankton bloom, changes on the phytoplankton species composition would have a major impact.

20 Global Warming and Antarctic Marine Ecosystems

CONTENTS

20.1 INTRODUCTION

Paleontological records indicate that fluctuations in the concentration of natural "greenhouse" gases such as carbon dioxide (CO_2), methane (CH_2) and nitrous oxide (N_2O) have been closely correlated with the repeated cycling of the Earth's glacial and interglacial periods (Petit et al. 1999; Monmin et al. 2001, and others). Recent increases in the concentration of greenhouse gases have been largely the result of human activities such as the burning of fossil fuels, agriculture, and changes in land use. Since the last industrial revolution, for example, CO_2 concentrations in the atmosphere have increased by 31% (Hoyer et al. 2001).

Scientific and technical assessments of climate change and impacts have been conducted by the Intergovernmental Panel on Climate Change (IPPC), which has published three assessment reports (Houghton et al. 1990a, 1990b, 1992, 1994, 1995, 1996, 2001; IPPC 1990, 1992, 1995a, 1995b, 2001; McCarthy et al. 2001; Metz et al. 2001; Watson et al. 2001). Over the last 140 years, the best estimate is that the global surface temperature has increased by 0.6°C (0.2°C) (Haughton et al. 2001). Based on a number of future scenarios and climate models, projections for future increases in global averaged surface temperatures to 2,100 range between 1.4°C and 5.8°C. The IPPC reports also stated that the temperature increases and their impacts are likely to be greater in the polar regions than elsewhere (Watson et al. 2001).

There is growing evidence that climate warming is occurring and long-term monitoring studies, especially in the terrestrial environment, suggest that recent climate trends are affecting species distributions and phenology (Hughes 2000). There is incomplete data on the impact of this warming on components of the marine environment in the Southern Ocean.

A salient feature of marine ecosystems in the Southern Ocean is their variability. Climate change is likely to accentuate this variability, in particular changes in extreme and episodic events. The following questions need to be addressed when analysing the impact of global warming on the Southern Ocean:

1. What are the important connections between ocean dynamics and biogeochemical cycles for the Southern Ocean?
2. On what time scales do the dominant processes influencing primary production and carbon flux occur?
3. What are the physical conditions regulating spatial variability and Southern Ocean ecosystems, community composition and structure?
4. What is the interannual variability of Southern Ocean carbon flux and what are the factors regulating these fluxes?
5. What changes might occur in the thickness and extent of sea ice?
6. What will the future changes be in primary production and phytoplankton community composition?
7. How will biogenic sedimentation change?
8. What will the future changes be in zooplankton species composition and abundance?
9. How will the distribution and abundance of krill be affected?
10. What impact will changes in the pelagic ecosystem have on the higher predators?
11. What changes might occur in the composition and biomass of the benthic communities?

20.2 THE PHYSICAL ENVIRONMENT

20.2.1 The Role of Antarctica in Global Warming

Our understanding of Antarctica's role in the global climate system has advanced dramatically in recent years as new atmospheric, oceanographic and cryosphere data sets have become available. We now know that ice-albedo feedbacks and radiative processes (mainly related to clouds) are extremely important over the continent and the sea ice zone, as they account for the large inter-annual variability of temperature at high latitudes.

Antarctica is the main heat sink in the Southern Hemisphere and there is a southward flux of heat in response to the radiatively-induced Equator-to-Pole temperature difference. The bulk (80%) of the heat is carried by the atmosphere, with the ocean transporting the remaining 20%. The circumpolar water circulation is central to inhibiting the poleward flux of heat via the ocean, and it plays a critical role in the glaciation of the continent. Ocean eddies are of great importance in the transport of heat and momentum in the Southern Ocean and they play an crucial role in controlling the strength of the Antarctic Circumpolar Current (ACC).

20.2.2 The Semi-Annual Oscillation (SAO) and the El Nino-Southern Oscillation (ENSO)

One of the first indications of high-low latitude coupling was the SAO. This was identified in the mean sea level pressure (MSLP) observations from stations around the coast of the Antarctic Continent, which showed that pressures were at a minimum (maximum) during autumn and spring, summer and winter. This was associated with a southward movement and a deepening of the circumpolar trough, which rings the Antarctic over 60–70° S. The circumpolar trough is present because of the large number of storms in the coastal region, as systems either develop in the strong thermal gradient at the edge of the Antarctic Continent or move south from the mid-latitudes. An SAO is also found in the amount of precipitation in coastal regions.

The ENSO is the largest climate cycle on earth, operating on a time scale of years to decades; variations in the cycle have world-wide implications. During El Nino events, a Rossly wave train becomes established from the central tropical Pacific across the South Pacific to the Bellingshausen Sea. On average, this results in colder, drier conditions over the Antarctic Peninsula, and warmer temperatures and higher levels of precipitation over coastal regions of the Southern Amunsden Sea (Turner 2004). Meridith et al. (1996, 2004) noted a deepened mixed layer and enhanced salinity at the western Antarctic Peninsula in response to increased ice production during the decay of the 1997–1998 ENSO. There is, however, considerable variability in the nature of ENSO events and their impact.

20.2.3 Air, Sea Ice and the Oceanic Thermohaline Circulation System in the Southern Ocean

Figure 20.1 is a schematic showing the dominant interactions between the air/sea/ice/ocean circulation system of the high

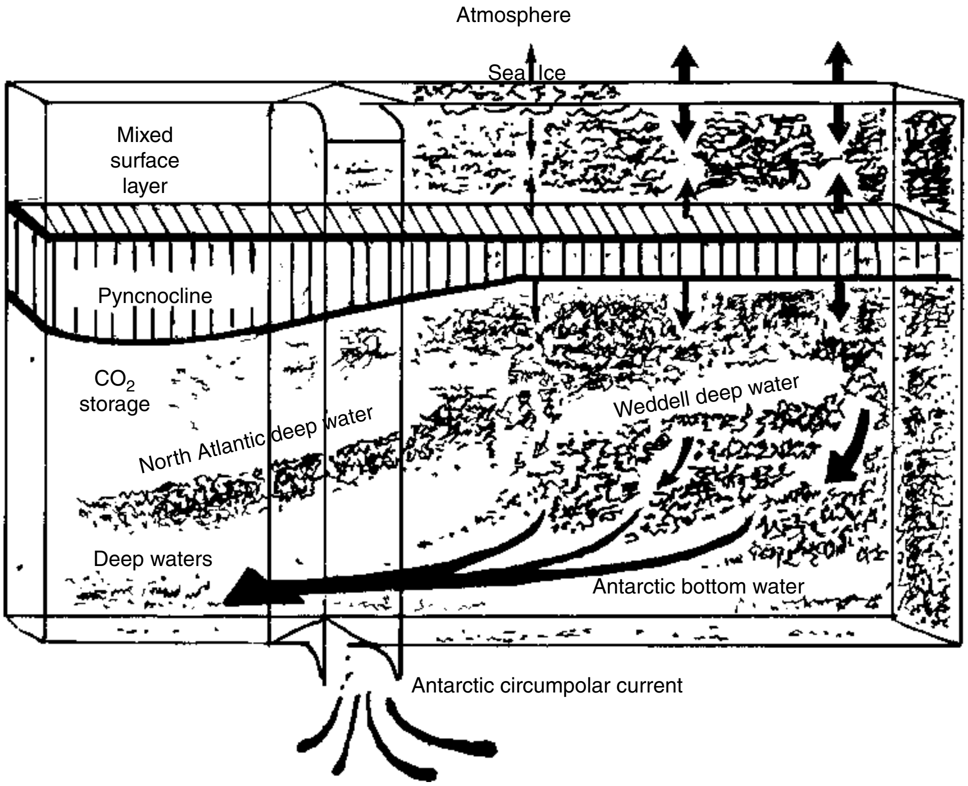


FIGURE 20.1 Diagram showing the dominant interactions between the various components of the air/sea/ice system in the high latitudes of the Atlantic sector of the Southern Ocean. The North Atlantic Deep Water represents both the southward-flowing North Atlantic and the Circumpolar Deep Water, which supply deep water to the Southern Ocean. Also shown is the Antarctic Bottom Water, which flows out of the Southern Ocean into the North Atlantic. The pycnocline represents the steep density gradient separating the colder, fresher surface waters from the significantly warmer and saltier deepwater below. (From Martinson, D.G., *International Conference on the Role of Polar Regions in Global Change*, University of Alaska, Fairbanks, AK, 270, 1990. With permission.)

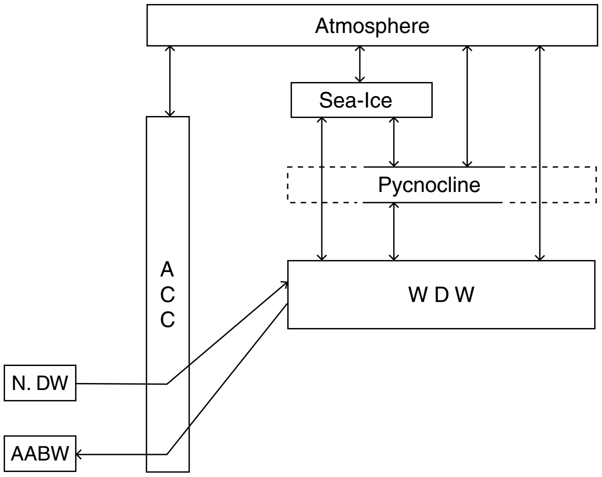


FIGURE 20.2 Overview of the main interactions occurring in Figure 20.1, showing the nature of the air/sea/ice coupling. A change in any component will influence all the other components in the system. (From Martinson, D.G., *International Conference on the Role of Polar Regions in Global Change*, University of Alaska, Fairbanks, AK, 270, 1990. With permission.)

latitudes of the Atlantic sector of the Southern Ocean. South of the ACC; the impact of the sea ice on the ocean-atmosphere exchanges is shown, with an enhanced effect in the open water (polyna) region. The pycnocline represents the steep density gradient separating the colder, fresher surface waters from the significantly warmer and saltier water below. The southward-flowing North Atlantic and Circumpolar deep water (CDW) is diagrammed, as well as the formation of the northward flowing Antarctic bottom water (AABW).

The formation of dense cold AABW close to the continent pays a major role in oceanic circulation, constituting the abyssal layer of the global overturning circulation (Schmitz 1995). It has been hypothesized that changes in the production and/or properties of the AABW could exert a long-term influence on the global climate. The bulk of the AAWB formation requires dense shelf water as a precursor; sea ice formation is a key process, as it increases the salinity of the ocean to raise its density. Consequently, climatically driven changes in sea ice production could play a profound role in altering AABW formation. Similarly, changes in the mass balance of the Antarctic ice sheets could affect the glacial freshwater contribution to the adjacent ocean, again with possible consequences for the production of AABW.

In addition to the AABW, other Southern Ocean water masses key in the global climate system. For example, the Antarctic intermediate water (AAIW) and Subantarctic mode water (SAMW) form important parts of the "upper cell" of the global overturning circulation, and show properties that depend strongly on atmospheric forcings. In addition, these water masses are responsible for around 40% of the total uptake of anthropogenic carbon dioxide and nutrients exported from the Southern Ocean. SAMW has been shown to support around 75% of global export production. It is believed that such mode waters are very susceptible to atmospherically-driven climate changes, and hence are strong markers of the ocean's response to such changes. Furthermore, changing ocean conditions can be important drivers of Antarctic and global climate change. Recent observations indicate that CDW, the most prevalent water mass of the ACC, is warming at a much greater rate than the global ocean as a whole (Gille 2002).

Atmospherically, this region modulates the climate through the strong insulating effect and high albedo of the seasonal ice cover. The sea ice field, however, is intimately coupled to the ocean/atmosphere system, because its temporal and spatial distribution is controlled by the ocean density structure and the atmospheric forcing. This atmospheric forcing is modified by the very presence of sea ice, and the ocean density structure is modified by the growth, decay and drift of the ice, as well as by the atmospheric forcing directly.

This strong feedback loop thus couples the local-, regional- and global-scale processes; this coupling is summarized in Figure 20.2. It assures that a change in any one component of the system will influence all other components. The stability across the pycnocline represents the weak link in the system (Gordon 1981). This coupling thus plays a pivotal role, because a relatively small change in any component will influence the vertical stability, which can force a large system response. For example, an excess growth of $\sim 15\%$ of ice during a winter would in some regions be sufficient to destabilize the water column, resulting in deep convection (Martinson 1990). The associated convective heat flux would eliminate the ice cover and the salt flux would precondition the water column for convection in the following year (Martinson et al. 1981; Motoi et al. 1987). Destabilization may be sensitive, among other things, to eddies or topographic influences.

Thus the main external parameters in the models of the ocean/sea ice system include: (1) the depth of the pycnocline; (2) the ratio of heat to salt through the pycnocline: (3) the strength of the pycnocline; and (4) the magnitude of atmospheric cooling. Assuming global warming, the anticipated changes in these variables suggests that the Southern Ocean may become less stable, leading to reduced ice cover and enhanced deep water ventilation (Martinson 1990).

20.2.4 THE ANTARCTIC ICE SHEETS

The melting of the Antarctic ice sheets would have important implications for Antarctic marine ecosystems. For example, a one-sixth variation in the annual mass gain is equivalent to a 1 mm a^{-1} sea level change. The ice sheet mass balance is the sum of the surface mass balance over the upper surface of the ice sheet, losses in the lower boundary, and discharge at the margin (Drewery and Morris 1992). Drewery and Morris (1992) estimate that the sea level response to a 2°C rise in the mean annual temperature over 40 years would, on a 10- to 100-year time scale, produce a net rise in sea level. However, climate change models are unable to predict the response of the ice sheets to global change scenarios with any degree of accuracy.

20.2.5 CHANGES IN SEA ICE CONCENTRATION AND THICKNESS

Sea ice is a major component of the ice and albedo feedback process that is largely responsible for the projected amplification of global warming in high latitudes. Associated ice growth and decay affect the ocean salinity and density structure and deep-water formation. Ice also isolates the atmosphere from the underlying fluxes in ocean heat and moisture.

Sea ice also plays a central role in the ecology of the Antarctic sea-ice zone. Sea ice microalgal production is a significant component of algal primary production in the Southern Ocean and ice edge algal blooms are a key contributor to the overall primary production. Many species, such as the cryopelagic community, copepods, krill, seabirds, seals and whales, are dependent on the pack and fast ice at various stages of their life cycle. The potential impact of reductions in sea ice concentration will be discussed in detail below.

20.3 EVIDENCE OF GLOBAL WARMING IN THE SOUTHERN OCEAN

20.3.1 INTRODUCTION

There is accumulating evidence that changes that have already occurred as a consequence of global warming and that such changes are accelerating.

20.3.2 AIR TEMPERATURE INCREASE

Comprehensive studies of land surface air temperature variation over the last century indicate a long-term warming trend of approximately 0.5°C or 0.6°C. Jones (1990) combined climatological station data and air temperature records from 26 overwintering stations in the Antarctic Peninsula and Ross Sea sectors of Antarctica to produce a time series of mean annual air temperatures from 1909 to 1987. Jones estimated annual air temperature values for each expedition site as anomalies from the reference period 1957 to 1975. Four of the five Antarctic regions Jones studied exhibited warming trends of at least 2°C over the past century. Jones concluded that the Antarctic is now at least 1°C warmer than it was at the beginning of the twentieth century.

The time series of annual average surface air temperatures (British Antarctic Survey 1998) from 1945 to 1997 shows this warming trend (Figure 20.3). The least-squares regression of the warming trend, which is significant at the 94% confidence level, is due in large part to the high frequency of warm years during the last three decades. Air temperatures at the Faraday Station have been above average for 20 of the 27 years from 1970 to 1996.

20.3.3 SEA TEMPERATURES

There is little evidence of changes in surface sea temperatures. Winter surface sea temperatures at Heard Island appear to have increased by 1°C over the last 50 years (Marchant, personal communication).

20.3.4 COASTAL ICE SHEET DECLINE AND GLACIAL RETREAT AND ADVANCE

Recent years have seen an increasing number of examples of declining ice cap coverage in coastal regions and on islands in particular. Woehler and Bengstrom (2004) have provided information on the decline of ice cover on Heard Island. Temperature records show that air temperatures in all months of the year have increased by approximately 1°C, which has resulted an a rapid increase in the ice-free areas of the island, estimated at 37%. Biotic responses have included the expansion of plant communities into the deglaciated areas and an increase in plant community composition at lower altitudes. Concomitantly, seabird populations have increased (King Penguins, Black-browed and Light-mantled Sooty Albatrosses) or oscillated (Gentoo Penguins and Southern Giant Petrels). Additional breeding areas have been provided for fur seals.

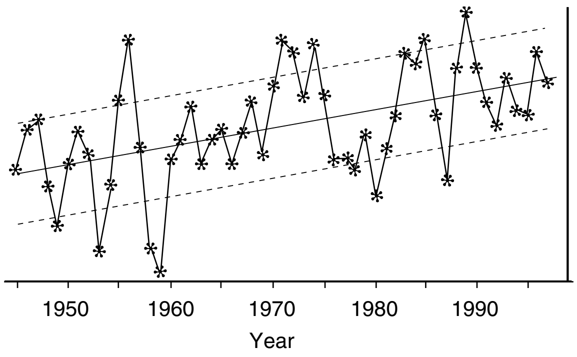


FIGURE 20.3 Faraday Station annual average temperatures, 1945–1997. The solid line is the least-squares regression line with a gradient of 0.050°C yr^{-1}, and the dotted lines indicate standard deviation from this line. The linear regression model using the effective number of independent observations ($n = 12.9$) is significant at the 94% confidence level. Data are from the British Antarctic Survey (1998). (From Smith, R.C., Ainley, D., Baker, K., et al., *Bioscience*, 49, 393, 1999. With permission.)

Cook et al. (2005) have analyzed data on the advance and retreat of 244 glaciers on the Antarctic Peninsula over the past half century (Figure 20.4). Of the glaciers studied, 87% have retreated, and a clear boundary between the mean advance and retreat has migrated progressively southward. They concluded that the pattern was broadly compatible with retreat driven by atmospheric warming, but that the rapidity of the igratin suggested that warming may not be the sole driver of the glacial retreat.

20.3.5 DISINTEGRATION OF ICE SHELVES ON THE ANTARCTIC PENINSULA

Savarka et al. (1999) and Smith et al. (1999) have reviewed the retreat and disintegration of a number of ice shelves on the Antarctic Peninsula. Twenty-six years ago, Mercer (1978) predicted the disintegration of ice shelves along the Antarctic Peninsula in response to global warming trends. Since Mercer's statement, several ice shelves in this region have retreated to some extent, some quite significantly. The Wordie Ice Shelf was the first to suffer major retreat, beginning at the end of the 1980s. It declined by 1300 km^2 between 1966 and 1989 (Doake and Vaughan 1991). Lucchitta and Rosanova (1998) derived and area loss of 993 km^2 from 1974 to 1995 for the northern margin of the George VI Ice Shelf and a decrease of 1.360 km^2 between 1974 and 1995 for the Wilkins Ice Shelf.

However, the most remarkable changes and losses during the last two decades were seen on the Larsen Ice Shelf, the largest ice shelf on the Antarctic Peninsula. Figure 20.5 depicts the losses, which occurred over a 16-year period from 1963 to 1997. Between 1975 and 1986, the edge of the ice shelf retreated about 540 km^2 (Skavarca 1993), and from 1986 to 1997, the retreat totaled another 2,624 km^2 (Rott et al. 1995, 1998). During the same period, the Larsen B Ice Shelf decreased in area by 1,720 km^2. More recently, the Wilkins Ice Shelf has started breaking up. The estimated total decrease in the area of the ice shelves over the period from 1960 to 1975 amounts to about 10,000 km^2. It is anticipated that further losses will occur in the Peninsula area as a consequence of global warming.

Recent research has found that due to the breakup of the ice shelves, nearby glaciers which had been prevented from entering the sea by the ice shelves have begun to flow more quickly. The Hectoria, Green and Evans Glaciers were flowing eight times faster in 2003 than in 2000, while the Jorum and Crame had doubled in speed by early 2003 and had trebled by the end of the year. Although the melting of the ice released by the breakup of the ice shelves would not result in an appreciable rise in sea level, the outflow of the glaciers could cause a rise in the sea level.

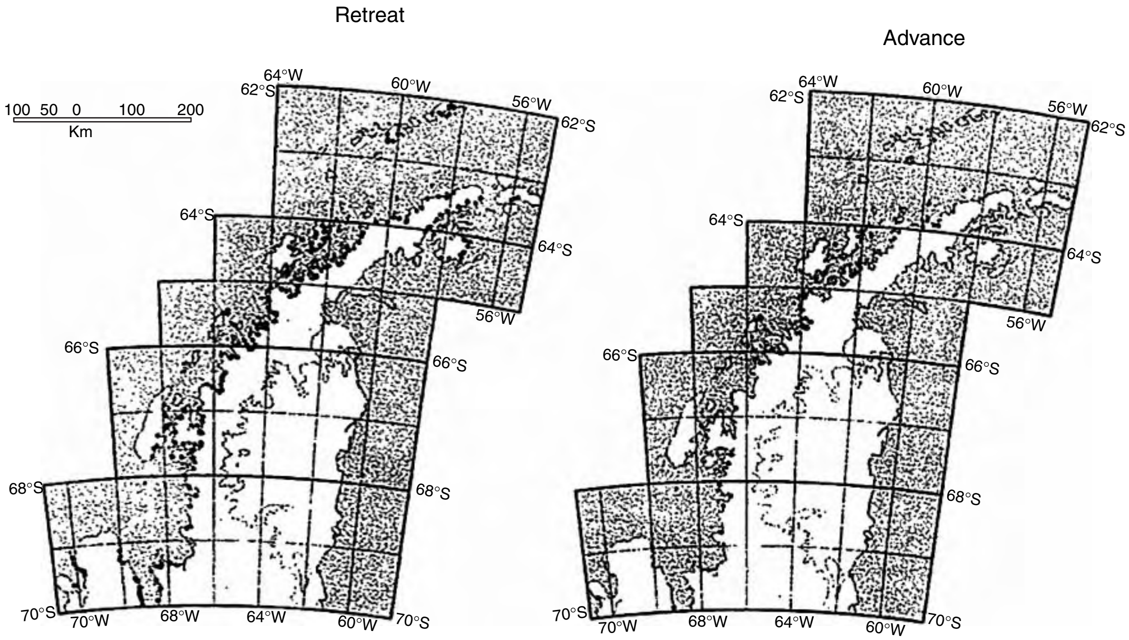


FIGURE 20.4 Overall change observed in Antarctic Peninsula glacier fronts since the earliest records. (From Cook, A.J., Fox, A.J., Vaughan, D.G., Ferringo, J.C., *Science*, 308, 542, 2005. With permission.)

20.3.6 EXTENT AND THICKNESS OF SEA ICE

Because of the considerable interannual and long-term variation in the extent of sea ice coverage, isolating trends due to global warming has proved difficult. Early whaling records suggest a historical reduction in the extent of the sea ice (de la Mare 1997). Whale catches are generally located at the edge of the sea ice. Over the period from 1840 to the late 1980s, catches have progressively moved south, towards the continent (Figure 20.6). However, there is some dispute as to the validity of De La Mare's conclusions (Jaca and Budd 1998).

According to Parkinson (2004), climate model simulations indicate little change in sea ice extent and thickness. This contrasts with the Northern Hemisphere Arctic region, where the sea ice has decreased at approximately 30,000 km^{-2} yr^{-1} over the period from 1972 to 2002 (Deser et al. 2002). Satellite observations have shown that a highly variable Southern Ocean sea ice cover decreased significantly in the 1970s, but overall, it has increased since the late 1970s. However, in the last three years, from 1999 to 2002, sea ice coverage has decreased (Figure 20.7). Interannual variability, however, is quite significant. In addition, a number of studies (Kwock and Comiso 2002; Ackley et al. 2003) have indicated that ice cover is associated with El Nino events.

20.3.7 ULTRAVIOLET RADIATION

As detailed in Chapter 19, greenhouse gas emissions have resulted in increased ultraviolet radiation, with consequent impacts on marine ecosystems. Such impacts are most pronounced in the Antarctic region.

20.3.8 CARBON DIOXIDE

As Karentz (2003) points out, "While changes in temperature will affect physiological rates relative to enzyme kinetics, changes in CO_2 may have an even greater impact on primary producers by regulating the carbon fixation process, and in turn the global carbon cycle" (Smith and Steenkamp 1990; Sarmiento and Le Quere 1996; Beardall et al. 1998; Falkowski and Rosenthal 2002; Falkowski et al. 2000). Under present environmental conditions, the annual production of Antarctic phytoplankton is believed to be limited by he seasonal light regime and possibly nutrients (e.g., iron), not the availability of CO_2 (Priddle et al. 1992). However, there are distinct differences between phylogenetic groups from different geographic areas in the affinity of ribulose-1,5-biphosphate carboxylase-oxygenase (RubiaCO) for carbon dioxide and oxygen (Tortell 2000). Species-specific variation in the thermokinetics of RubiaCO determines if carbon fixation or photorespiration will occur under different conditions of CO_2 concentration and temperature. This provides a further mechanism for the regulation of primary productivity and autotrophic diversity under a changing CO_2 regime and provides a feedback mechanism for CO_2 drawdown.

20.3.9 CHANGES IN KRILL POPULATIONS

Recently, Atkinson et al. (2004) used an extensive data bank covering the summers of 1926–1939 and 1976–2003 to

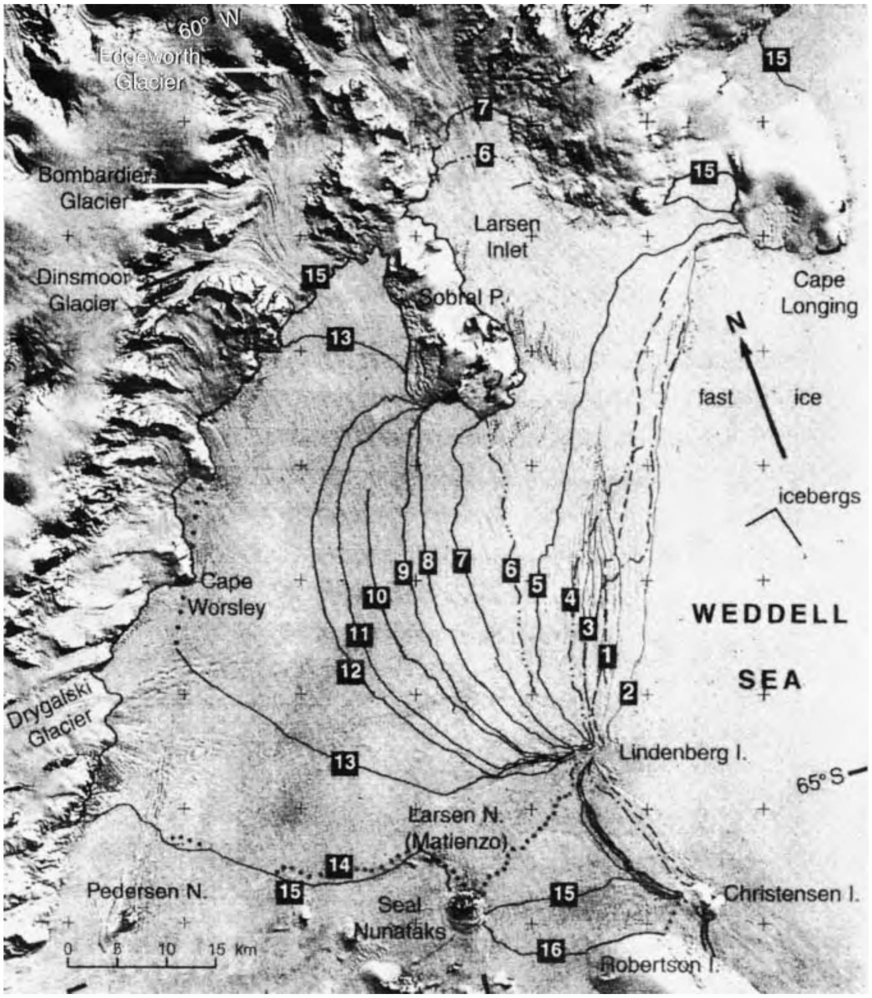


FIGURE 20.5 A time series illustrating the retreat for the Larsen Inlet and the Larsen Ice Shelf in different years. 1: August 30, 1963; 2: October 3, 1978; 4: February 20, 1979; 5: March 1, 1986; 6: November 5, 1989; 7: December 8-January 1993; 9: February 16, 1993; 10: October 23, 1994; 11: January 25, 1995; 12: January 28, 1995; 13: January 30, 1996; 14: March 8, 1995; 15: March 2, 1997. (From Skvarca, P., et al., *Polar Rec.*, 205, 1999. With permission.)

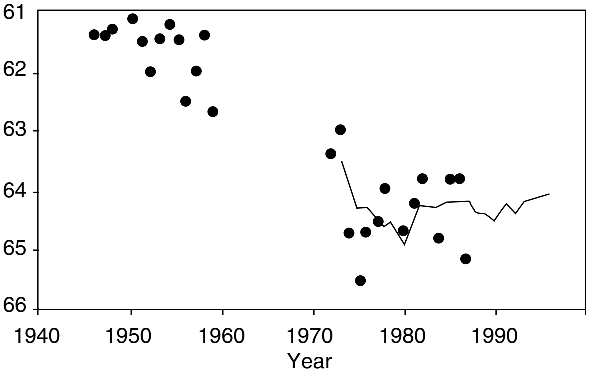


FIGURE 20.6 Mean annual extent of sea ice and whaling records over time. (Data from de la Mare, W.K., *Nature*, 389, 389, 1997.)

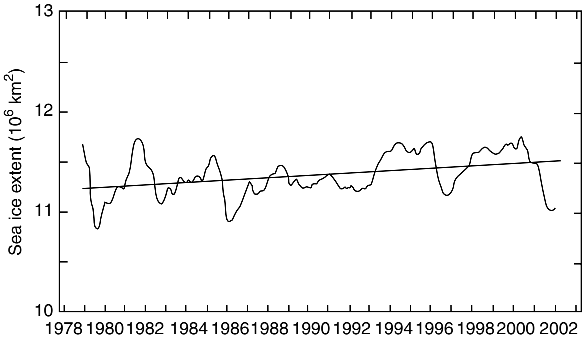


FIGURE 20.7 Annual sea ice extent over the period from 1978 to 2002 as estimated from satellite images.

analyze krill and salp density distributions in the Southwest Atlantic Sector of the Southern Ocean. Their analysis indicated that overall krill densities had declined (Figure 20.8). High densities depend on the summer phytoplankton blooms and extensive sea ice coverage to provide plentiful sea ice microalgal food for adults and larval stages during the winter. Concomitantly with the decline in the krill populations, those of the salps increased dramatically. Salps are small particle feeders, and this decline in population indicated a substantial change in the phytoplankton species composition.

If the krill biomass were to decline or their patterns of distribution were to change, this could have an indirect (flow-on) impact on those species that rely on krill as their principal

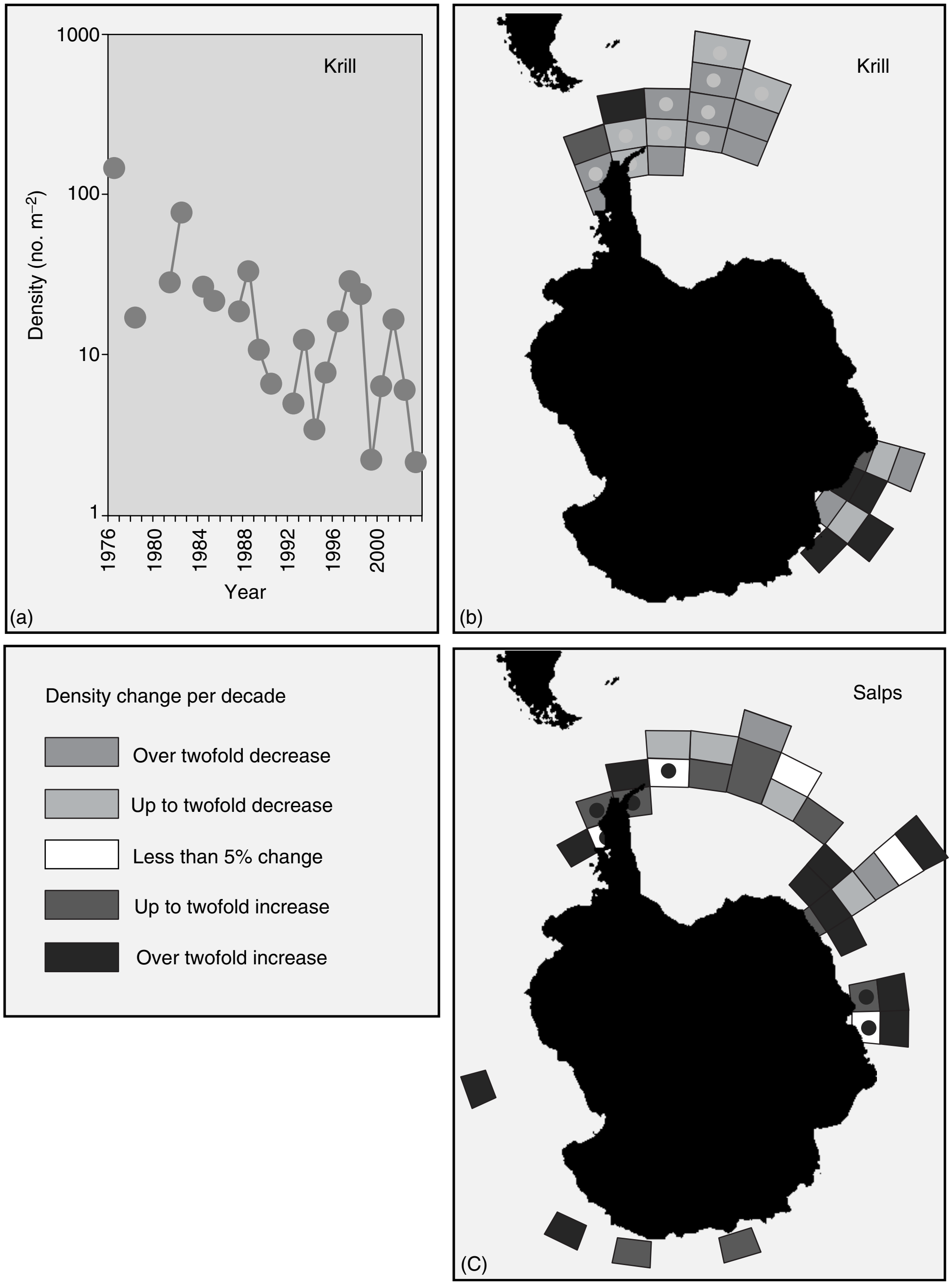


FIGURE 20.8 Temporal change of krill and salps. (a) Krill density in the SW Atlantic sector (4,948 stations in years with more than 50 stations). Temporal trends include (b) post-1976 krill data from scientific trawls; (c) 1926–2003 circumpolar salps data south of the SB. (From Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., *Nature*, 432, 101, 2004. With permission.)

food item, including squid, some fish species, birds (especially penguins), and Ross, Crabeater and Weddell seals. The degree to which these species could switch to alternative food sources is unknown. However, it is clear that, should the possible consequences of global warming occur, those changes could have a considerable impact on the higher consumers in the Antarctic marine ecosystem.

20.3.10 CHANGES IN POPULATIONS OF BIRDS, SEALS, AND WHALES

Changes in seal and whale populations during the past two centuries were caused by human over-exploitation. The populations of both fur seals and whales have increased since this exploitation ceased. Data on bird populations indicate that some populations have been stable over the period for which data is available, while other populations have increased or decreased.

Croxall (1992) has discussed in detail environmental change and its impact on seabird populations. All adequately documented populations of Adélie and chinstrap penguins in the Antarctic Peninsula region increased between the late 1940s and the mid 1970s (Croxall 1992; Smith et al. 1999) (Figure 20.9). In the last decade or so, these Adélie and chinstrap populations have fluctuated without any clear overall trend (Trivelpiece et al. 1990; Fraser et al. 1992; Trivelpiece and Fraser 1996). Antarctic Continent populations of Adélie penguins appear to have been relatively stable. Population declines during the late 1960s in the Ross Sea were followed by substantial increases from the late 1980s (Taylor and Wilson 1990; Taylor et al. 1990; Wilson 1990; Wilson et al. 2001). These increases brought the population levels to three times those of the mid-1960s, followed by fluctuating growth, especially at Cape Royds (Wilson et al. 2002). All Ross Sea colonies changed in a similar manner (Taylor and Wilson 1990). While increasing temperatures may have been a contributing factor in the population increase, sea ice extent and concentration are considered to be the most important factors involved in the populations of Adélie penguins (Wilson et al. 2001).

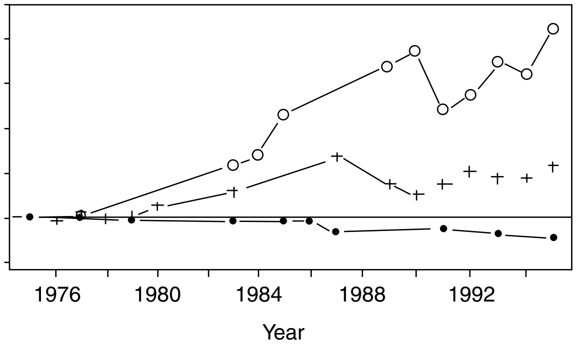


FIGURE 20.9 Twenty-year trends in chinstrap and Adélie penguin populations at Arthur Harbor (Palmer Station). Open symbols, chinstrap penguins; solid symbols, Adélie penguins; crosses, Adélie penguins at Cape Royds, Ross Island. In the west Antarctic Peninsula region, the two species have exhibited opposite trends, with chinstrap penguins increasing over 500% since the mid-1970s and Adélie penguins decreasing by nearly 25%. Trends in Adélie penguin populations at Cape Royds show an increase throughout the 1980s, with roughly stable populations thereafter. (From Smith, R.C., Ainley, D., Baker, K., et al., *Bioscience*, 49, 399, 1999. With permission.)

In the West Antarctic Peninsula region, Adélie penguin populations have been stable or declining, whereas chinstrap penguin breeding populations have increased by several hundred percent (Fraser et al. 1992; Fraser and Patterson 1997; Smith et al. 1999). Adélie penguins are obligate associates of winter pack ice (Ribic and Ainley 1988; Ainley et al. 1994), whereas chinstrap penguins occur almost exclusively in open water (Ainley et al. 1994; Smith et al. 1999). It would appear that in recent years, there has been less winter pack ice and more open water. Figure 20.10 depicts the impact of sea ice extent on the reproductive success of Adélie and Chinstrap penguins at King George Island over the period from 1976 to 1988.

Studies of abandoned rookeries (Emslie et al. 1998) have shown that Adélie penguins have occupied the West Antarctic Peninsula area for at least the past 600 years, whereas the recent population expansion of Chinstrap and Gentoo Penguins southwards along the Peninsula appears to be correlated with regional warming during the past 50 years (Fraser et al. 1992; Trivelpiece and Fraser 1996).

Weimerskirch et al. (2003) discuss evidence that trends in bird and seal populations in the southern Indian Ocean are indicators of a system shift. They highlight changes in air temperatures recorded at seven sites in this sector (Figure 20.11). These temperatures have steadily increased over the past 50 years, at rates ranging from 0.07° to 0.30°C per decade in the mid 1960s and stabilized in the mid 1980s, being particularly important in the Subantarctic sector.

The population abundance of most top predators, except two species, King Penguins and Amsterdam fur seals, started to decline at the end of the 1960s (Figure 20.12). The decrease took place for all species during the 1970s, and for some species continued into the early 1980s. For several species, the decline during the 1970s was followed by a large (Adélie penguins, southern fulmar) or a partial (wandering albatrosses on Crozet and Kerguelen, black-browed albatross at Campbell) recovery of the population, while other species (emperor penguins, elephant seals) did not recover and their populations remained at low levels. Two species, Amsterdam fur seals and king penguins at Crozet and Kerguelen, and showed increases in their numbers at the same time.

The changes in environmental conditions due to global warming have probably produced profound functional consequences in the ecosystem of the southern Indian Ocean, as illustrated by the decline in the concentrations of chlorophyll *a* and zooplankton concentration after the late 1970s (Hunt et al. 2001). This suggests that decreases in food availability at lower trophic levels may underlie the general decrease of top predator populations. This decrease occurred with a lag compared to the increase in temperature. Seabird and sea mammals are long-lived and consequently

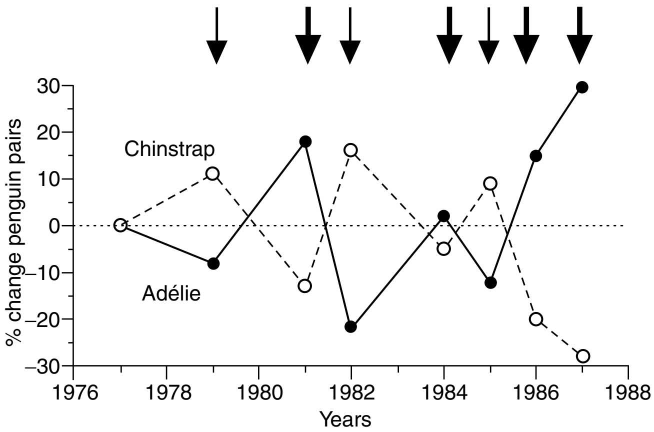


FIGURE 20.10 Effect of sea ice extent on the reproductive success of Adélie (closed circles) and Chinstrap (open circles) Penguins at King George Island. Thickness of the arrows indicates the density of the pack ice during the preceding year. (From Fraser, W.R., Trivelpiece, W.Z., Ainley, D.G., Trivelpiece, S.G., *Polar Biol.*, 11, 50, 1992. With permission.)

factors affecting demographic parameters, such as reproduction or recruitment, could be expected to have a delayed effect on population size (Thompson and Ollason 2001). Because air and sea temperatures have reached a plateau since the mid 1970s and have not returned to their original values, the pattern that occurred in the Indian Ocean is likely to be a regime shift, i.e., a jump from one stable state to another (Scheffer et al. 2001; Weimerskirch et al. 2003).

Population increases were seen for only two species (King penguins and Amsterdam fur seals) during the period of general decline in top-predators and of increase in temperatures. While the species whose populations have decreased are mainly squid eaters, and to a lesser extent crustacean or fish predators (Cherel and Klages 1998), King penguins and Amsterdam fur seals specialize in feeding on myctophid fish (Guinet et al. 1996). Penguin species that have decreased (emperor, Adélie and rockhopper) are principally krill feeders; the krill prey is likely to have declined as a consequence of a decrease in the extent of the sea ice.

Subsequently, Weimerskirch et al. (2004) used the long-time series available on demographic parameters of four Antarctic and Subantarctic seabirds and combined them with long-time series of climatic parameters. The results showed that over the past 40 years, the seabird populations fluctuated with a three- to five-year periodicity that was also detected in environmental factors such as sea ice extent, temperature and the Southern Ocean Oscillation index, suggesting strong environmental forcing on the populations. The system shift that occurred on the late 1970s was also detected. Over the past 50 years, emperor penguins in Terre Adélie have declined by 50% because of a decrease in adult survival during the late 1970s. During that period, there was a prolonged abnormally warm period with reduced sea-ice extent. Mortality rates increased when warm sea-surface temperatures occurred in their foraging area, and when the annual sea-ice extent was reduced. In a population of Blue Petrels (*Halobaena caerulea*) in the Kerguelen Archipelago, 70% of the mortality occurred in the winter and was linked to climatic factors. The strength of the density-dependence was affected by climate, with population crashes occurring when poor conditions coincided with high densities. An exceptionally long-lasting warming caused a ~40% decline in the population.

Overall, the results underlined the strong effects of oceanographic processes on the demography of the seabirds through complex interactions between mortality, density-dependent effects, and their high susceptibility to climate change. There was strong evidence that most of the mortality occurred during the winter months and that it was affected by climate fluctuations.

The results detailed above contrast with those of Nicol and Jouventin (2001), who investigated population trends for seven seabird species at Pointe Geologie (Terre Adélie). Trends from 1985 showed that for the whole archipelago, excluding islands where nesting sites had been destroyed by construction of an airstrip, Adélie Penguins and South Polar skuas were the only species to show a significant decrease (>3.5% annual change). The other species showed opposite trends, three increasing lightly (southern fulmars +0.4%, cape petrels +2.3%, snow petrels +0.9%). Three species particularly affected by the destruction of their breeding habitat (Adélie penguin, cape petrel, snow petrel) showed the capability to restore their populations. Species feeding on krill (Adélie penguins and cape petrels) increased more than the other species. In contrast to other regions where environmental trends have resulted in significant population changes (e.g., Antarctic Peninsula, Fraser et al. 1992; South Orkney Islands, Tratham et al. 1996; Admiralty Bay, King George Island, Fraser et al. 1992; Antarctic Peninsula, Poncet and Poncet 1987; Fraser and Patterson 1997; Ross Sea region, Taylor and Wilson 1990), no apparent trends were detected at Terre Adélie.

Sun et al. (2004) have estimated the historical seal populations at King George Island for the past 1,500 years from seal-hair abundance, bioelement concentration. The total organic carbon (TOC) and total nitrogen (TN) in a

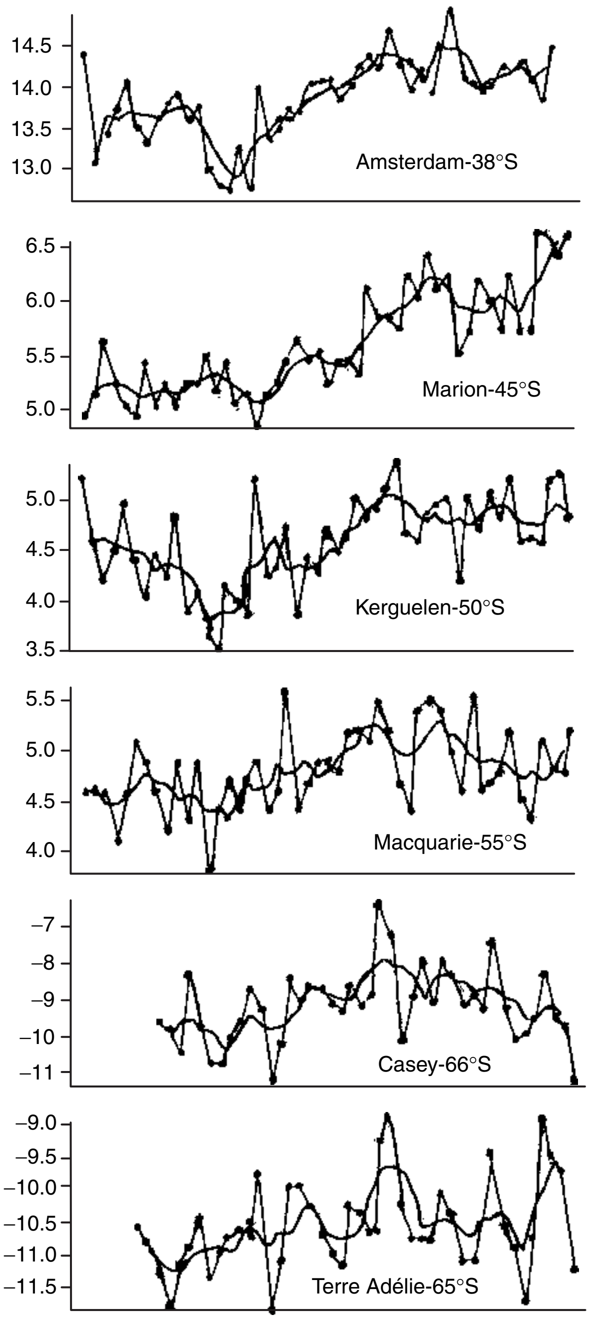


FIGURE 20.11 Changes in the average annual air temperatures at several sites in the Southern Indian Ocean. The points and the thin line indicate average values, and the solid line is the moving average (average over three years). (From Weimerskirch, H., Inchausti, P., Guinet, C., Barbraud, C., *Antarctic Sci.*, 15, 250, 2003. With permission.)

terrestrial sediment sequence are influenced by seal excrement. Prior to human harvesting of the seals, the seal populations exhibited dramatic fluctuations, with two peaks during 760–500 and 1,400–1,100 years before the present and two troughs during 1,100–750 and 500–300 years before the present. A comparison with historical climates suggested that seal populations may be limited by climate-related factors, such as sea ice coverage and atmospheric temperature.

20.4 THE POTENTIAL IMPACT OF GLOBAL WARMING ON ANTARCTIC MARINE ECOSYSTEMS

20.4.1 INTRODUCTION

As detailed above, the impact on Antarctic marine ecosystems of global warming due to the increase which has occurred in greenhouse gas emissions, has already been observed. Although there is considerable uncertainty over the relative magnitude of the different sinks in the global carbon cycle, it is known that approximately half of the anthropogenic CO_2 emitted to the atmosphere rapidly enters other pools and that much of this is taken up by the oceans (IPPC 1992). It is known that the oceans provide a long-term sink for atmospheric CO_2, partly through the production of particulate material in the euphotic zone and its subsequent export to deeper water and the sediments: the so-called “biological pump” (see Longhurst 1991). Current climate models do not accurately depict the role of the Antarctic sea ice zone in future climate change. However, it is agreed that temperature increases will occur. With our increasing knowledge of the functioning of Antarctic marine ecosystems, it is possible to predict how this increase will result in changes to these ecosystems.

20.4.2 STABILITY OF THE ANTARCTIC ICE SHEETS

Climate models predict different scenarios for the West and East Antarctic Ice Sheets (Drewery and Morris 1992). The models predict that atmospheric evaporation will result in increased snowfall over the Antarctic Continent, so that the east Antarctic Ice Sheet will remain stable (Quilty 1992; Simmonds 1992; Malakoff 2002). However, as we have seen, changes are already occurring in West Antarctica and it is possible that the West Antarctic Ice Sheet may disintegrate. This would result in a rise in sea level of up to 4–6 m and a large input of fresh water as the ice melts. This could have a major impact on water column properties, primary production and the zooplankton.

20.4.3 INCREASE IN SEA TEMPERATURES

The temperature of the Antarctic marine environment ranges from $-2°C$ (the temperature at which seawater freezes) to $+2°C$ near the Antarctic Continent and $+3°$ to $+6°C$ around the Subantarctic Islands. There is also little seasonal variation in these temperatures. Many invertebrates and fishes are stenothermal, with their lethal temperatures at the most a few degrees above the ambient temperatures. Members of the microbial community, especially protists and some phytoplankters, are living at temperatures below those required for optimal growth (Vincent 1988). Thus, an increase in sea temperatures would promote the growth of these species.

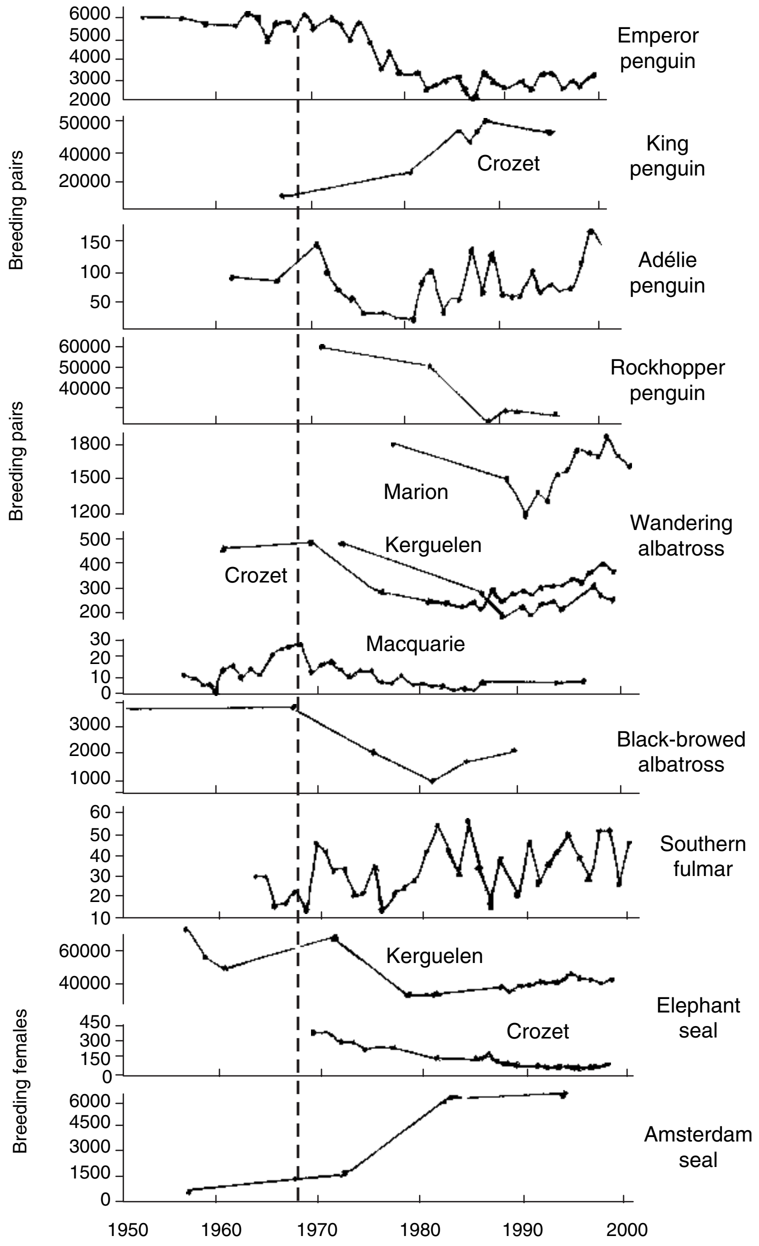


FIGURE 20.12 Changes in the size of population of nine species of seabirds and seals breeding in the Southern Indian Ocean. The dashed line indicates the approximate time when the population changes started to occur. (From Weimerskirch, H., Inchausti, P., Guinet, C., Barbraud, C., *Antarc. Sci.*, 15, 252, 2003. With permission.)

Freezing has been the primary selection pressure shaping the current Antarctic marine biota (Clarke and Crame 1997a; Clarke 1993). Polar temperatures not only limit the availability, viscosity and gas content of the water, but also lower the rate of most enzyme reactions. While for some species the optimum temperature are above ambient levels, for others, a rise of a few degrees would be lethal.

Many stenothermal invertebrates and fishes can survive over a very narrow temperature range. When the temperature of the water is raised to 4°C, the large nemertine worm *Parborlasia corrugatus* suffers a loss of muscle tone and death. Most Antarctic fish, including the cryopelagic species *Pagothenia borchgrevinki*, have an upper lethal limit of 5°C. Davidson and Lowe (2002) and seebacher et al. (2005) found that when this species was acclimated to 4°C for a month, there were major changes in its physiology, such as decreased osmotic pressure of the body fluids and increased swimming performance at high temperatures, even up to 10°C (Figure 20.13). This result suggests that some nototheniids may not be as stenothermal as currently believed, and if given time to acclimate, they may be able to tolerate increases in environmental temperatures.

It is important to note that individual enzymatic processes within an organism can be regulated differently

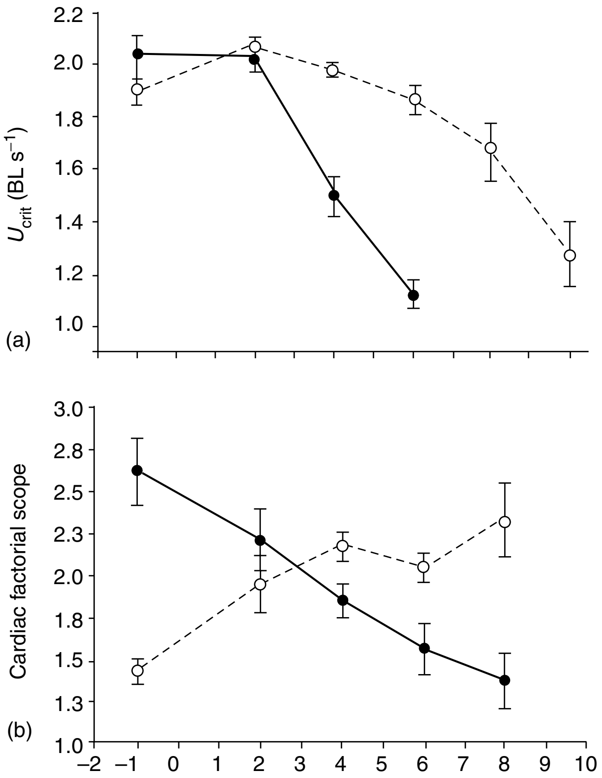


FIGURE 20.13 (a) Sustained aerobic swimming performance (maximal critical swimming speed: U_{CRIT} mean ± s.e.) and (b) factorial cardiac scope (mean ± s.e.) of *Pagothenia borchgrevinki* acclimated to natural temperatures (−1°C; closed circles, solid lines) and to 4°C (open circles, broken lines) for 4–5 weeks. BL, body length. (From Seebacher, F., et al., *Biol. Lett.*, 1, 152, 2005. With permission.)

by temperature. For instance, there is evidence that some physiological processes associated with photosynthesis are uncoupled from temperature, while respiration of fixed carbon increases with temperature (Thomas et al. 1992). Thus the efficiency of carbon assimilation will be affected by temperature change and even small thermal increments could cause some significant shifts in the competitive balance between species and the flux of carbon in the ecosystem (Martinez 1996; Simon et al. 1999).

Additionally, life history stages are differentially affected by changes in temperature. Temperature control of physiology can alter other aspects of reproduction, such as the timing of reproductive events. Temperature can also define limits for the survival of gametes and embryos. Therefore, environmental change that alters reproductive effort could in turn uncouple existing species interactions and restructure reproductive trophic relationships.

The extremes of the Antarctic environment provide a barrier to the import of species from warmer climates, but climate change may ameliorate the present environment and foster the reproductive success and establishment of invading species, possibly at the expense of the current taxa. Thus changes in species distribution patterns are a likely consequence of climate change. *Euphausia superba* lives at temperatures in the range of −2°C to about +5°C. In the Scotia Sea, they are living close to this upper limit. An increase in the water temperature would, most likely, lead to the northern limit of their range moving southwards. An increase in water temperature could make some shelf areas too warm for the present fish species. It is likely that these species would be replaced with other species more tolerant of warmer water. It is also probable the Antarctic Convergence would move southwards, resulting in many species having their distributions extended to the south. Any changes in their prey species composition would impact the higher predators, such as seabirds and seals.

20.4.4 DECREASE AND POSSIBLE DISAPPEARANCE OF THE SEA ICE

One of the most dramatic consequences of global warming could be changes in sea ice concentration and distribution, eventually resulting in its disappearance. If this were to happen, the impact on the community composition and ecosystem dynamics of the Southern Ocean ecosystem would be pronounced.

Sea ice plays a crucial role in the ecology of the Southern Ocean (Martinson 1990). Warmer temperatures will reduce ice, which in turn will promote further warming (Budd 1991). Increased areas of open water at high latitudes modify ocean/atmosphere gas and heat exchange, restructuring local and global atmospheric and oceanic circulation (Bromwich et al. 1998).

The presence of sea ice around Antarctica is, as discussed above, directly involved in the production of AABW. Thus the loss of sea ice would inhibit the pattern of vertical circulation south of the Polar Frontal Zone that produces the high concentration of nutrients (nitrate, phosphate and silicate) characteristic of the Southern Ocean marine ecosystem. Changes in the production of AABW could also affect productive processes further north in the world's oceans.

The ecological impact of sea ice decline could be considerable. Possible impacts include:

1. Reduced sea ice microalgal production; this would reduce or eliminate a major component of primary production in the Southern Ocean.
2. Reduction in the biomass of the sea ice microbial community, thus providing less inoculum to "seed," the bloom of phytoplankton that follows the decay and melting of the sea ice.
3. Decrease and possible elimination of food sources for the cryopelagic community.
4. Elimination of habitat for those copepod species associated with the sea ice at some stage of their life cycle.
5. Reduction or elimination of a food source (sea ice microalgae) for adult krill during the breakup of

the sea ice and for larval krill during the winter (Brierly et al. 1999).

6. Reduction in the marginal sea ice zone phytoplankton blooms, which are a major contributor to overall primary productivity in the Southern Ocean.
7. A decrease in sea ice would permit more light to enter the water column, which could promote phytoplankton growth.
8. In inshore waters, the decline or disappearance of the sea ice would allow more light to penetrate the water column leading, to enhanced growth of benthic microalge and macroalgae with consequent impacts on the benthic community.
9. The lessening of the sea ice cover would lead to increased exposure of the primary producers, invertebrate and vertebrate, to UV radiation. The impact of this increased UV radiation would depend on the degree to which individual species have developed UV-B absorbing compounds (Marchant et al. 1991).
10. Any diminution in the amount of sea ice would represent a change in the habitat for those species that utilize it (Croxall 1992) (see Chapter 4, Section 9 below).

20.4.5 Potential Impact of a Decline in Sea Ice Cover on Phytoplankton Production

Antarctic sea ice cover was predicted to shrink by 25% over the next 100 years in a Global Climate Model in which atmospheric CO_2 was increased by 1% per year. If this were to occur, the relative sizes of the POOZ, the MIZ and the SIZ would shift. This would have an impact on phytoplankton primary production.

Arrigo and Thomas (2004) have estimated the changes that occur in primary production with 50% and 5% of the current sea ice cover (Figure 20.14). With 50% of the current sea ice cover, sea ice algal production would decrease from 43 to 6 Tg C yr^{-1}, and production in the MIZ would decrease from 409 to 250 Tg C yr^{-1}. On the other hand, production on the open ocean would increase by ~28%, from 3,919 to 5,012 Tg C yr^{-1}. The net gain in production resulting from a 50% loss of the sea ice cover would be ~900 Tg C yr^{-1}, an increase of 25%. Thus an expected 25% loss of sea ice cover over the next century would increase primary production in the Southern Ocean by approximately 10%, resulting in a slight negative feedback on global warming. A number of factors could modify these estimates, including: (1) changes in the species composition of the phytoplankton community; (2) a reduction in the seeding of the water column upon melting of the sea ice; and (3) a reduction in the concentration of iron in the surface waters causing a decline in phytoplankton production. Iron accumulates in the sea ice and its release upon the melting of the ice could increase the surface water concentration of iron by about an order of magnitude.

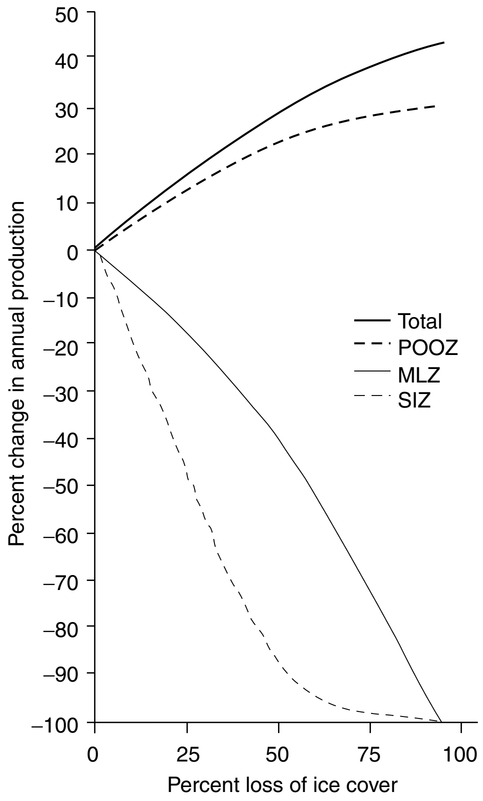


FIGURE 20.14 Percentage change in annual phytoplankton production in various regions of the Southern Ocean. (From Arrigo, K.R., Thomas, D.N., *Antarctic Sci.*, 16, 2004. With permission.)

20.4.6 Impact of Global Warming on Phytoplankton

In most of the world's oceans, phytoplankton is nutrient-limited. In contrast, in the Southern Ocean, the concentration of inorganic nutrients (N, P, Si) remains high throughout the year. The Southern Ocean is not a uniform system; it is clearly heterogeneous, with no single factor controlling primary production (Treguer and Jacques 1992). Ice cover and vertical mixing influence algal growth rates by modulating radiance flux. Micronutrients, especially iron, may limit growth in some areas. Primary production is also suppressed by high removal rates of algal biomass. Grazing by zooplankton is the major factor determining the magnitude and quality of vertical flux. Several of the controls on phytoplankton production, such as water temperature, wind-induced mixing and sea ice cover, are sensitive to climate change. With global warming, there could be an increase in wind stress over the Southern Ocean, deepening the mixed layer and inhibiting phytoplankton bloom development.

In temperate and tropical waters, chrococcoid cyanocacteria (blue green algae) are reported to have a growth rate of 2.6 doublings per day; they constitute a significant component of the food web, accounting for 30–40% of the standing crop of these organisms (Iturriaga and Mitchell 1986). The abundance of these organisms decreases exponentially with temperature across the Southern Ocean (Marchant et al. 1987). Temperature appears to be the principal determinant of their abundance. Under the present climate regime cyanobacteria, because of their low abundance, play a minor role in the Antarctic marine ecosystem. In temperate and tropical waters, however, cyanobacteria account for 25–90% of the phytoplankton biomass (in terms of chlorophyll) and 20–80% of the primary productivity (Li et al. 1983). Marchant (1992) points out that an increase in water temperatures would lead to a marked increase in the abundance of cyanobacteria in the Southern Ocean. The consequences of this would most likely be a change in the species composition and in the abundance of the microheterotropds utilizing the cyanobacteria. As a result, the prey for krill and other grazers would change, with consequent alterations in the ecosystem dynamics.

As discussed above, global warming could result in a change in the species composition of the phytoplankton community, with a decrease in the populations of large-celled diatoms and an increase in the picoplankton, especially cyanobacteria, autotrophic flagellates and coccolithophorids. These species form the basis of the microbial loop (see Figure 20.15). This could impact diatom consumers, especially krill. Another consequence could be an increase in the populations of the pymnesiophyte *Pharocystis antarctica* (Marchant 1992), which produces UV-B absorbing compounds (Marchant et al. 1991), the concentration of which are 5–10 times higher in Antarctic strains of this alga than in other species of *Phaeocyctis* examined from other parts of the world's oceans (Marchant and Davidson 1991). A decline in diatom production and an increase in that of *Phaeocystis* could have effects on trophodynamics and vertical carbon flux (Marchant and Davidson 1991). As the nutritional value of *Phaeocystis* is substantially lower than that of diatoms (Claustre et al. 1990), there is the possibility of nutrient limitation on higher trophic levels. The food resource available to zooplankton, especially krill, could be reduced. This would impact krill consumers such as cephalopods, fish, seabirds (especially penguins) and seals.

Conditions promoting the growth of the colonial stage in the life cycle of *Phaeocystis* would lead to an increase in the production of dimethylsulphide (DMS). *Phaeocystis* is reported to be the principal producer of DMS in Antarctic waters, contributing as much as 10% of the total flux of DMS to the atmosphere (Gibson et al. 1989). The major source of cloud condensation nuclei (CCN) over the sea appears to be sulphate aerosol particles formed by the oxidation of DMS produced by marine algae. The increased cloud cover has an impact on atmospheric albedo, heat flux to the ocean surface and the flux of photosynthetically available radiation.

Figure 20.16 depicts the likely consequences of a temperature increase, which would lead a decrease in the extent of the sea ice and an increased in the impact of UV-B radiation on Southern Ocean organisms and processes.

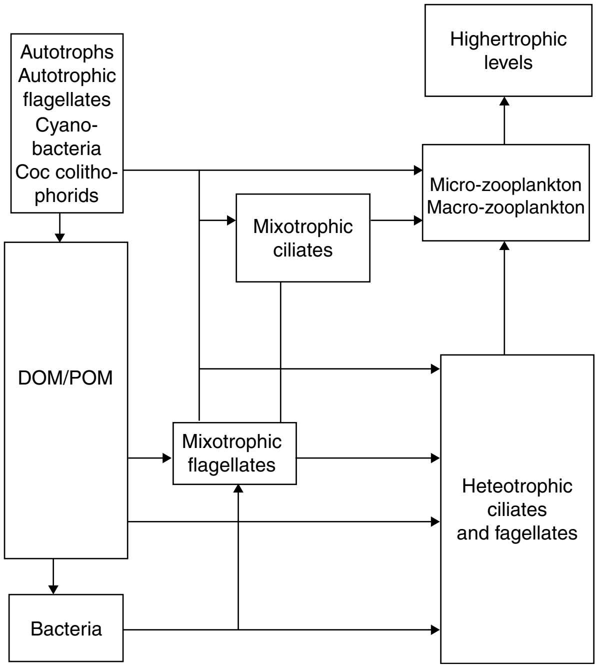


FIGURE 20.15 The principal functional components of the lower levels of the Antarctic pelagic food web. The arrows indicate the direction of energy flow between the components. (From Marchant, H.T., *Impact of Climate Change on Antarctica–Australia*, Australian Govt. Publ. Ser., Canberra, 27, 1992. With permission.)

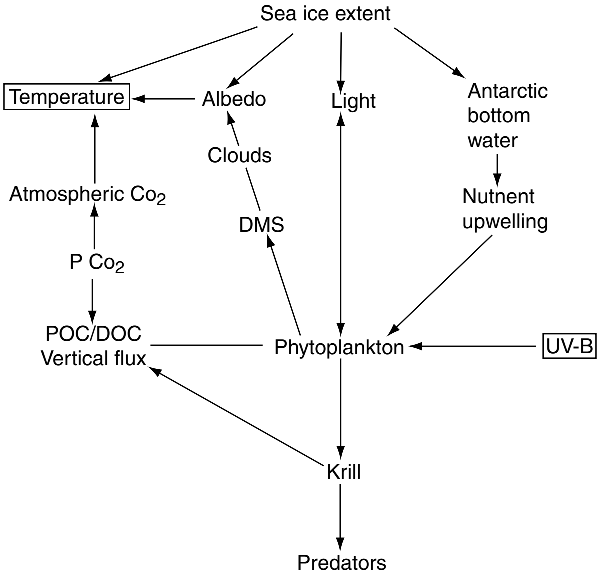


FIGURE 20.16 Conceptual diagram of the principal indirect impacts of climate change on both temperature and UV irradiance to Southern Ocean organisms and processes. (From Marchant, H.T, *Impact of Climate Change on Antarctic–Australia*, Australian Govt. Publ. Ser., Canberra, 30, 1992. With permission.)

20.4.7 Impact of Global Warming on Particle Flux to the Benthos

The determining factor in the magnitude and quality of the vertical particle flux is zooplankton grazing (Smetacek et al. 1990). Smetacek et al. (1990) point out that much of the antarctic pelagic ecosystem is dominated by a recycling community in which primary production and grazing are very tightly coupled. The members of the community are typically small and the grazers are dominated by protozoans (Figure 20.17) and small copepods. Superimposed on this system are the blooms of larger-celled phytoplankton (diatoms and *Phaeocystis*), which are grazed by the larger copepods and krill. This component is highly patchy.

The loss of phytoplankton through sinking removes particulate organic matter from the euphotic zone. However, evidence from sediment traps does not disclose large-scale sedimentation. Figure 20.17 depicts the relationship between the wind regime, mixed layer depth and vertical particle flux. At high wind stress, the mixed layer is deep and the phytoplankton biomass low. As wind stress decreases the mixed layer becomes shallower, algal biomass increases and larger and colonial phytoplankton taxa become more important. The shallower the mixed layer, the faster the growth rate and the sooner the available nutrient pool is exhausted (Smetacek and Passow 1990). Nutrient exhaustion triggers aggregate formation and mass sinking of diatom flocs. With increasing mixed layer depth, nutrient exhaustion no longer occurs and a recycling community is found. As the mixed layer depth decreases, vertical flux increases and it is dominated by the faecal pellets of the larger grazers (Peinert et al. 1989). Sediment trap data show that the bulk of the sedimenting organic matter is composed of large fecal pellets, especially those of krill.

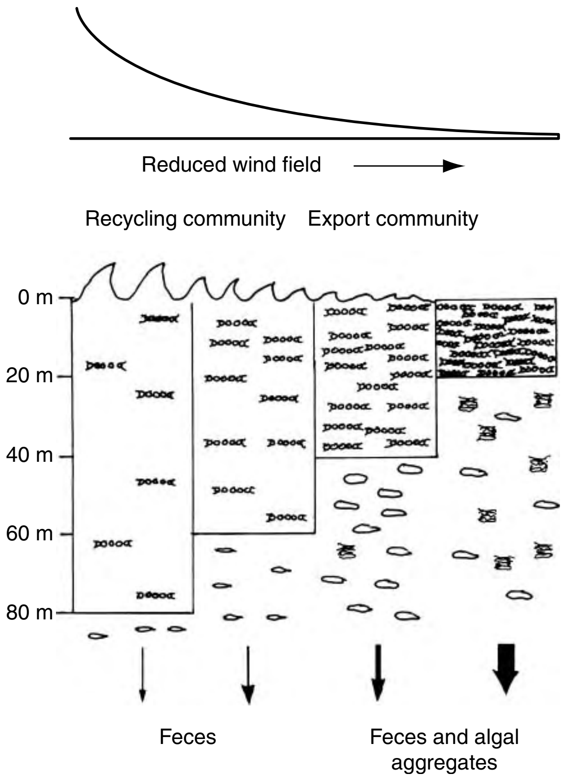


FIGURE 20.17 Schematic relationship between wind regime, mixed layer depth, and vertical particle flux. At high wind stress, the mixed layer is deep phytoplankton biomass is low and vertical flux of particles, predominantly as small fecal pellets, is small. As the mixed layer becomes more shallow, under reduced wind forcing, algal biomass increases and colonial taxa become more important. Vertical particle flux also increases, and is dominated by flocs and fecal pellets of large grazers. (From Priddle, J., Smetacek, V., Bathmann, U., *Philos. Trans. R. Soc. Lond. B*, 292, 1992. With permission.)

Diatoms have a high sinking rate and a deep mixed layer is required to retain them in the upper layers of the water. Smetacek et al. (1990) reviewed vertical fluxes of organic matter as documented by sediment trap studies in the Bransfield Strait and the Weddell Sea. At one extreme, they point out that perhaps only 0.1% of the primary production in the Weddell Sea may reach the seafloor, whereas krill grazing may produce rapid sedimentation of faecal material, representing a significant proportion of annual primary production (perhaps 10%). Thus global warming may influence the processes discussed above by increasing wind stress. Additionally, if krill populations were to decline (see Section 20.4.8 below) there would be a lessened consumption of diatoms and a decline in the flux of organic matter to the benthos, which would impact the biomass and the growth of the benthic fauna.

20.4.8 Potential Impact of Global Warming on Zooplankton, Especially Krill

Changes in the stocks and distribution of krill due to global warming could be caused by a decline in their food supply or by changes in circulation patterns. Everson (1992) has discussed possible impacts of changes in circulation patterns and concluded that on a Southern Ocean scale it is not possible to detect change, but that on a local scale, such as at South Georgia, major changes are detectable. At South Georgia, periods of krill scarcity can persist for several months. The most likely cause of this change in abundance is variation in the pattern of the Circumpolar Current in the Scotia Sea and the east Pacific sector of the Southern Ocean. It is thus clear that changes in circulation patterns can have a major impact on the abundance of krill in specific areas of the Southern Ocean. However, it is not currently possible to predict what changes might occur in the future. Such changes, coupled with possible changes in the food supply as described above could result in a decline in the abundance of krill.

Krill stocks appear to have decreased in the Antarctic Peninsula region over the last two decades (Siegel and Loeb 1995; Loeb et al. 1997). Recently Atkinson et al. (2004), based on an extensive data bank covering the summers of 1926–1939 and 1976–2003, analyzed krill and salp density distributions in the southwest Atlantic Sector of the Southern Ocean. Their analysis indicated that overall krill densities had declined (Figure 20.18). High densities depend on the summer phytoplankton blooms and extensive sea ice coverage providing plentiful sea ice microalgal food for the adults and larval stage during the winter. Concomitantly with the decline in the krill populations, those of the salps increased dramatically. Salps are small particle feeders and this indicated a substantial change in the phytoplankton species composition.

Loeb et al. (1997), Siegel (2000a, 2000b), and Brierley et al. (2002) have provided data on a close relationship between krill, the pelagic tunicate *Salpa thompsoni*, and the extent and duration of the sea ice. Following winters with reduced sea ice cover, during which the recruitment of krill is not favored, extensive salp blooms tend to form. Salp blooms can severely affect the reproduction and survival of krill (Figure 20.19). On the other hand, long periods of extensive sea ice cover favors krill recruitment and induces a delayed seasonal spring phytoplankton bloom, enabling krill to out-compete the salps, and krill tend to dominate in open waters. If global warming leads to a reduction in the extent of the sea ice, then salps would dominate and krill populations would be reduced.

If the krill biomass were to decline or the patterns of distribution were to change, this could have a flow on impact on those species that rely on krill as their principal food item, such as Ross, Crabeater and Weddell seals, some fish species, and birds, especially penguins. The degree to which they could switch to alternative food sources is largely unknown. However, it is clear that if climate changes which may be due to global warming become more dramatic, this could have a considerable impact on the higher consumers in the Antarctic marine ecosystem.

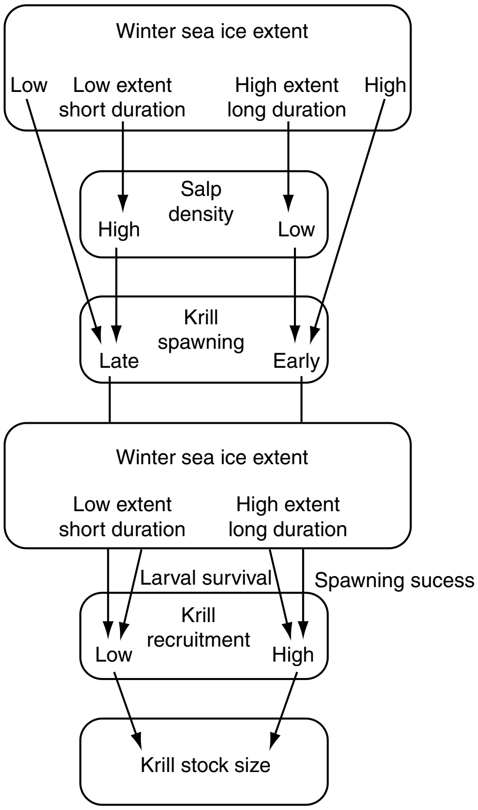


FIGURE 20.19 Hypothesis on the relationship between krill recruitment success, sea ice conditions and biological factors (salp abundance, spawning time). (From Schnack-Schiel, S.B., *Sea Ice. An Introduction to its Physics, Biology, Chemistry and Geology*, Thomas, D.N., Dieckmann, G.S., Eds., Blackwell Science, Oxford, 211, 2003. With permission.)

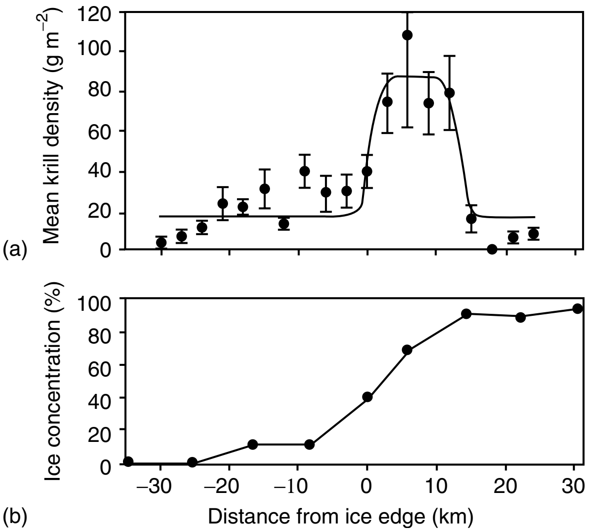


FIGURE 20.18 Krill distribution relative to the sea ice edge and ice concentration. (a) Krill density by distance (in 3km bits, positive is under sea ice) from the local sea ice edge. The line is a highly significant regression, error bars are ±SEM. (b) Sea ice concentration. (From Brierley, A.S., Fernandes, P.G., Bromley, M.A., *Science*, 295, 2002. With permission.)

20.4.9 POTENTIAL IMPACT OF GLOBAL WARMING ON THE BENTHOS

It is difficult to predict how the existing benthic fauna would react to an increase in global warming (Clarke and Crame 1992). However, it is certain that the fauna would change, as it has throughout time. Many of the possible environmental changes discussed above will have impacts of varying degrees on the benthic fauna. The present thermal regime in the Southern Ocean is very stable (Clarke 1983), particularly close to the Antarctic Continent, although there are signs of change; this is associated with a high level of sternothermy in the fauna. Taken together, these factors would suggest that any warming of the seas surrounding the Antarctic Continent might have severe consequences for the fauna. This is because the present fauna has been selected for a physiology that is tuned to a narrow range of temperatures, which may limit their ability to adapt to a higher range of temperatures. Such species could be eliminated from the benthos.

The question then is, could such species be replaced by the immigration of species from the north? A number of factors would limit such invasions. The continental shelves around the Antarctic Continent are isolated from other shallow water areas by large tracts of deep water. Many cool-temperate species that could potentially migrate onto the Antarctic shelf have reproductive strategies that would appear to limit their dispersal ability (e.g., low fecundity because of large eggs, direct development or brooding, and reduced larval stages). Additionally, for many taxa the Polar Frontal Zone acts as a strong (but not necessarily absolute) barrier to dispersal into or out of the Southern Ocean. The collapse of the sea ice and changes in primary production, food supply and sedimentation of particulate organic matter may limit the ability of some species to survive and reproduce.

The possible increase in benthic microalgae and macroalgae in shallow waters would bring about changes in the composition and abundance of the species in the benthic community. Herbivores such as gastropod molluscs and benthic grazers feeding on the microalgal mats and surface deposit feeders ingesting the surface layer of the soft sediments would predominate. Changes in the intensity and species composition of phytoplankton blooms would have an impact on those species consuming sedimented phytoplankton and particulate organic matter.

20.5 POTENTIAL CHANGES IN ECOSYSTEM STRUCTURE AND DYNAMICS

20.5.1 Shallow-Water Ecosystems

The impact on shallow water ecosystems is likely to be considerable. These changes will be due to:

1. The reduction and eventual disappearance of the ice foot, which would release substrates for colonization by sessile species. There would be intense competition for space, and it is likely that certain species would dominate, e.g., some erect bryozoan species (Barnes 1999).
2. An increase in the benthic microalgal biomass and production in shallow waters providing a substantial food resource for benthic deposit feeders, whose abundance is likely to increase. On the other hand, resuspension of the microalgae would provide food for suspension feeders.
3. An increase in the benthic macroalgal biomass and production would provide an enhanced food resource for herbivorous crustaceans and gastropods, whose populations would consequently increase. Macroalgal decay would provide an enhanced input of particulate organic matter.
4. A reduction or disappearance of the sea ice would permit enhanced penetration of UV radiation. The impact of this on the algae and invertebrates would depend on the degree to which individual species had evolved protective and repair mechanisms. On the other hand, an increase in available light (PAR) would favor the growth of phytoplankton and enhance biogenic sedimentation. This would in turn provide enhanced food supplies for herbivorous planktonic invertebrates, especially crustaceans.
5. Some stenothermal species could be eliminated from the ecosystem, especially benthic species. On the other hand, warmer water species could recruit to the area.

20.5.2 Sea Ice Zone Ecosystems

Considerable changes could occur in the sea ice zone following a reduction or disappearance of the sea ice and the formation of a deeper mixed layer. Such changes could include:

1. A loss of ice edge phytoplankton blooms, resulting in a reduction in primary production. This would impact the planktonic invertebrates that depend on this food resource.
2. Warmer water could lead to lowered primary production.
3. Coupled with changes in the nutrient supply, light availability, and increased UV radiation, there would be a change in the species composition of the phytoplankton community with a shift from diatoms to the smaller nano- and picophytoplankton. An increase in water temperatures would favor the development of a community dominated by cyanobacteria, which are currently a minor component of the phytoplankton assemblages (Marchant 1992).
4. Increased penetration of UV radiation following the decline or elimination of the sea ice could lead to the dominance of the UV-tolerant *Phaeocyctis* (Marchant et al. 1991; Davidson and Marchant 1994; Marchant 1997), because *Phaeocystis* is not consumed to any extent by herbivores. This would then have an impact on the higher predators, birds and seals, which feed on these species.
5. With the change in phytoplankton species composition, there would be lessened biogenic sedimentation, which would reduce the food supply available to the benthos.
6. With the disappearance of the sea ice, there would be a reduction in the overall primary production due to the loss of the sea ice microalgal production, estimated at 30% of the total. In addition, populations of a number of herbivores, especially copepods and krill, which graze on the sea ice microlagae, would be reduced due to the loss of a critical food resource.
7. A reduction in sea ice microalgal production would likely to lead to a decline in the krill-based ecosystem, with a shift towards a system centered more strongly on salps.

8. With the reduction and disappearance of the sea ice, some higher predators, especially seals, could be impacted by the loss of haul-out and breeding sites.
9. Populations of land- or ice-breeding seabirds could be affected by changes in their food supply, especially krill, and the availability of foraging zones.
10. There would be an increase in the number of icebergs and consequently a great increase in the impact of iceberg scour.

20.6 SOME GENERAL CONCLUSIONS

The palaeontological record and data extracted from ice cores show that the Antarctic marine ecosystem has undergone considerable fluctuations in the past in response to periods of cooling and warming. Currently, we are in a man-induced warming episode. Models predict that the warming trend will continue. Consequences for the Southern Ocean marine ecosystems include:

1. Further increases in air temperatures.
2. Increases in sea temperatures.
3. Changes in the mean position of the circumpolar atmospheric low-pressure though, the Antarctic Convergence Line (ACL) (Smith et al. 1999); this would influence not only the semi-annual cycle of temperature, pressure, wind and precipitation, but also the distribution of sea ice.
4. Changes in the thermohaline circulation and the distribution of oceanic fronts with consequent changes in the distribution of the water masses.
5. Changes in the depth and strength of the pycnocline.
6. A decrease in the formation of AABW, with a consequent impact on global oceanic circulation patterns.
7. A decrease in and possible disappearance of the sea ice.
8. Changes in the ratio of new to regenerated nutrient supply.

The changes in the air/sea ice/thermohaline circulation could have profound consequences for the species composition and dynamic functioning of the Antarctic marine ecosystems. As outlined above, changes are already occurring. Smith et al. (1999) have diagrammed the idealized relationship between the sedimentary record and overlying biological flux and biological production. This model represents the modern continuum from polar to subpolar conditions along a south-to-north response to climate change. At the cold end of this climate gradient, perennial sea ice is present in surface waters. Under these conditions, the contribution of sedimentation from melting ice is low. Thick multi-year sea ice also reduces light penetration, resulting in little or no biological production. The net result is low accumulation of biogenous and terrigenous sediments (approximately 0.01–0.02 mm yr^{-1}).

With climate change, the advance and retreat of annual sea ice controls the composition and volume of material settling to the sea floor. Although terrigenous input increases with increased meltwater, the impact of warming on the biological system is even more significant. High primary production is associated with the marginal ice zone. Under these conditions, biogenous material dominates the particle flux and overall sedimentation rates range from 1 to 4 mm yr^{-1} (Leventer et al. 1996).

At the warm end of this climate gradient, the region experiences longer ice-free periods. Without sea ice melt to stratify the upper water column, the open water system undergoes increased wind mixing, resulting in lower annual average primary production and organic flux to the sea floor. However, due to the relatively warm conditions, glacial meltwater input of terrigenous material is high, leading to sediment accumulation rates of up to 10 cm yr^{-1} (Domack and McDenny 1996).

The most profound change as a result of global warming would be the reduction in sea ice cover, with consequences as outline above in Section 20.4. Lowered primary production would impact the composition and abundance of the phytoplankton community, with flow-on effects on the zooplankton community. A possible effect would be a reduction in the krill biomass, which would have an impact on the consumers of krill at the higher trophic levels, namely seabirds, seals and whales. Some top predators, especially seals, would lose substrate for haul-out and breeding.

21 Human Impact

CONTENTS

21.1 INTRODUCTION

Although Antarctica is the most isolated area on the globe, it nevertheless has been impacted by man's activities. The earliest impacts resulted from the exploitation of seals and whales (see Chapter 8 and Chapter 9). More recently, there has been the exploitation of krill and fish stocks resulting in considerable reduction in the populations of some fish species. Fishing activities, especially by long-liners, has severely impacted on some bird species, especially albatrosses. The establishment of bases by various countries and the activity of research parties have also had an impact on the pristine environment, resulting in environmental problems of solid waste management, fuel spills, and the disposal of liquid wastes with consequent impacts on marine communities. Tourism, which has grown considerably in recent years, has added to human impact. Research vessels and the increasing number of tour ships have raised the possibility of oil spills. Mans release of greenhouse gases resulting in ozone depletion and global warming have impacted Antarctica (see Chapter 19 and Chapter 20). All of such impacts will be discussed below.

21.2 IMPACT OF WASTE DISPOSAL

21.2.1 Solid Wastes

The impact of waste disposal is illustrated with reference to McMurdo Station, Scott Base, Terra Nova Bay, and Casey Station. In the early days of station operations, waste disposal was not handled well. However, this question has been addressed by the Scientific Committee on Antarctic Research and the Antarctic Treaty System. Strict regulations have been put in place to regulate waste disposal practices.

The following account is based upon information in New Zealand Antarctic Institute (2001). Until the mid-1980s to early 1990s, it was normal practice at McMurdo Station and Scott Base to dispose of solid wastes at dump sites close to the stations and directly onto the sea ice. For example, at McMurdo Station all solid wastes (including metal, rubber, plastics, and food wastes) were originally disposed at a dump site on the shores of Winter Quarters Bay. Combustible wastes were burnt in open piles, aided by the addition of waste fuels, and some material, including large items of equipment, was dumped on adjacent sea ice, eventually sinking to the sea bed. The seabed adjacent to McMurdo Station is littered with such waste material. Dayton and Robilliard (1969) reported on the abundance of this material and noted that "Inorganic matter on the bottom at McMurdo is dramatic: fuel lines, barrels, honey buckets, rope, clothing, tractors, pieces of aeroplanes, thousands of beer cans, and many other types of trash are everywhere.… litter is commonly seen as far a 6 km to the north."

Debris is also evident offshore at Scott Base, where dumping on the sea ice was a practice. This was halted by the mid-1980s. Recent heavy metal analyses of the seabed material in the vicinity of the base has recorded values higher than those that would have been expected to occur naturally (Anderson and Chague-Goff 1996). Elevated levels of trace metals, including silver, copper, cadmium, nickel, zinc, mercury, lead, and chromium have been found in drains and meltwaters in and around Scott Base that eventually discharge to the sea (Sheppard et al. 1997).

Disposal of wastes at the coastal dump site at McMurdo Station was discontinued in the 1980/1981 season and a new dump site was constructed further inland. Combustible wasters were soaked with waste fuel and burned. Open burning ceased in the 1990/1991 season and the landfill was closed. Subsequently, combustible wastes were burnt in an incinerator until all burning of waste was phased out in 1994. Since then, all waste matter is now returned either to the United States or New Zealand.

At Terra Nova Bay Station, solid wastes have never been disposed onto land or into the sea. There, combustible solid wastes have been disposed of by incineration, with the residues retrograded to Italy, along with all other noncombustible solids and hazardous wastes. Studies of marine chemical contamination in the vicinity of Terra Nova Bay Station indicates that although PCB levels are slightly elevated, the overall level of contamination is still very low despite 15 years of operation (Focardi, Bargagli, and Cotsolini 1995).

The early methods of waste disposal by incineration has the potential to contaminate the marine environment with pollutants. Sediments in Winter Quarters Bay are heavily contaminated with a range of organic contaminants, including polycyclic aromatic hydrocarbons (PAHs) and persistent organo–chlorine compounds, polychlorinated biphenels (PCBs), and polychlorinated terphenyls (PCTs). Elevated concentrations of some heavy metals such as copper, cadmium, lead, and zinc are present, although levels of most other heavy metals are not significantly different from remote reference sites. Although the concentrations of heavy metals are only 2–3 times greater than at reference sites, hydrocarbon concentrations were elevated by several orders of magnitude. There is evidence that marine animals living in the vicinity of McMurdo Station may be adversely affected by these substances. Lenihan et al. (1995) found that the diversity and density of animals living within the sediments were significantly poorer than those found outside Winter Quarters Bay and that benthic organisms transferred into the bay did not survive. Bivalves and fish from the vicinity of Winter Quarters Bay have been found to contain significantly elevated concentrations of PAH compounds in their tissues (McDonald et al. 1994). However, the aerial extent of the contamination is restricted to an area of 80,000 m^2. Levels of contaminants fall to near-background levels by several hundred meters from the bay's mouth.

The impact of waste disposal practices at Casey Station, East Antarctica have been studied by Deprez, Arens, and Locher (1999), Snape et al. (2002), and Stark and Riddle (2003). The potential contaminated areas that have been identified at the Australian Station of Casey; these are two old waste dumps (the Old Casey waste dump on the shore of Brown Bay and the Wilkes waste dump on the shore of Newcomb Bay). In addition, there are two sewage outfalls in Shannon Bay and Casey Wharf (Stark 2000). Benthic community composition was ascertained in reference and contaminated areas and manipulative experiments were carried out to assess whether contamination of marine sediments affected the development of communities through the recolonization of defaunated sediments. Assemblages at potentially impacted locations were significantly different to reference locations, and displayed attribute characteristics of disturbed communities. The differences between reference and polluted locations were highly correlated with concentrations of heavy metals. In the field experiments, it was found that contamination of marine sediments resulted in significantly different assemblages in comparison to control sediments. Thus, a potential causal link was established for the difference between reference and impacted locations around Casey Station. There were several amphipod species that appeared to be responding in an opportunistic manner to disturbance because they were very abundant at impacted localities. One of these species (*Orchomene franklini*) was also the most affected by the hydrocarbon treated sediments, suggesting that it may cope with some types of contamination (e.g., heavy metals) better than others (e.g., hydrocarbons). Most of the differences in the assemblages could be attributed to heavy metal contamination. These metals, such as lead, copper, zinc, tin, and cadmium, are known to have anthropogenic origins and are associated with materials that are found in the tips. Although the effects of contaminated sediments were complex and variable, differences were found between control and contaminated sediments.

21.2.2 SEWAGE

One of the major environmental problems facing base operators is the discharge of sewage to the ocean. In the early years of base occupation, sewage was discharged to the sea without treatment. The most extensively investigated sewage outfall is that of McMurdo Station (Lenihan et al. 1990, 1995; Lenihan 1992; Conlon et al. 2000, 2003; Edwards, McFeters, and Venkatsan 1998). Sewage release offshore is of concern because anthropogenic organic matter is three times as slow to be degraded at $-1.8°C$ Antarctic seawater as in 20°C seawater (Howington, McPeters, and Smith 1994). Although the sewage was originally discharged at the shore edge in 1990/1991, the discharge point was shifted to about 50 m offshore in a depth of about 20 m. Records of wastewater at McMurdo Station for the 1997–1998 season show a release from 52,517 $l\ day^{-1}$ during the winter low season to 271,547 $l\ day^{-1}$ during the summer high season. This waste is macerated and diluted with from the reverse osmosis plant and the aquarium, giving a total flow of 648,087–2,175,294 $l\ day^{-1}$. No other treatment was applied. Large particles, including food and faces, deposit at the mouth of the outfall, accumulating in a pile up to 2 m high (Conlon et al. 2000).

Howington et al. (1992) found coliform bacteria in the water column from Hut Point to the station's intake and to 300 m offshore in 1990 and 1991. Edwards, McFeters, and Venkatsan (1998) found the human bacterium *Clostridium perfringens* at the discharge point and as far as 824 m southeast in the seabed sediment. Although the predominant current flow is southwards, a near-shore anticlockwise gyre in McMurdo Sound carries material from the outfall northwards towards Winter Quarters Bay, with occasional flow reversal to the south. A measurable but declining plume of sewage extends for up to 1 km along the McMurdo shoreline and up to 300 m seaward from the outfall (Figure 21.1). Conlon et al. (2000) noted that the benthic fauna was assimilating sewage-derived products along the coast as far as 824 m downcurrent of the sewage outfall.

Conlon et al. (2003) documented the benthic changes that had occurred over the ten years from 1988 to 1998. Outside the contaminated area, there was a highly diverse benthic community composed of abundant deposit feeders, suspension feeders, and predators. Downstream from the outfall, there was a mix of fauna typical of both the outfall site and unpolluted reference sites, along with species unique to the area. Multivariate analyses showed a marked reduction in the diversity of the fauna following the extension of the sewage outfall in 1992 but some increase in 1998 (Figure 21.2a). In 1993, faunal abundance at the outfall site increased more than six-fold (Figure 21.2b). After the extension of the sewage outfall, taxonomic diversity and distinctness declined sharply, and in 1993 and 1998 were significantly less than at a down-current reference site (1993) and at an up-current reference site (1998). By the last sampling time in 1998, however, diversity and abundance had returned to about 60% of 1992 levels. It is clear that the benthic community was responding to changes in the sewage discharge system. A sewage treatment plants was installed in 2003 and it will be of interest to follow further changes as they occur.

Similar, but less extensive studies have been undertaken on the smaller sewage and wastewater outfalls at Scott Base and Terra Nova Station. The Scott Base outfall discharges up to 17.000 l of domestic wastewater daily in the summer. Redvers (2000) has shown that the effects of the discharge on water quality around the discharge point in terms of nutrients, BOD, trace metals, copper, and zinc, and fecal coliforms are localized and relatively insignificant.

21.3 IMPACT OF TOURISM

Tourism is a relatively recent phenomenon in Antarctica, but it has been growing rapidly. Shipboard cruising currently accounts for 90% of Antarctic tourism. In the 2000/2001 season, there were 131 Antarctic ship tourist voyages, the bulk of which were to the Antarctic Peninsula area. Significant pollution could arise from the sinking or grounding of one of these ships, in particular from the release of fuel oil.

There also has been concern about the potential impact of tourist activity, especially at landing sites that are designed to allow the tourists to see Antarctic wildlife, especially breeding colonies of penguins and haul-out or breeding site of seals (Enzenbacker 1992; Stonehouse 1992). Although it is generally agreed that the breeding success of the smaller Adélie penguin colonies, in particular, are significantly affected by human disturbance, other causes of population declines need to be taken into account. Fraser and Patterson (1997), in an investigation of the impact of humans (especially tourists) on Adélie penguin populations at Palmer Station, concluded that their data suggested that the potentially adverse effects of tourism and research may be negligible relative to the effects imposed by long-term changes in other environmental variables. Human impact on breeding populations of marine birds will be further considered in the next section.

21.4 DISTURBANCE OF NESTING SEABIRDS

Long-term studies on penguin colonies indicate that the populations of these birds may decrease at sites where they co-occur with humans (Thompson 1977; Wilson 1990; Wilson, Taylor, and Barton 1990; Woehler et al. 1994). However, see Fraser and Patterson (1997). This implies that somehow man can affect population size. It is therefore

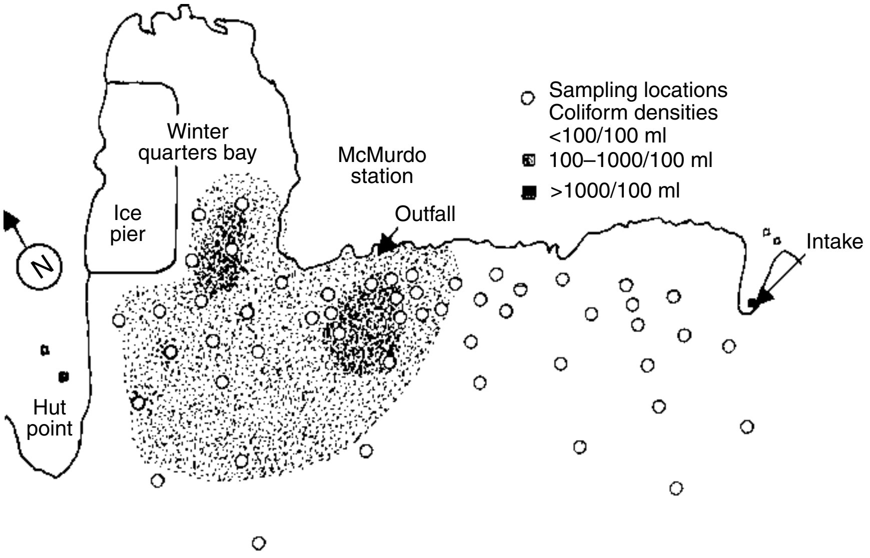


FIGURE 21.1 The sewage plume near McMurdo Station, Ross Island during December 1991. Bacterial coliform densities are mapped. For scale the small squares at 25 m on each side. Material is carried from the outfall, north into Winter Quarters Bay, and the plume extended for up to 1 km along the shoreline. (From McFeters, G.A., Barry, J.P., Howington, J.P., *Water Res.*, 27, 645, 1993. With permission.)

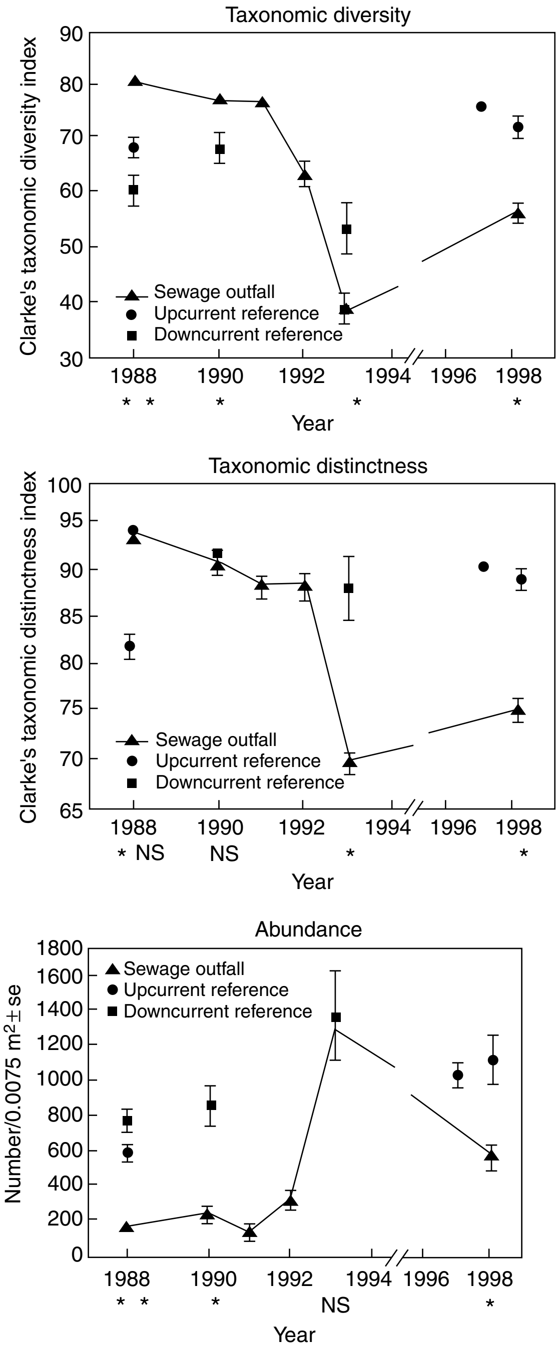


FIGURE 21.2 Abundance, Taxonomic diversity and taxonomic distinctiveness at the McMurdo Station sewage outfall and down-current and up-current reference sites. Differences between the means at the outfall site and the reference sites are indicated by a * (significant) or NS (not significant) at $p=0.05$. (From Conlon, E.C., Rau, G.H., McFeters, G.A., Kvick, R.G., *Antarctic Ecosystems: Models for Wider Understanding, New Zealand Natural Sciences*, University of Canterbury, Christchurch, 315, 2003. With permission.)

necessary to understand what contributes disturbance and what are the consequences for the impacted species, so that procedures can be put into place to avoid disturbance. Apart from an increasing number of tourists visiting penguin colonies in recent years, scientists engaged in research could have an impact on penguin colonies. Research on penguins necessitates direct contact with the birds at some time (e.g., during weighing, marking, or instrument attachment). In addition, there has been concern that the marking of penguins with flipper bands can affect their survival. Some studies have demonstrated the effects of humans on penguin physiology and behavior (Wilson et al. 1991), breeding performance (Reid 1968; Woehler et al. 1994; Giese 1996) and distribution and abundance (Woehler et al. 1994). A single approaching person has been shown to increase nesting penguin heart rates (Culik et al. 1990; Wilson et al. 1991), suggesting that animals may be stressed even though no external changes are observable. Others have failed to detect any effects on physiology (Nimon, Schroter, and Stonehouse 1995), abundance (Parmelee and Parmelee 1987) or breeding success (Oelke 1975; Fraser and Patterson 1997). It would thus appear that simple behavioral observations are not a reliable indicator of the presence or absence of disturbance. Physiological parameters such as heart rate, body temperature (Boyd and Sladen 1971) and corticosterone levels (Le Maho et al. 1992; Fowler 1993) can allow quantification of the degree of response to disturbance.

Controversy continues concerning the impact of disturbance on penguins. Regel and Putz (1997) measured the stomach temperatures of molting emperor penguin chicks and adults while the birds were exposed to various man-induced stimuli (Figure 21.3). Stimuli resulted in typical temperature rises that varied with the duration and strength of the stimulus. On average, the temperature rose by 1.5 K, the maximum being 2.6 K following a stimulus of more than 2 h duration. Minimal energy costs inducing temperature rises could be estimated. Depending on the intensity of the stimulus, minimal energy expenditure ranged between 3.2 kJ kg^{-1} and 9.7 kJ kg^{-1}, being slightly higher in the chicks. This represented up to 10% of the daily energy demand during the molt. The estimated minimal increase in metabolic rate during stress averaged 2.3 W/kg in chicks and 2.0 W kg^{-1} in adults (maximum of 4.2 W kg^{-1} and 3.3 W kg^{-1}, respectively).

Energy reserves in molting emperor penguins are limited (these penguins do not feed for between 30 and 40 days [Groscolas 1978]). Therefore, stress that increases energy expenditure must be balanced by additional prey to compensate. For example, if the observed emperor colony of 6,000 breeding pairs with associated chicks to be disturbed by a helicopter and tourists, as in an experiment carried out by Regal and Putz, the energy expended by the colony for a single visit would be at least 9.8×10^5 kJ. Assuming that the birds feed mainly on krill (Putz 1995) with an energy content of 4.35 kJ g^{-1} (Croxall et al. 1984), and an assimilation efficiency of 75%, 310 kg would be required to compensate for such a disturbance. This approach shows promise for assessing the impact of disturbances on penguins.

Colby and Shears (1999) investigated the impact of tourist visits on breeding gentoo penguins at Port Lockley on the Antarctic Peninsula. Comparisons were made between treatment areas (visited by 35–55 tourists every 1–2 days) and control colonies (not visited by tourists). There were no differences between the two groups in the proportion of birds that laid, in hatching success, or the proportion of single-chick broods. Nests monitored in a disturbed colony and a control colony showed no differences in chick mass or survival up to 20 days of age. The overall breeding success, based on counts of creched birds, was similar to other southern populations of gentoo penguins. It was concluded that disturbance from tourist visits was unlikely to have been a major determinant of gentoo penguin population change at Port Lockley.

In contrast to the findings of Colby and Shears (1999), and Woehler et al. (1994) found that visitor impacts reduced overall breeding success an a colony of Adélie penguins at Shirley Island, near Casey Station. Breeding population success was compared at Whitney Point and Shirley Island. At Whitney Point, the breeding populations increased from 1,112 pairs in 14 colonies in 1959/1960 to 4,714 pairs in 36 colonies in 1992/1993. On Shirley Island, the total breeding population remained at 7,770 pairs between 1968/1969 and 1992/1993, except in 1990/91, when the population peaked at 8,719 pairs. Newly established colonies increased more rapidly than established ones. Breeding success (chicks fledged per nest) was significantly lower for Shirley Island colonies than for those at Whitney Point. Human visitors to Shirley Island from Casey Station were believed to be responsible for the observed changes in the distribution and abundance and for maintaining the stable population by educing overall breeding success through disturbance associated with visits.

Fraser and Patterson (1997) investigated changes in Adélie penguin populations near Palmer Station, Antarctic Peninsula. Human activities (tourism and research) near Palmer Station has increased significantly since 1975. Initially, these activities were focused on the large and easily accessible populations of Adélie penguins on Litchfield and Torgersen Islands. Litchfield Island became a specially protected area (SPA) in 1978. This ended tourism on the island and reduced research-related activity to negligible levels. Despite SPA status, the total breeding population of Adélie penguins on Litchfield Island decreased by 43% between 1975 and 1992. In contrast at Torgensen Island, where tourism and research-related activities continued to increase over the same time period, the decrease in these populations was only 19%.

21.5 CONTAMINATION OF MARINE BIOTA BY POLLUTANTS

Although Antarctica is the most isolated and least-inhabited continent, it is not free of environmental contaminants. Global atmospheric and marine circulation provides a mechanism for pollutants that have been generated outside Antarctic to find their way south. For example, residues of persistent organochlorine compounds such as dichloro–diphenyl–trichloethane (DDT) have been found in Antarctic marine organisms since the mid 1960s (Sladen, Menzie, and Reichel 1963). Risebrough et al. (1976) suggested that organo–chlorine pollutants found in the guano of Adélie penguins had been transported to the Antarctic ecosystem through the atmosphere, not from local contamination. Chemicals such as polychlorinated biphenyls (PBCs) have also been found in South Polar skuas and in the tissues of Antarctic seals.

On a local scale, shipping and base activities, especially waste disposal methods and incineration, have caused contamination by heavy metals, pesticides, and polychlorinated biphenyls (PBCs). These localized sites may be contaminated to levels comparable to industrial sites elsewhere (Berkman and Nigro 1992). PBCs and other persistent chemicals such as DDT have the potential to accumulate in Antarctic organisms. Because of their high levels of body fat, marine mammals and birds are particularly at risk.

Most studies have found that the levels of persistent contaminants in the Antarctic marine ecosystem to be quite low, certainly much lower than levels measured in the Northern Hemisphere (Table 21.1). It would appear that global concentrations of some compounds, including DDT, are actually gradually declining, as are corresponding levels in the Ross Sea (Larsson, Jarnmnark, and Sodergren 1992; Court et al. 1997), due to their banning in most Western nations.

Focardi, Bargagli, and Cotsolini (1995), and Corsolini and Forcardi (1998) have investigated the bioconcentration of polychlorinated biphenyls in the pelagic food chain in the Ross Sea. The mean concentration of PBC was 1 ng g^{-1} in phytoplankton, 4.23 ng g^{-1} in zooplankton, 9.39 ng g^{-1} (body burden) in silverfish and 124.76 ng g^{-1} in penguin liver. The values of bioconcentration factor (BCF) show that the largest increment in BCP concentration was from water to phytoplankton.

Bargagli et al. (1998) investigated the biomagnification of mercury in marine sediments and the biota of the inner shelf in Terra Nova Bay, Ross Sea. Hg levels in the finest fraction of the sediments were among the lowest ever reported for coastal marine environments (0.012 ± 0.007 μg g^{-1} dry wt). A progressive increase in Hg concentrations was found in organisms at different levels of the marine food web (phytoplankton <zooplankton and benthic primary consumers

TABLE 21.1
Concentration of Polychlorinatedbiphenyls (Range in ng l^{-1}) in Seawater from Different Latitudes

Latitude	Concentration (ng l^{-1})
40°59′ N	0.23–0.49
38°19′ N	0.33–0.50
29°59′ N	0.35–0.83
16°39 N	0.35–0.64
69°S 39°E	0.035–0.069

Source: From Tanabe, S., Tatsukawa, R, *Proceedings of the BIOMASS Colloquim in 1982*, National Institute of Polar Research, Tokyo, 576, 1983; Corsolini, S., Forcardi, S., *Ross Sea Ecology*, Fernando, F.M., Gugliemo, L., Ianora, I., Eds., Springer, Berlin, 576, 1998. With permission.

<detritovores and opportunistic invertebrates <epipelagic fish <demersal fish and plankton-feeding seabirds, fish-eating penguins and Weddell seals). In general, primary producers and consumers showed slightly lower Hg concentrations ($0.076 \pm 0.023\ \mu g\ g^{-1}$ dry wt) than organisms of related species from other seas, but values in feathers ($2.91 \pm 1.03\ g\ g^{-1}$ dry wt) of the Antarctic skua and in tissues of a Weddell seal (44.0 and 24.0 $\mu g\ g^{-1}$ dry wt in the liver and spleen) were similar to those in skuas and seals from the Northern Hemisphere. The results of the study show that despite the very low concentrations of Hg in the marine sediments, Hg levels in Terra Nova Bay organisms were only slightly lower than or in the same range as those reported for similar species from other parts of the world (Sadiq 1992).

21.6 IMPACT OF OIL SPILLS

An increasing number of ships, including research and supply vessels, ice breakers, tourist ships, and private yachts, are operating in Antarctic waters. Accidental discharges of fuel have often occurred, but the impact of these has been minor. However, there is always the possibility of the grounding or sinking of a ship with the consequent release of large quantities of fuel oil. One major event was the grounding of the Argentian supply ship *Bahia Paraiso* on shoals in Arthur harbour off Anvers Island, about 2 km from the National Science Foundation's Palmer Station on January 28, 1989. An estimated 6×10^5 l of oil, primarily diesel fuel arctic, spilled into the surrounding bays causing slicks within the first few days that covered 100 km^2 of sea surface (Kennicutt 1990; Kennicutt et al. 1991, Kennicutt 1992a, 1992b). The affected area consisted of nearly 20 small islands within a 2-km radius of Palmer Station. The heaviest oiling occurred along rocky shores. Penhale, Coosen, and Marschoff (1997) have reviewed the history of the impacts of the oil spill.

Early observation showed that by four days after the Bahia ran aground, a 30 km^2 area surrounding Palmer Station was covered by an oil slick (Kennicutt 1990). Rocky inertidal sites showed the first signs of ecological damage. By February 4, a 50% mortality of inertidal limpets was estimated and algal mats in the inertidal area also appeared to be dead (Penhale 1989). The initial impact on seabirds in the area varied. Although few dead birds were observed, most adult birds appeared to have been exposed to fuel oil (Fraser and Patterson 1997). Initial surveys of Adélie penguin colonies indicated that more than 80% of the birds had been exposed to the spill. The exposure of the various species in the area depended on their behavior. Adults were exposed primarily through feeding on krill and fish present in the area. Because the spill occurred during the period of peak chick growth for many species, chicks were exposed to oiled parents and oiled food.

Initial observations on other ecosystem components suggested negligible effects (Kennicutt 1990). Marine mammals (which were primarily absent from the area in February and March) and benthic fish appeared not to have been affected by the spill. Initial results of microbial degradation of the hydrocarbons indicated low levels of activity (Kennicutt et al. 1991). Preliminary examination of the subtidal community suggested little impact. Analysis of hydrocarbon component of macroalgae (*Monostroma* sp. and *Leptospma simplex*), limpets (*Nacella concinna*) (Kennicutt et al. 1992a, 1992b), birds (*Phalocrocorax atricepts*, *Catharacta maccormicki*, *Larus dominicanus* and *Pygoscelis adeliae*), clams (*Laternula elliptica*), bottom-feeding fish (*Notothenia coriiceps neglecta* and *Harpagifer antarcticus*) and sediments collected over several months after the spill showed contamination to varying degrees (Kennicutt et al. 1992a, 1992b). Kennicutt et al. (1991) concluded that the relatively small size of the volatile fuel in the high-energy environment resulted in limited toxic effects. Samples taken a year following the spill showed some contamination, primarily in the sediments in the vicinity of the *B. Paraiso*, due to low-level release from the ship. Studies conducted two years after the spill (Kennicutt et al. 1992a, 1992b) showed little contamination in limpets and subtidal sediments.

Studies of the subtidal communities showed little effect (Hyland et al. 1994). Macrofaunal assemblages at most stations examined were characterized by very high densities and numbers of taxa. There were no significant differences ($P < 0.05$) between oil-spill and control sites in numbers of individuals, species, or families, nor were there any major differences in dominant fauna or overall community composition. The assemblage at the shallower of the two historical sites that were sampled, however, showed a substantial change over the 18-year period between studies. This change consisted of a shift towards a more species-rich and abundant macrofauna characteristic of the more physically stable part of the harbor. This change was probably related to the fact that the glacier face near this site had retreated approximately 250 m over the last 20-odd years, resulting in less physical disturbance of the adjacent sea floor.

Laboratory studies were conducted on the short-term (3–7 days) effects of diesel fuel arctic on sediment microbial processes in the Palmer Station vicinity: the acute effects appeared negligible (Karl 1992). Longer-term (120 days) exposure showed either no effect or a slight stimulatory effect on metabolic activity and production. Very low rates of microbial hydrocarbon oxidation potential were located in both the oil-spill area and control areas.

The effect of the oil spill on the seabird community varied with time and with species. Both during the time of the oil spill and in subsequent years, results showed that the adult breeding population of giant petrels (*Macronectes giganteus*), brown skuas (*Catharacta skua*) and South Polar skuas (*C. maccormicki*) were not adversely affected (Fraser and Patterson 1997). At the time of the oil spill, however, a population-wide mortality of South Polar Skua chicks occurred. Alternative hypotheses exist as to whether this was due to the oil spill, weather conditions, or regional food limitation, or a combination of these factors (Eppley and Rubega 1990; Trivelpiece et al. 1990; Eppley 1992).

Comparison of changes in Adélie penguin populations in the vicinity of Palmer Station with those receiving no exposure to oil suggests that colonies exposed to oil lost an additional 16% of their numbers, when the loss due to natural mortality was less than 3% (Fraser and Patterson 1997). Populations exposed to oil showed no significant differences compared with control sites in subsequent years. Cormorants (*P. atriceps*) showed a near 100% mortality of chicks following the spill; in subsequent years, the number of active nests had deceased by approximately 85% (Fraser and Patterson 1997). The number of active nest sites of the Kelp Gull (*L. dominicanus*) has shown a steady decline since 1989. This was probably due to a decline in their staple food the limpet *N. concinna*.

The only other oil spill incident was the grounding of the Australian research and supply ship the *Nella Dan* at Macquarie Island. Smith and Simpson (1995) assessed the impact of the oil spill on the community structure of invertebrates inhabiting the holdfasts of the bullkelp *Durvillaea antarctica*. The grounding resulted in the release of 270,000 l of oil, mostly light marine diesel on the northeastern coast of the island. Large mortalities of marine invertebrates were evident within the last few days following the oil spill with thousands of animals washed ashore along a 2-km stretch of the coastline immediately north of the grounding site.

The results of an inertidal study comparing distribution patterns with earlier work on inertidal zonation (Kenny and Hayson 1962; Simpson 1976a, 1976b) indicated that there were marked reductions in the abundance of marine invertebrates in the lower littoral zone at oiled locations when compared to the controls (Pople, Simpson, and Cairns 1990). More specifically, effects were localized to the kelp and lower red zones. The upper inertidal areas showed little difference among sites, which suggested minimal impact in these areas. Holdfasts from oiled sites were characterized by heavy sediment loads, a dominance of capitellid, cirratulid, and spionid polychaetes, and the rarity of the isopod *Limnoria stephenseni*. In contrast, samples from the control sites were dominated by peracarid crustaceans and, in particular, by the herbivorous isopod *L. stephenseni*. Analysis of differences in the size distribution patterns of the four most common species (the isopod *L. stephenseni*, the amphipods *Parawaldeckia kidderi*, and *Hyale novae zealandiae*, and the gastropod *Laevilittorina caliginosa*) suggests that impacts occurred across all sizes for *L. stephenseni* and *P. kidderi*. At the heavily oiled sites, size distribution patterns for the gastropod *L. caliginosa* were skewed towards larger individuals, suggesting a differential mortality of smaller individuals. It was suggested that the rarity of *L. stephenseni* at oiled sites may have resulted from the accumulation of sediment within the internal chamber of the holdfast producing a habitat more suitable for polychaete worms. It is clear that the oil spill had two effects on the benthic community: (1) direct toxicity and (2) longer-term modification of the habitat. In addition, the presence of hydrocarbon residues within the sediments may limit the fauna to opportunistic species with tolerance to these persistent oil fractions.

There have been a very limited number of studies of the impact of petroleum on cold-adapted Antarctic macro- and microorganisms, and the rates of degradation of petroleum products in the Antarctic marine environment. Fiala and Delille (1999) investigated the impact of diesel fuel and "Arabian light" crude oil on sea ice microalgae in land fast sea ice on the coastal shelf of Terre Adélie. In uncontaminated sea ice, chlorophyll *a* concentration showed two maxima, one in April (50 mg m^{-3}) during sea ice formation, and a second one in spring just before the ice thaw (20 mg m^{-3}). The crude oil and diesel fuel contamination induced a negative effect on ice-microalgal biomass, which remained at a weak level throughout the ice-covered period (Figure 21.3a). However, the inhibitory effect of diesel contamination occurred after the autumn phytoplankton bloom. The effect of bioremediation, (Floodgate 1995) a process designed to increase the rate of natural cleaning processes, was also tested. Inoculation with hydrocarbon-degrading microorganisms and/or addition of nutrients are the most studied strategies. Nutrient addition has been shown to stimulate the biodegradation of oil on a number of contaminate shorelines (Bragg et al. 1994). However, little was known about hydrocarbon degradation processes in cold environments. The addition of fertilizer (Inipol EPA-22) to diesel and crude oil had a clearly favorable effect in the sea-ice microalgae (Figure 21.3b).

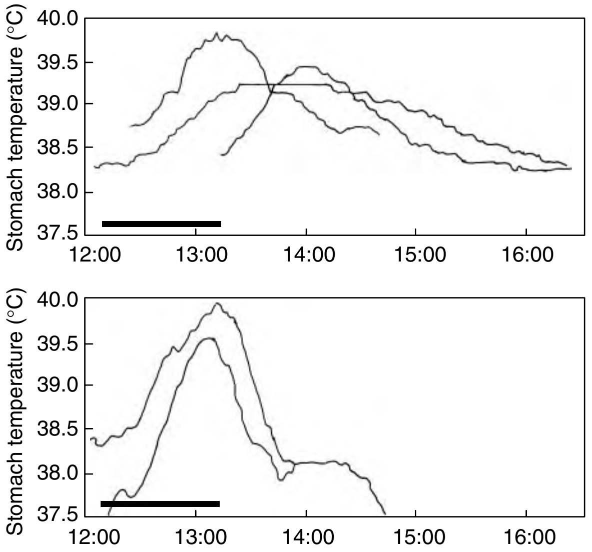


FIGURE 21.3 Stomach temperatures of three adults (a) and two chicks (b) reacting to "chicks weighing." Note that adults were not handled and neither were parents of the chicks. The stress event is marked by a bar. (From Regal, J., Putz, K., *Polar Biol.*, 18, 249, 1997. With permission.)

21.7 THE IMPACT OF RESOURCE EXPLOITATION

Probably the major human impact on the Antarctic marine ecosystem has been the exploitation of living resources. The first resource to be exploited was the stocks of whales, followed by seals and, more recently, krill and various fish species. The impact of the exploitation of these resources has been discussed in detail in Chapter 16 and Chapter 17.

Epilogue

From the accounts given in the various chapters of this book, the extent to which our understanding of the functioning of the Antarctic marine ecosystem has changed is evident. Prior to research carried out since the 1950s, the prevailing view of the Southern Ocean pelagic ecosystem could be summarized as follows:

1. High-diatom-dominated primary production, flourishing in a environment where nutrients were never limiting
2. A system dominated by short food chains (e.g., diatoms-krill-baleen whales)
3. Little information was available on the roles of bacteria and heterotrophic Protozoa. It was believed that they did not play as prominent a role as in temperate and tropical waters
4. Antarctic marine bacteria were believed to be temperature-limited in their activity, and their populations were believed to be much lower than those of temperate and tropical regions
5. There was practically no information on the vertical flux of organic matter and its remineralization
6. It was believed that krill (*Euphausa superba*) has a life span of 2, or a maximum of 3 years, that they spawned only once, and that they did not feed during the long Antarctic winter
7. Information on the distribution and magnitude of the krill stocks was scarce
8. Although the existence of the sea ice microbial community had been known for about 150 years, there was practically no information its composition, dynamics, and role in the Antarctic marine ecosystem
9. Although enhanced diatom production at the ice edge had been known for some time, there was little appreciation of the importance of ice edge processes
10. There was little available information on the impact that the decline in whale stocks had on the ecosystem
11. There was a prevailing view that the system was largely predictable and fragile
12. Although the taxonomy of the species of the benthic communities was reasonably known, there was little information on the biomass of the benthos, the ecology of the individual species, their adaptation to low temperatures (near the freezing point of sea water, the synchronization of life cycles to the brief input of organic matter during the spring–summer phytoplankton bloom, and of community dynamics

In contrast, the current view can be summarized as follows:

1. We now know that much of the phytoplankton production, especially in the open-water zone and the seasonal pack-ice zone, following the diatom and *Phaeocystis* blooms, is dominated by small nano- and picophytoplankton that can account for up to over 70% of the total net primary production. Although temporary reduction in nutrient levels occur during the blooms they are seldom reduced to levels where they become limiting.
2. We now understand the relative contributions of new (nitrate) and regenerated (ammonium) nutrients to the primary production process.
3. Although the diatom-krill-vertebrate consumer food chain is an important component of the marine food web, we now know that krill consume only something on the order of 2–5% of the phytoplankton primary production. However, locally, they can have a major impact on the phytoplankton community composition by their intensive grazing activity in which they contribute to the pool of regenerated nutrients (ammonium), and bring about a change to a system dominated by autotrophic microflagellates and heterotrophic miroflagellates and ciliates.
4. We now know the microbial food web in the Antarctic marine ecosystem is the same as in other oceans, and that the pelagic food web is a very complex one. Rather than categorizing areas of the Southern Ocean as *eutrophic* or *oligotrophic*, it is now considered that, at different times, any particular area can occupy the total spectrum from oligotrophic to eutrophic.
5. As a result of recent research, we now know that heterotrophic protozoa are as abundant as those in other oceans and that they play a similar role in the pelagic ecosystem.
6. Our views of the roles of bacteria have changed dramatically. They are as abundant as in other

oceans and, although their activity may approach that found in temperate seas, the metabolic rates are, to some degree determined, by the prevailing low temperatures.

7. Research has shown that the vertical flux from the euphotic zone to deeper waters and the sediments occurs mainly during the diatom blooms, and that at other times such flux is negligible or low. When the pelagic primary production is dominated by the small nano- and picophytoplankton, organic matter is recycled within the euphotic zone, with remineralization resulting in the production of regenerated nitrogen (ammonium).
8. There has been a dramatic change in our view of krill and its role in the Southern Ocean marine ecosystem. We now know that krill may live up to at least 7 years (instead of three) and that they may spawn at least over three seasons. We now have much information on krill swarming and the factors influencing it, although we are still unable to estimate its absolute abundance. In contrast to the idea that krill did not feed during the Antarctic winter, it has been established that in the pack ice during the winter they have an abundant food supply, feeding on the sea-ice microalgae. This food supply is of particular importance to the fucilia larvae.
9. A considerable body of information has now accumulated on the dynamics of the sea-ice microbial community. The development, growth rates, and physiological ecology of the sea-ice microalgae is now reasonably well known; estimates of the right order of magnitude can be made of the sea ice microbial contribution to the overall primary productivity of the Southern Ocean. We now have a better understanding of the composition and ecological roles of the sea-ice bacteria, protozoa, and metazoa. It is now clear that the release of the sea ice microalgae upon the melting of the ice seeds the water column giving rise to the marginal ice edge blooms. The role of the sea ice as a nursery for the development stages of some copepod species has been established and the role of the under-ice cryopelagic community is now well known.
10. As a result of the research carried out, the importance of the marginal-ice-edge primary production and its role in supporting primary consumers and higher trophic levels is now clear. If this ice-edge production is taken into account, then the apparent anomaly of the overall low primary production in the high nutrient-low chlorophyll regions that comprise large areas of the Southern Ocean and the large populations of vertebrate consumers and the often high rates of biogenic sedimentation can be resolved.
11. We now know that the decline in the baleen whale stocks has resulted in changes in the demographic parameters of krill consumers (birds, seals, and minke whales), although we do not yet know what new equilibrium will reached.
12. Far from being stable and predictable, the Southern Ocean system has been shown to be highly variable on a range of scales. This is particularly evident in the distribution and abundance of krill, which we now know fluctuates widely from year to year in any given location. The system is subject to natural perturbations of varying intensity and duration; this results in a system that is resilient and not fragile.
13. Research has established that the Antarctic benthos is not impoverished, but is characterized by very high biomass levels—several times that of the benthos—at comparable depths in the Arctic, with infaunal densities, especially in shallow shelf areas, equal to the highest densities recorded elsewhere in the world's oceans. It is now known that the benthos of the deep Antarctic bottoms is much richer than previously thought, and the meiofaunal diversity and density is comparable to that of other areas. Considerable progress has been made in understanding the considerable impact of iceberg scour on benthic communities. More information is now available on the adaptation of the benthic species to the prevailing low temperatures.
14. Previously little was known concerning the possible impact of increased ultraviolet radiation on Antarctic marine ecosystems. As a result of recent research, we now have a good understanding of its impact.
15. Recent research has documented the impact of global warming on Antarctic marine ecosystems and we are now in a position to be able to predict future changes that may occur.

In spite of the considerable advances that have been made, there are still many gaps in our understanding of the functioning of Antarctic marine ecosystems. As discussed in Chapter 15, the system is characterized by considerable variability, not only in the physical features of the environment, but also in its biological components. This variability, which occurs on a variety of scales (interannual, annual, meso-, and large-scale, etc.), needs to be understood, both as a basis for the management of the living resources of the Southern Ocean and for the assessment and prediction of future change.

As detailed in Chapter 14, we now know that the Southern Ocean pelagic ecosystem resembles that of other oceanic areas in the roles played by bacteria and heterotrophic protozoans in the microbial network and in the remineralization of organic detritus. However, much more research is required on the rates of formation of particulate organic particle and dissolved organic matter, the rates of decomposition of POC in the water column, and the rates and quantities of particulate vertical flux to the sediments. Although the shelf benthic communities have densities and biomasses comparable to the most productive communities elsewhere in the world's oceans, only a few studies have been carried out on the dynamics of the communities.

Attention is increasingly being paid to how the unique characteristics of the Antarctic marine environment can be protected from man-induced changes. Although many view the Antarctic region as pristine, it has suffered destructive exploitation of its living resources, whales, seals, and fish for over 200 years. In addition, there has been an increasing human presence in the form of logistic and research bases, while Antarctic tourism is on the increase. Although in the past this has resulted in localized negative impacts, the Scientific Committee on Antarctic Research (SCAR) countries have adopted measures designed to minimize such impacts.

Exploitation of the living resources of the Southern Ocean, as discussed in Chapter 16, is now controlled by CCAMLR. This provides a framework for the regulation of fisheries for krill, fish, and squid and any other living marine resource, apart from seals and whales. As we have seen, the convention is unusual in that its ecological emphasis requires that exploitation should not be allowed to progress to the point at which nontarget species are at risk. Although the current exploitation of krill does not have a significant overall impact on dependent species, the exploitation of fish has resulted in every commercially attractive fish stock being allowed to decline below its most productive level. CCAMLR has been moving, at a pace that has been criticized as too slow, to conserve heavily depleted stocks and ensure their recovery. However, uncertainty regarding aspects of the dynamics of Antarctic marine ecosystems, and in particular the magnitude of the krill stocks and their production rates, has made practical management difficult. It can be said that, as far as CCAMLR is concerned, the jury is still out; however, every encouragement should be given to it in its endeavours to develop sound, sustainable management of the living resources of the Southern Ocean.

The SCAR has played a lead role in Antarctic conservation and in coordinating research on Southern Ocean ecosystems. Over the years, it developed a series of multinational scientific research programmes, such as the BIOMASS Program, that carried out much of the research discussed in this book. Recently, SCAR has developed a series of new multidisciplinary research programs, two of which are particularly relevant to Southern Ocean ecosystems: the Antartic and the Global Climate System Program (a Scientific Program on AGCS) and the Evolution and Biodiversity in the Antartica Program (EBA).

The AGCS Program aims to investigate the nature of the atmospheric and oceanic linkages between the climate of Antarctica and the rest of the Earth system, as well as the mechanisms involved therein. The EBA Program—the response of life to change—will involve a suite of modern techniques and an interdisciplinary approach to explore the evolutionary history of selected Antarctic biota to examine how modern biological diversity in the Antarctic influences the way present-day ecosystems function, and thereby predict how the biota may respond to future environmental change. An integral component of the programme will be the Circum-Antarctic Census of Marine Life (CirAntCML).

Research carried out under these two programs will provide critical information on the functioning of Antarctic marine ecosystems.

References

Abrams, R.W., Energy and food requirements of pelagic aerial seabirds in different regions of the African sector of the Indian Ocean, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M. Eds., Springer, Berlin, 1985a, 466–472.

Abrams, R.W., Environmental determinants of pelagic seabird distribution in the African sector of the Southern Ocean, *J. Biogeogr.*, 12, 473–492, 1985b.

Accornero, A., Marino, C., Arrigo, K.P., Martion, A., Tucci, S., Vertical flux of particulate matter in the polyna of Terra Nova Bay, Part I: Chemical constituents, *Antarc. Sci.*, 15, 119–132, 2003.

Accornero, A., Marino, C., Esposito, F., Gambi, M.C., Vertical flux of particulate matter in the polyna of Terra Nova Bay, Part II: Biological components, *Antarc. Sci.*, 15, 175–188, 2003.

Ackley, S.F., Ice-scavenging and nucleation: Two mechanisms for incorporation of algae into newly-forming sea ice, *EOS Trans., Am. Geophy. Union*, 63, 54–55, 1982.

Ackley, S.P., Sullivan, C.W., Physical controls on the development and characteristics of Antarctic sea ice biological communities—a review and synthesis, *Deep-Sea Res.*, 41, 1583–1604, 1994.

Ackley, S.F., Taguchi, S., Buck, K.R., Sea ice algal relationships in the Weddell Sea, *Antarc. J. U.S.*, 13, 7–10, 1978a.

Ackley, S.F., Taguchi, S., Buck, K.R., Primary productivity in sea ice of the Weddell Region, *U.S. Army Corps of Engineers Cold Regions Research and Engineering Report*, 78, 191–217, 1978b.

Ackley, S.F., Buck, K.R., Taguchi, S., Standing crop of algae in the sea ice of the Weddell Sea region, *Deep-Sea Res.*, 26A, 269–381, 1979.

Ackley, S.F., Dieckmann, G.S., Shen, H., Algal and foram incorporation into new sea ice, *EOS Trans. Am. Geophys. Union*, 68, 1736, 1987.

Ackley, S.F., Bengston, J.L., Boveng, P., Castellini, M., Daly, K.L., Jacobs, S., Kooyman, G.L., Laake, J., Quetin, L., Ross, R., Siniff, D.B., Stewart, B.S., Stirling, I., Torres, J., Yochem, P.K., The top-down multidisciplinary study of the structure and function of the pack ice ecosystem in the eastern Ross Sea, Antarctica, *Polar Rec.*, 39, 219–230, 2003.

ACMRR (FAO), *Report on the Scientific Consultation on the Conservation and Management of Marine Mammals and their Environment and ACMRR Working Party on Marine Mammals*, Bergen, Norway, 31 August–9 September 1976, 1976.

Acosta Pomer, M.-L.C., Bruni, V., Maugeri, T.L., Picoplankton biomass in the Ross Sea, Antarctica, *Polar Biol.*, 13, 1–6, 1993.

Adams, N.J., Brown, C.R., Dietary differentiation and trophic relationships in the sub-Antarctic penguin community at Marion Island, *Mar. Ecol. Prog. Ser.*, 57, 249–258, 1989.

Adams, N.J., Klages, N.T., Seasonal variation in the diet of king penguins (*Aptenodytes patagonicus*) at subAntarctic Marion Island, *J. Zool. (Lond.)*, 212, 303–324, 1987.

Adams, N.J., Klages, N.T., Temporal variation in the diet of gentoo penguins (*Pygoscelis papua*) at Marion Island, *Colonial Waterbirds*, 12, 30–36, 1989.

Adelung, D., Buchholz, F., Calik, B., Keck, A., Fluoride in the tissues of krill (*Euphausia superba* Dana and *Meganyctiphanes norvegica* M.Sars) in relation to the moult cycle, *Polar Biol.*, 7, 43–50, 1987.

Adie, R.J., Geological history, in *Antarctic Research: A Review of British Scientific Achievement in Antarctica*, Priestley, R., Adie, R.J., de Q Robin, G., Eds., Butterworths, London, 1964, 118–162.

Admiral, W., Venekamp, A.H., Significance of tintinnid grazing during blooms of *Phaeocystis pouchetii* (Heptophyceae) in Dutch coastal waters, *Neth. J. Sea Res.*, 20, 61–66, 1986.

Agnew, D., Review of the CCAMLR Ecosystem Monitoring Program, *Antarc. Sci.*, 9(3), 235–242, 1997.

Aguaya, A., The present status of the Antarctic fur seal, *Arctocephalus gazella*, at the South Shetland Islands, *Polar Rec.*, 19, 167–176, 1978.

Ahlgren, J.A., DeVries, A.L., Comparison of antifreeze glycoproteins from several Antarctic fishes, *Polar Biol.*, 3, 93–97, 1984.

Ahlgren, J.A., Cheng, C.C., Schrag, J.D., DeVries, A.L., Freezing avoidance and the distribution of antifreeze glycopeptides in body fluid and tissues of Antarctic fish, *J. Exp. Biol.*, 137, 549–563, 1988.

Ahn, L.V., Kang.Y.-C., Preliminary study on the macrobenthic community of Maxwell Bay, South Shetland Islands, *Korean J. Polar Res.*, 2, 61–71, 1991.

Ainley, D.G., Biomass of birds and mammals in the Ross Sea, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, W.R., Laws, R.M., Eds., Springer, Berlin, 1985, 498–515.

Ainley, D.G., Boekelheide, R.J., An ecological comparison of oceanic seabird communities in the South Pacific Ocean, *Stud. Avian Biol.*, 8, 2–23, 1983.

Ainley, D.G., DeMaster, D.P., Survival and mortality in a population of penguins, *Ecology*, 61, 522–530, 1980.

Ainley, D.G., DeMaster, D.P., Upper trophic levels in polar marine ecosystems, in *Polar Oceanography, Part B: Chemistry, Biology and Geology*, Smith, W.O., Jr., Ed., Academic Press, San Diego, CA, 1990, 599–630.

Ainley, D.G., Jacobs, S.S., Seabird affinities for ocean and ice boundaries in the Antarctic, *Deep-Sea Res.*, 28A, 1173–1185, 1981.

Ainley, D.G., LeResche, R.E., The effects of weather and ice conditions on breeding Adélie Penguins, *Condor*, 75, 235–239, 1973.

Ainley, D.G., Sullivan, C.W., AMERIEZ 1983: A summary of activities on board RV *Melville* and USGS *Westwind*, *Antarc. J. U.S.*, 19, 100–102, 1984.

Ainley, D.G., LeResche, R.E., Sladen, W.J.L., *Breeding Biology of Adélie Penguins*, University of California Press, Berkeley, CA, 1983.

Ainley, D.G., O'Connor, E.F., Borkelheide, R.J., The marine ecology of the birds in the Ross Sea, *Ornithol. Monogr.*, 32, 1–97, 1984.

Ainley, D.G., Fraser, W.R., Sullivan, C.W., Torres, J.J., Hopkins, T.L., Smith, W.O., Jr., Antarctic mesopelagic micronekton: evidence from seabirds that pack ice affects community structure, *Science*, 232, 847–849, 1985.

Ainley, D.G., Fraser, W.R., Daley, K.L., Effects of pack ice on the composition of micronekton communities in the Weddell Sea, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin, 1988, 140–146.

Ainley, D.G., Fraser, W.R., Smith, W.O., Jr., Hopkins, T.L., Torres, J.J., The structure of upper-level pelagic food webs in the Antarctic: effect of phytoplankton distribution, *J. Mar. Syst.*, 2, 111–122, 1991.

Ainley, D.G., Ribec, C.A., Fraser, W.R., Does prey preference affect habitat choice in Antarctic seabirds?, *Mar. Ecol. Prog. Ser.*, 90, 207–221, 1992.

Ainley, D.G., Ribic, C.A., Fraser, W.R., Ecological structure among migrant and resident seabirds of the Scotia–Weddell confluence region, *J. Anim. Ecol.*, 63, 347–364, 1994.

Alberti, G., Kils, U., The filtering basket of *Euphausia superba*, *ICES CM 1980/L*, 54–63, 1990.

Alder, V.A., Boltavoskay, D., The ecology and biogeography of tintinnid ciliates in the Atlantic sector of the Southern Ocean, *Mar. Chem.*, 35(1–4), 337–346, 1991.

Alexander, V., Interrelationships between seasonal sea ice zone and biological regimes, *Cold Reg. Sci. Technol.*, 2, 157–178, 1980.

Alexander, V., Niebauer, J.H., Oceanography of the eastern Bering Sea ice-edge zone in spring, *Limnol. Oceanogr.*, 26, 1111–1125, 1981.

Aleyev, Y., *Nekton*, Dr. W. Junk Publishers, The Hague, 1977.

Allanson, B.R., Hart, R.C., Lutjeharms, J.R., Observations on the nutrients, chlorophyll, and primary production of the Southern Ocean south of Africa, *S. Afr. J. Antarc. Res.*, 10/11, 3–14, 1981.

Allanson, B.R., Boden, B., Parker, L., Duncombe, R., A contribution to the oceanology of the Prince Edward Islands, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 38–43.

Alldredge, A.L., Madin, L.P., Pelagic tunicates: unique herbivores in marine plankton, *BioScience*, 32, 655, 1982.

Alldredge, A.L., Silver, M.W., Characteristics, dynamics, and significance of marine snow, *Prog. Oceanogr.*, 20, 41–82, 1988.

Allen, K.R., Some methods for estimating exploited populations, *J. Fish. Res. Board Canada*, 23(10), 1553–1574, 1966.

Allen, K.R., Simplification of a method for estimating exploited populations, *J. Fish. Res. Board Canada*, 25, 270–1143, 1968.

Allen, K.R., Relation between production and biomass, *J. Fish. Res. Board Canada*, 28, 1573–1581, 1971.

Allen, K.R. *Conservation and Management of Whales*, University of Washington Press, Seattle,WA, 1980.

Almeida Prado-Par, M.S., Diel vertical migration of zooplankton at a fixed station in the Bransfield Strait, summer 1985, *Pesquisa Antártica Brasileira*, 1, 89, 1989.

Alvarifio, A., Bathymetric distribution of chaetognaths, *Pac. Sci.*, 18, 64–82, 1964.

Amaratunga, T., Population Biology, in *Cephalopod Life Cycles*, Vol. 2, Boyle, P.R., Ed., Academic Press, London, 1987, 239–252.

AMERIEZ A Research Plan for Antarctic Marine Ecosystem Research at the Ice Edge Zone (AMERIEZ). (1983), AMERIEZ Steering Committee, Washington, DC, 1983.

Amos, A.F., Distribution of krill (*Euphausia superba*) and the hydrography of the Southern Ocean: Large-scale processes, *J. Crustacean Biol.*, 4(Special Issue No.1), 306–329, 1984.

Amsler, C.D., Rowley, R.J., Laur, D.R., Quetin, L.B., Ross, R.M., Vertical distribution of Antarctic peninsular macroalgal cover: Biomass and species composition, *Phycologia*, 34, 424–430, 1995.

Anderson, H.T., *The Biology of Marine Mammals*, Academic Press, New York, 1969.

Anderson, V., Filtration and ingestion rates of *Salpa fusiformis* Cuvier (Tunicata: Thaliacea): effects of size, individual weight and algal concentration, *J. Exp. Mar. Biol. Ecol.*, 87, 13–27, 1985.

Anderson, H.T. Ed., *The Biology of Marine Mammals*, Academic Press, New York, 1999.

Anderson, B., Chague-Goff, C., *Benthic Foraminifera and Trace Metals in Sediments off the Scott Base Sewer Outfall, Antarctica*, Antarctic Data Series No. 18, Antarctic Research Centre, Research School of Earth Sciences, Victoria University, Wellington, 1996, 1–12.

Anderson, P., Fenchel, T., Bactivory by microheterotrophic flagellates in sea water samples, *Limnol. Oceanogr.*, 30, 198–202, 1985.

Anderson, V., Nival, P., A pelagic ecosystem model simulating production and sedimentation of biogenic particles: role of salps and copepods, *Mar. Ecol. Prog. Ser.*, 44, 37–50, 1988.

Andersson, A., Azam, F., Hagstrom, A., Release of aminoacids and inorganic nutrients by heterotrophic marine microflagellates, *Mar. Ecol. Prog. Ser.*, 23, 99–106, 1995.

Andreae, M.O., Ocean–atmosphere interactions in the global biogeochemical sulfur cycle, *Mar. Chem.*, 30, 1–29, 1990.

Andreev, M.P., Bykov, V.P., Smirov, V.M., Investigation of the influence of post-modem in krill on the quality of processed flesh, in *Krill Processing Technology*, Bykov, V.P., Ed., VNIRO, Moscow, 1981, 68–72.

Andrew, D., Review of the CCAMLR Ecosystem Monitoring Program, *Aust. Sci.*, 9, 235–242, 1997.

Andrews, K.J.H., The distribution and life-history of *Calanoides acutus* (Giesbrecht), *Discov. Rep.*, 34, 117–162, 1966.

Andriashev, A.P., A general review of the Antarctic fish fauna, in *Biogeography and Ecology of Antarctica*, van Oye, P., van Meigham, J., Eds., Dr. W. Junk, The Hague, 1965, 491–550.

Andriashev, A.P., The problem of the life community associated with the lower layer of the Antarctic fast ice, *SCAR/SCOR/IABO/IUBS Symposium on Antarctic Oceanography, Santiago, Chile, 13–16 September, 1966*, Currie, R.I., Ed., 1968, 147–155.

Andriashev, A.P., Butskaya, N.A., Faleeva, T.I., Polovye tsikly antarkticheskih ryb *Trematomus bernachii i Pagothenia borchgrevinki* (Notheniidae) v sviazis adaptatsiei k usloviian obitaniia, *Dolklady Akademii Nauk SSSR*, 248, 400–502, 1979.

Angel, M.V., Detrital organic fluxes through pelagic ecosystems, in *Flows of Energy and Materials in Marine Ecosystems: Theory and Practice*, Fasham, M.J., Ed., Plenum Press, New York, 1984, 475–516.

Angel, M.V., Fasham, M.J.R., Eddies and biological processes, in *Eddies in Marine Science*, Robinson, A.R., Ed., Springer, Berlin, 1983, 492–524.

Anonymous, FIBEX acoustic survey design, *Biomass Rep. Ser.*, 20, 1–14, 1980.

Anonymous, Post-FIBEX data interpretation workshop, *Biomass Rep. Ser.*, 20–27, 1981a.

Anonymous, Convention on the conservation of Antarctic Marine Living Resources, *SCAR Bull.*, 67, 383–395, 1981b.

Anonymous, Technical group on programme implementation and coordination, Third Meeting, *Biomass Rep. Ser.*, 29, 1–28, 1982.

Anonymous, Second Post-FIBEX Hydrograhic Data Interpretation Workshop, Hamburg, F.R. Germany, 16–20 May 1983, *Biomass Rep. Ser.*, 31, 1–26, 1983.

Anonymous, Results of research into distribution and status of stocks of target species in the Convention area—Atlantic, Indian and Pacific Ocean Sectors of Antarctica, in *Selected Papers Presented to the Scientific Committee of CCAMLR 1982–84, Part I*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1984a, 227–325.

Anonymous, General circulation of the Southern Ocean: Status and recommendations for research: a report by SCOR Working Group 74, *World Climate Programme Series No. 108*, 1–50, 1984b.

Anonymous, An approach to a management strategy for the Antarctic marine ecosystem, in *Selected Papers Presented to the Scientific Committee of CCAMLR, Part II*, Convention on the Conservation of Antarctic Marine Living Resources, Hobart, 1985a, 1–14.

Anonymous, Ecosystem management: Proposal for undertaking a coordinated fishing and research experiment at selected sites around Antarctica, in *Selected Papers Presented to the Scientific Committee of CCAMLR, Part II*, Commission on the Conservation of Antarctic Marine Living Resources, Hobart, 1985b, 285–294.

Anonymous, Post-FIBEX acoustic workshop, Frankfurt, Federal Republic of Germany, September 1984. *Biomass Rep. Ser.* No. 40, 1–106, 1986.

Anonymous, *Report of the Workshop on Southern Elephant Seals*, CCAMLR Wg-GEMP-91/92, 8 pp, 1991.

Antezana, T., Ray, K., Aggregation of *Euphausia superba* as an adaptive group strategy to the Antarctic ecosystem, *Berichte zur Polarforschung*, 4, 199–215, 1983.

Antezana, T., Ray, K., Active feeding of *Euphausia superba* in a swarm north of Elephant Island, *J. Crustacean Biol.*, 4(Special Issue No.1), 142–155, 1984.

Antezana, T., Ray, K., Melo, C., Trophic behaviour of *Euphausia superba* in laboratory conditions, *Polar Biol.*, 1, 77–82, 1982.

Antz, W.E., T. Brey, Eds. The expedition of *ANTARKTIS XVII/3* (EASIZ) of the RV *Polarstern* in 1998, *Ber. Polarforsch.*, 1–229, 402.

Antz, W.E., Gutt, J., Eds., The expedition of the *ANTARKTIS XIII*/3 (EASIZ) of the RV *Polarstern* to the eastern Weddell Sea in 1996, *Ber. Polarforsch.*, 249, 1–239, 1997.

Antz, W.E., Gutt, J., Eds., The expedition of *ANTARKTIS XV*/3 (EASIZ II) of the RV *Polarstern* in 1998, *Berichte zur Polarforschung*, 301, 1–148, 1999.

Antz, W.E., Brey, T., Gerdes, D., Gorny, M., Gutt, J., Hosin, S., Klages, M., Pattern of life history and population dynamics of benthic invertebrates under the high conditions of the Weddell Sea, Antarctica, *Polar Biol.*, 11, 169–177, 1992.

Antz, W.E., Brey, T., Gallardo, V.A., Antarctic zoobenthos, *Oceanogr. Mar. Biol. Annu. Rev.*, 32, 241–304, 1994.

Antz, W.E., Gutt, J., Klages, M., Antarctic marine biodiversity: an overview, in *Antarctic Communities: Species, Structure, and Survival*, Antz, W.E., Gutt, J., Klages, M., Eds., Cambridge University Press, Cambridge, UK, 1997, 3–13.

Archer, S.D., Leakey, R.J.G., Burkill, P.H., Sleigh, M.A., Appleby, C.J., Microbial ecology of sea ice at a coastal Antarctic site: Community composition, biomass, and temporal change, *Mar. Ecol. Prog. Ser.*, 135, 179–195, 1996.

Aristegui, J., Montero, M.F., Batesteros, S., Basterretx, G., van Lenning, K., Plankton primary production and microbial respiration measured by ^{14}C assimilation and dissolved oxygen changes in coastal waters of the Antarctic Peninsula during austral summer: Implications of carbon flux studies, *Mar. Ecol. Prog. Ser.*, 132, 191–201, 1996.

Armstrong, A.J., Siegfried, W.R., Consumption of Antarctic krill by Minke whales, *Antarc. Sci.*, 3(1), 13–18, 1991.

Arnaud, P.M., Nature de l'entagement du benthos algal et animal dans l'Antarctique, *Compt. Rendu. Acad. Sci., Paris*, 262, 16–26, 1965.

Arnaud, P.M., Frequency and ecological significance of necrophagy among benthic species in Antarctic coastal waters, in *Antarctic Ecology.*Vol. I, Holdgate, W.M., Ed., Academic Press, London, 1970, 259–267.

Arnaud, P.M., Contribution a la bionomie marine benthique des regions antarctiques et subantarctiques, *Tethys*, 6, 467–653, 1974.

Arnaud, P.M., Adaptations within the Antarctic marine benthic ecosystem, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 135–157.

Arnaud, P.M., Jazdzewski, K., Presler, P., Sicinski, J., Preliminary survey of benthic invertebrates collected by Polish Antarctic expeditions in Admiralty Bay (King George Island, South Shetland Island), *Pol. Polar Res.*, 7(1–2), 7–24, 1986.

Arnould, J.P.V., Whitehead, M.D., Diet of Antarctic petrels, cape pigeons, and southern fulmars rearing chicks at Prydz Bay, *Antarc. Sci.*, 3, 19–27, 1991.

Arrigo, K.R., Impact of ozone depletion on phytoplankton growth in the Southern Ocean: Large-scale spatial and temporal variability, *Mar. Ecol. Prog. Ser.*, 114, 1–12, 1994.

Arrigo, K.R., McClain, C.R., Spring phytoplankton production in the western Ross Sea, *Science*, 226, 261–263, 1994.

Arrigo, K.R., Sullivan, C.W., The influence of salinity and temperate covariation on the photophysical characteristics of Antarctic sea ice microalgae, *J. Phycol.*, 28, 746–756, 1992.

Arrigo, K.R., Thomas, D.N., Large-scale importance of sea ice biology in the Southern Ocean, *Antarc. Sci.*, 16, 471–486, 2004.

Arrigo, K.R., Robinson, D.H., Sullivan, C.W., A high resolution study of the platelet ice ecosystem in McMurdo Sound, Antarctica: Photosynthetic and bio-optical characteristics of a dense algal bloom, *Mar. Ecol. Prog. Ser.*, 98, 173–185, 1993.

Arrigo, K.R., Dieckmann, G., Gosselin, M., Robinson, D.H., Fritzen, C.H., Sullivan, C.W., High-resolution study of the platelet ice ecosystem in McMurdo Sound, Antarctica: Biomass, nutrient, and production profiles within a dense microalgal bloom, *Mar. Ecol. Prog. Ser.*, 127, 255–268, 1995.

Arrigo, K.A., Worthen, D.L., Lizotte, M.P., Primary production of near-surface communities within Antarctic pack ice, *Antarc. Res. Ser.*, 73, 23–43, 1998.

Arrigo, K.R., Ditullio, G.R., Dunbar, R.B., Robinson, D.H., van Woert, M., Worthen, D.L., Lizotte, M.P., Bio-optical properties of the southwestern Ross Sea, *J. Geophys. Res.*, 103, 21683–21695, 2000.

Aseev, Y.P., Size structure and longevity of krill populations from the Indian Ocean sector of Antarctica, in *Antarctic Krill: Distribution Pattern and Environment*, Lubimov, T.G., Ed., Trudy VNIRO, Moscow, *Sbornik Nauk Trudy Vses Nauchno-issled Rybnogoz Khoziaistra Okeanografii*, 1983, 103–110.

Asencio, G., Moreno, C.A., Dieta y selectividad alimentaria de *Protomyctophum bolini* Fraser-Brunner (Pisces: Myctophidae) en el paso Drake (Antarctica), *Serie Científico del Instituto Antártico Chileno*, 31, 85–96, 1984.

Asheimer, H., Krause, H., Rakusa-Suszczewski, S., Modelling individual growth of the Antarctic krill, *Euphausia superba*, *Polar Biol.*, 4, 65–73, 1985.

Ashmole, N.P., Seabird ecology and the marine environment, in *Avian Biology,* Vol. I, Farner, D.S.F., King, K., Eds., Academic Press, New York, 1971, 192–304.

Ashmole, N.P., Ashmole, M.J., Comparative feeding ecology of sea birds of a tropical oceanic island, *Bull. Peabody Mus. Nat. Hist.*, 24, 1–131, 1967.

Atkinson, A., Distribution of six major copepod species around South Georgia during an austral summer, *Polar Biol.*, 9, 3–11, 1989.

Atkinson, A., Peck, J.M., A summer-winter comparison of the zooplankton in the oceanic area around South Georgia, *Polar Biol.*, 8, 463–473, 1988.

Atkinson, A., Peck, J.M., The distribution of zooplankton in relation to the South Georgia shelf in summer and winter, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin, 1990, 159–165.

Atkinson, A., Sinclair, T.D., Zonal distribution and seasonal vertical migration of copepod assemblages in the Scotia Sea, *Polar Biol.*, 23, 46–58, 2000.

Atkinson, A., Snyder, R., Krill-copepod interactions at South Georgia, Antarctica, I: Omnivory by *Euphausia superba*, *Mar. Ecol. Prog. Ser.*, 160, 63–76, 1997.

Atkinson, A., Whitehouse, M.J., Ammonium excretion by Antarctic krill Euphausia superba at South Georgia, *Limnol. Oceanogr.*, 45, 55–63, 2000.

Atkinson, A., Whitehouse, M.J., Ammonium regeneration by Antarctic mesoplankton: an allometric approach, *Mar. Biol.*, 139, 301–311, 2001.

Atkinson, A., Ward, P., Williams, R., Poulet, S.A., Diel vertical migration and feeding of copepods at an oceanic site near South Georgia, *Mar. Biol.*, 113, 583–593, 1992.

Atkinson, A., Shreene, R.S., Pakhomov, E.A., Priddle, J., Blight, S.P., Ward, P., Zooplankton response to a phytoplankton bloom near South Georgia, Antarctica, *Mar. Ecol. Prog. Ser.*, 144, 195–210, 1996.

Atkinson, A., Ward, P., Hill, A., Brierley, A.S., Cripps, G.C., Krill-copepod interactions at South Georgia, II: *Euphausia superba* as a major control on copepod abundance, *Mar. Ecol. Prog. Ser.*, 176, 63–79, 1999.

Atkinson, A., Whitehouse, M.J., Priddle, J., Cripps, G.C., Ward, P., Brandon, M.A., South Georgia Antarctica: a productive cold-water pelagic system, *Mar. Ecol. Prog. Ser.*, 216, 279–308, 2001.

Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., Long-term decline in krill stocks and increase in salps within the Southern Ocean, *Nature (Lond.)*, 432, 100–103, 2004.

Ayala, F.J., Valentine, J.W., Zumwalt, G.S., An electrophoretic study of the zooplankter *Euphausia superba*, *Limnol. Oceanogr.*, 20, 635–640, 1975.

Azam, F., Ammerman, J.W., Cycling of organic material by bacterioplankton in pelagic marine ecosystems: Environmental considerations, in *Flows of Energy and Materials in Marine Ecosystems*, Fasham, M.J.R., Ed., Plenum Press, New York, 1984, 345–360.

Azam, F., Hodson, R.E., Multiphasic kinetics for D-glucose uptake by assemblages of natural marine bacteria, *Mar. Ecol. Prog. Ser.*, 6, 213–222, 1981.

Azam, F., Ammerman, J.W., Cooper, N., Bacterioplankton distributional patterns and metabolic activities in the Scotia Sea, *Antarc. J. U.S.*, 16, 164–165, 1981.

Azam, F., Ammerman, J.W., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, F., The ecological role of water-column microbes in the sea, *Mar. Ecol. Prog. Ser.*, 10, 257–263, 1983.

Azam, F., Smith, D.C., Hollibaugh, J.T., The role of the microbial loop in Antarctic pelagic ecosystems, *Polar Res.*, 102, 239–243, 1991.

Azam, F., Beers, R.J., Campbell, L., Carlucci, A.F., Holm-Hansen, O., Reid, F.M.H., Occurrence and metabolic activity of organisms under the Ross Ice Shelf, Antarctica, at Station J9, *Science*, 203, 451–453, 1998.

Azzali, M., Kalinowski, J., Spatial and temporal distribution of krill (*Euphausia superba*) biomass in the Ross Sea (1989–1990 and 1994), in *Ross Sea Ecology*, Farando, F.M., Guglielmo, L., Ianova, A., Eds., Springer, Berlin, 1998, 433–455.

Azzali, M., Kalinowski, J., Castagnani, R., *How much krill is there? Results of the 5th Italian Expedition to the Ross Sea, 1989/90*, BIOMASS Newsletter, Biomass/Scar/IABO/ACMRR, Vol. 13, Texas A&M University, College Station, TX, 1991, 6–7.

Azzali, M., J. Kalinowski, N. Saino, Estimation of biomass of krill (*Euphausia superba*) and birds and mammal census during Xth Italian Expedition to the Ross Sea, November–December 1994, *DOC WB-EMM 96/63 Agenda Item No. 3*, Commission for the Conservation of Antarctic Marine Living Resources, CCAMLR Hobart, 1996, 21–26.

Baarud, T., Klem, A., Hydrological and chemical investigations in the coastal waters off More in the Romsdatfjord, *Hvalradets Skrifter*, 1, 1–88, 1931.

Bada, J.L., Lee, C., Decomposition and alteration of organic compounds dissolved in seawater, *Mar. Chem.*, 5, 523–534, 1977.

Baines, P.G., Condie, S., Observations and modelling of Antarctic downslope flows: A review, in *Interactions at the Antarctic Continental Margin*, Jacobs, S.S., Weiss, R., Eds., *Antarct. Res. Ser.*, 75, 20–49, 1998.

Baker, A.deC., The circumpolar continuity of Antarctic plankton species, *Discov. Rep.*, 29, 201–218, 1954.

Baker, A.deC., The distribution and life history of *Euphausia tricantha* Holt and Tattersall, *Discov. Rep.*, 29, 309–340, 1959.

Baker, A.deC., The problem of keeping animals alive in the laboratory, *J. Mar. Biol. Assoc. U.K.*, 43, 291–294, 1963.

Baker, D.J., Polar oceanography II: South Ocean, *Rev. Geophys. Space. Phys.*, 17, 1578–1585, 1979.

Balbontin, F., Garreton, M., Newling, J., Composicion del alimento y tarnano de las presas en larvas de peces del estrecho Bransfield (SIBEX Fase II-Chile), *Serie Científica del Instituto Antártico Chileno*, 35, 25–144, 1986.

Balech, E., *Clave ilustrada de dinoflagelados Antarcticos*, Buenos Aires: Instituto Antártico Argentino Direccion Nacional del Antartico, Publ. IAA No. 11, 99 pp, 1975.

Bannister, J.L., The biology and status of the sperm whale off Western Australia—an extended summary of results of recent work, *Int. Whaling Committee Rep.*, 19, 70–76, 1969.

Bannister, J.L., Baker, A.deC., Observations on food and feeding of baleen whales off Durban, *Norwegian Whaling Gazette*, 56, 78–82, 1967.

Banse, K., Determining the carbon-to-chlorophyll ratios of natural phytoplankton, *Mar. Biol.*, 41, 199–212, 1977.

Banse, K., Does iron really limit phytoplankton production in offshore subarctic Pacific?, *Limnol. Oceanogr.*, 35, 772–775, 1990.

Barber, R.T., Smith, R.L., Coastal upwelling systems, in *Analysis of Marine Ecosystems*, Longhurst, A.R., Ed., Academic Press, New York, 1981, 32–68.

Bargagli, R., Monachi, F., Sanchez-Hernandez, J.C., Cateni, D., Biomagnification of mercury in an Antarctic food web, *Mar. Ecol. Prog. Ser.*, 169, 65–76, 1998.

Bargmann, H.E., The development and life history of adolescent and adult krill (*Euphausia superba*), *Discov. Rep.*, 23, 103–176, 1945.

Barkley, E., Nahrung und Filterapparat des Walkrebschens *Euphausia superba* Dana, *Zeitschrift für Fischerei und deren Hilfswissenschaften*, 1, 65–156, 1940.

Barlow, R.G., Phytoplankton ecology in the Southern Benguela Current III: Dynamics of a bloom, *J. Exp. Mar. Biol. Ecol.*, 63, 239–248, 1998.

Barnes, D.K.A., Sublittoral epifaunal commuities at Signy Island, Antarctica, I: The ice-foot zone, *Mar. Biol.*, 121, 553–564, 1995a.

Barnes, D.K.A., Sublittoral epifaunal communities at Signy Island, Antarctica, II: Below the ice-foot zone, *Mar. Biol.*, 121, 565–572, 1995b.

Barnes, D.K.A., The influence of ice on polar nearshore benthos, *J. Mar. Biol. Assoc. UK*, 79, 401–407, 1999.

Barnes, D.K.A., Invasions by marine life in plastic debris, *Nature (Lond.)*, 416, 808–821, 2002a.

Barnes, D.K.A., Human rubbish assists alien invasions of sea, *Directions Sci.*, 1, 107–112, 2002b.

Barnes, D.K.A., Brockington, S., Zooplankton diversity, biomass and abundance at Adélie Island, Antarctica, *Mar. Ecol. Prog. Ser.*, 249, 145–255, 2003.

Barrat, A., Note sur le petrel gris, *Procellaria cinerea*, *Comité National Français des Recherches Antarctiques*, 33, 19–24, 1974.

Barrat, A., Quelques aspects de la biologie et de l'ecologie du manchant royal (*Aptenodytes patagonicus*) de îles Crozet, *Comité National Français des Recherches Antarctiques*, 40, 9–52, 1976.

Barrat, A., Mougin, J.L., Donnes numeriques sur le zoogeographie de l'avifauna antarctique et subantarctique, *Comité National Français des Recherches Antarctiques*, 33, 1–10, 1974.

Barrera-Oro, E., Casaux, R., Ecology of demersal fish species from Potter Cove, *Berichte zur Polarforschung*, 299, 156–167, 1998.

Barrett-Hamilton, G.E.K., Seals, Expedition Antarctiques Belgique. Results Voyage "Belgica" 1897–1899, *Rap. Scient. Zool.*, 1–19, 1901.

Barry, J.P., Hydrographic patterns in McMurdo Sound, Antarctica and their relationship to local benthic communities, *Polar Biol.*, 8, 367–376, 1998.

Barry, J.P., Dayton, P.K., Current patterns in McMurdo Sound, Antarctica, and their relationships to local biotic communities, *Polar Biol.*, 8, 367–376, 1988.

Bartsch, A., Die Eislagenflora des Weddellmeeres (Antarktis): Antenzusammensetzung und Biomasse soeie Okophysologie augeuahlter Arten, *Berichte zur Polarforschung*, 63–70, 1989. In German with English abstract.

Basalaev, V.M., Petuchov, A.G., Experimental poutassou fishing in the Scotia Sea from the research factory ship *Academik Kripovich*, *Trudy VNIRO*, 66, 307–310, 1969. In Russian.

Basson, M., Beddington, J.R., Preliminary analysis of growth and mortality rates of Antarctic krill (*Euphausia superba*) from length frequency analysis, *Ant. Spec. Top*, 51–55, 1989.

Bates, T.S., Charlson, R.J., Gammon, R.H., Evidence for the climatic role of marine biogenic sulphur, *Nature (Lond.)*, 329(6137), 319–321, 1987.

Bathmann, U.V., Fischer, G., Müller, P.J., Gerdes, D., Short-term variations in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: Relation to water mass advection, ice cover, plankton biomass, and feeding activity, *Polar Biol.*, 11, 185–195, 1991.

Bathmann, U.V., Schanek, R., Klass, C., Dubischer, C.P., Smetacek, V., Spring development of phytoplankton biomass and composition in major water masses of the Atlantic sector of the Southern Ocean, *Deep-Sea Res. II*, 44, 51–67, 1997.

Battershill, C.N., Distribution and abundance of benthic marine species at Cape Armitage, Ross Island, Antarctica—initial results, *NZ Antarc. Rec.*, 9, 35–52, 1989.

Beardall, J., Beer, S., Raven, J.A., Biodiversity of marine plants in an era of climate change: some predictions based on physiological performance, *Botanica Marina*, 41(1), 113–123, 1998.

Beck, J.R., Food, moult, and age of first breeding in the cape pigeon, *Daption capensis Linneaus*, *Br. Antarc. Surv. Bull.*, 21, 33–44, 1969.

Beck, J.R., Breeding seasons and moult in some smaller Antarctic petrels, in *Antarctic Ecology,* Vol. 1, Holdgate, M.W., Ed., Academic Press, London, 1970, 542–550.

Becquevort, S., Mathot, S., Lancelot, C., Interactions in the microbial community of the marginal ice zone in the northwestern Weddell Sea through size distribution analysis, *Polar Biol.*, 12, 211–218, 1992.

Beddington, J.R., Cooke, J.G., Development of an assessment technique for male sperm whales based on length data in catches, with special reference to the Northwest Pacific stock, *Int. Whaling Committee Rep.*, 31, 747–760, 1981.

Beddington, J.R., Cooke, J.G., The potential yield of fish stocks, *FAO Fish. Tech. Papers*, 242, 1–47, 1983.

Beddington, J.R., de la Mare, W.K., Marine mammal fishery interactions, in *Selected Papers Presented to the Scientific Committee of CCAMLR 1982–1984, Part II*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1984, 155–178.

Beddington, J.R., de la Mare, W.K., Marine mammal-fishery interactions: Modelling and the Southern Ocean, in *Marine Mammals and Fisheries*, Beddington, J.R., Beverton, R.J., Lavigne, D.M., Eds., George Allen & Unwin, London, 1985, 94–105.

Beddington, J.R., Grenfell. B., *The Status of Major Zoological Groups in the Southern Ocean*, International Union for the Conservation of Nature, Gland, Switzerland, 1980, 1–237.

Beddington, J.R., May, R.M., Maximum sustainable yields in ecosystems subject to harvesting at more than one trophic level, *Math. Biosci.*, 51, 261–281, 1980.

Beddington, J.R., May, R.M., The harvesting of interacting species in a natural ecosystem, *Sci. Am.*, 247, 62–69, 1982.

Beddington, J.R., Beverton, R.J.H., Lavigne, D.M. Marine Mammals and Fisheries, George Allen & Unwin, London, 1985.

Beers, J.R., Trent, J.D., Reid, F.M.H., Shanks, A.L., Macroaggregates and their phytoplankton components in the Southern California Bight, *J. Plankton Res.*, 8, 475–487, 1986.

Bell, W., Mitchell, R., Chemotactic and growth responses of marine bacteria to algal extracellular products, *Biol. Bull., Mar. Biol. Lab., Woods Hole*, 143, 265–277, 1972.

Bellido, A., Les biocenoses du littoral rocheux aux Îles Kerguelen, *Colloque sur les Ecosystemes Subantarctiques, 1981, CNFRA*, 51, 81–93, 1982.

Bengtson, J.L., *Review of Information Regarding the Conservation of Living Resources of the Antarctic Marine Ecosystem*, Report prepared for the U.S. Mammal Marine Commission, Washington, DC, 1978.

Bengtson, J.L., Reproductive ecology of crabeater and leopard seals along the Antarctic Peninsula, *Antarc. J. U.S.*, 17(5), 185, 1982.

Bengtson, J. L.,Review of Antarctic marine fauna, in *Selected Papers Presented to the Scientific Committee of CCAMLR 1982–1984, Part I*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1 pp, 1985a.

Bengtson, J. L.,Monitoring indicators of possible ecological changes in the Antarctic marine ecosystem. in *Selected Papers Presented to the Scientific Committee of CCAMLR 1982–1984, Part II*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1985b, 43–154.

Bengtson, J.L., Long-term trends in the foraging patterns of female Antarctic fur seals at South Georgia, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin, 1988, 286–291.

Bengtson, J.L., Laws, R.M., Trends in crabeater seal age at maturity: an insight into Antarctic marine interactions, in *Selected Papers Presented to the Scientific Committee of CCAMLR 1982–1984. Part II*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1984, 341–368.

Bengtson, J.L., Laws, R.M., Trends in crabeater seal age at maturity: an insight into Antarctic marine ecosystem interactions, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 667–675.

Bengtson, J.L., Siniff, D.B., Reproductive aspects of female crabeater seals (*Lobodon carcinophagus*) along the Antarctic Peninsula, *Can. J. Zool.*, 59, 92–102, 1981.

Bengston, J.L., Boven, W.D., Jansen., S.K., Foraging areas of krill-consuming penguins and fur seals near Seal Island, Antarctica, *Antarc. J. U.S.*, 26(5), 217–218, 1991.

Berger, W.H., Herger, J.C., Reading the sedimentary record of the ocean's productivity, in *Primary Productivity and Biogeochemical Cycles in the Sea*, Falkowski, P.G., Woodhead, A.O., Eds., Plenum Press, Oxford, 1992, 455–486.

Bergstrom, B.I., Hempel, G., Marschall, H.P., North, A., Siegel, V.G., Stromberg, J.O., Spring distribution, size composition, and behaviour of krill (*Euphausia superba*) in the western Weddell Sea, *Polar Res.*, 26, 85–89, 1990.

Berkes, F., Some aspects of the feeding mechanisms of euphausiid crustaceans, *Crustaceana*, 29, 266–270, 1975.

Berkman, P.A., Ecological variability in Antarctic coastal environments: past and present, in *Antarctic Communities. Species, Structure and Survival*, Battaglia, B., Valencia, J., Walton, D.W.H., Eds., Cambridge University Press, Cambridge, 1997, 349–357.

Berkman, P.A., Nigro, M., Trace metal concentrations in scallops around Antarctica: Extending the Mussel Watch Programme to the Southern Ocean, *Mar. Pollut. Bull.*, 24, 322–323, 1992.

Berkman, P.A., Marks, D.S., Shreve, G.P., Winter sediment resuspension in McMurdo Sound and its ecological implications, *Polar Biol.*, 6, 1–3, 1986.

Berkmann, P.A., Waller, T.R., Alexander, S.P., Unprotected larval development in the Antarctic scallop *Adamussium colbecki* (Mollusca: Bivalvia: Pectinidae), *Antarc. Sci.*, 3, 151–157, 1991.

Berman, T., Holm-Hansen, O., Release of photoassimilated carbon as dissolved organic matter by marine phytoplankton, *Mar. Biol.*, 28, 305–310, 1974.

Berman, M.S., McVey, A.L., Ettertshank, G., Age determination of Antarctic krill using fluorescence and image analysis of size, *Polar Biol.*, 9, 267–271, 1989.

Bernard, K., Froneman, P.W., Mesozooplankton community structure in the Southern Ocean upstream of Prince Edward Islands, *Polar Biol.*, 25, 597–604, 2002.

Bernard, K., Froneman, P.W., Mesozooplankton community structure and grazing impact in the Polar Frontal Zone during the austral autumn 2003, *Polar Biol.*, 26, 268–275, 2003.

Bernard, K., Froneman, P.W., Trophodynamics of selected mesozooplankton in the west Indian sector of the Polar Frontal Zone, Southern Ocean, *Polar Biol.*, 28, 594–606, 2005.

Berruti, A., The breeding biologies of the sooty albatross, *Phoebetria fusca* and P. *palpebrata*, at Marion Island, *S. A. J. Antarc. Res.*, 8, 99, 1979.

Berry, A.J., The occurrence of a leopard seal (*Hydrurga leptonyx*) in the tropics, *Annual Magazine of Natural History, 13th series 1960 (1961)*, 587–591, 1961.

Bertram, G.C.L., The biology of the Weddell and crabeater seals, with a study of the comparative behaviour of the Pinnipedia, *British Grahamland Expedition 1934–37 Scientific Reports 1*, 1940.

Berzin, A.A. *The Sperm Whale*, Israel Program for Scientific Translations, Jerusalem, 1972.

Best, P.B., Distribution and feeding habits of baleen whales off the Cape Province, *Div. Sea Fish. Invest. Rep., S. Afr.*, 57, 1–44, 1967.

Best, P.B., The sperm whale (*Physeter catadon*) off the west coast of South Africa. 2. Reproduction in the female, *Div. Sea Fish Invest. Rep. S. Afr.*, 66, 1–32, 1968.

Best, P.B., The sperm whale (*Physeter catadon*) off the west coast of South Africa, 3: Reproduction in the male, *Div. Sea Fish. Invest. Rep., S. Afr.*, 72, 1–20, 1969.

Best, P.B., The sperm whale (*Physeter catadon*) off the west coast of South Africa, 5: Age, growth and maturity, *Div. Sea Fish. Invest. Rep., S. Afr.*, 79, 1–27, 1970a.

Best, P.B., Exploitation and recovery of right whale (*Eubalaena australis*) off the Cape Province, *Div. Sea Fish. Invest. Rep., S. Afr.*, 80, 1–20, 1970b.

Best, P.B., Status of the whale population off the west coast of South Africa and current research, in *The Whale Problem: A Status Report*, Schevill, W.E., Ed., Harvard University Press, Cambridge, MA, 1974a, 53–81.

Best, P.B., The biology of the sperm whale as it relates to stock management, in *The Whale Problem: A Status Report*, Schevill, W.E., Ed., Harvard University Press, Cambridge, MA, 1974b, 257–293.

Best, P.B., Social organization in sperm whales, *Physeter macrocephalus*, in *Behavior of Marine Mammals,* Vol. 3, Winn, H.E., Olla, B.L., Eds., Plenum Press, New York, 1979, 227–289.

Best, P.B., Seasonal abundance, feeding, reproduction and growth in minke whales off Durban (with incidental observations from Antarctica), *Rep. Int. Whal. Commun.*, 32, 755–786, 1982.

Bester, M.N., Laycock, P.A., Cephalopod prey of the sub-Antarctic fur seal *Arctocephalus tropicalis* at Gough Island, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 551–554.

Bester, M.N., Erickson, A.W., Ferguson, J.W.H., Seasonal changes in the distribution and density of seals in the pack ice of the Princess Martha Coast, Antarctica, *Antarc. Sci.*, 7(4), 357–364, 1995.

Beverton, R.J.H., Holt, S.J., A review of methods estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling, *Rapports et Proces Verbeux de Reunions, Council International pour l'Exploration de la Mer*, 140, 67–83, 1956.

Beverton, R.J.H., Lee, A.J., Hydrographic fluctuations in the North Atlantic Ocean and some biological consequences, in *The Ecological Significance of Biological Change in Britain*, Johnson, C.G., Smith, L.P., Eds., Institute of Biology Symposia, London, 1965, 79–107.

Beylev, G.M., Uschakov, P.V., Certain regularities in the quantitative distribution of the benthic fauna in Antarctic waters, *Dolklady Akademii Nauk SSSR*, 112, 137–140, 1957.

Bianchi, F., Brine investigations, *Ber. Polarforsch.*, 62, 95–97, 1989.

Bianchi, F., Boldrin, A., Coice, F., Nöthig, E.-M., Sehlstedt, P.L., Socal, G.T., Syverten, E.E., Phytoplankton distribution in relation to sea ice, hydrography, and nutrients in the northwestern Weddell Sea in early spring during EPOS, *Polar Biol.*, 12, 225–235, 1992.

Bianchi, M., Feliatra, F., Treguer, P., Vincendeau, M.A., Morvan, J., Nitrifiction rates, ammonium and nitrate distribution in upper layers of the water column and sediments of the Indian sector of the Southern Ocean, *Deep-Sea Res.*, 44, 1017–1032, 1997.

Bibik, V.A., Maslennikov, V.V., Delevin, A.S., Polonsky, V.E., Solyankin, E.N., The current system and distribution of waters of different modifications in the Cooperation and Cosmonaut Seas, in *Interdisciplinary Investigations of the Pelagic Ecosystem in the Cooperation and Cosmonaut Seas*, Makarov, R.R., Ed., NIRO Publishing, Moscow, 1988, 16–43.

Biddanda, B.A., Microbial synthesis of macroparticulate matter, *Mar. Ecol. Prog. Ser.*, 20, 241–251, 1985.

Biddanda, B.A., Structure and function of microbial aggregates, *Oceanologica Acta*, 9, 209–211, 1986.

Biddanda, B.A., Pomeroy, L.R., Microbial aggregation and degradation of phytoplankton-derived detritus in sea water, I: Microbial succession, *Mar. Ecol. Prog. Ser.*, 42, 79–88, 1988.

Bidenko, M.S., Rasulova, T.A., Odintsor, A.B., On the activity of proteolytic ferments in Antarctic krill, in *Research in technological characterization and processing of krill*, Bidenko, M.S., Ed., Atlant-VNIRO, Kalingrad, 1981, 15–18. In Russian with English summary.

Bidigare, R.R., Potential effects of UV-B radiation in marine organisms of the Southern Ocean: Distribution of phytoplankton and krill during austral spring, *Photochem. Photobiol.*, 50, 469–477, 1989.

Bidigare, R.R., Johnson, M.A., Duffy, J.D., Biggs, D.C., Nutrient chemistry of ammonium in Antarctic surface waters, *Antarc. J. U.S.*, 16, 168–170, 1981.

Bidigare, R.R., Itiarte, J.L., Kang, S.H., Ondrusek, M.E., Karentz, D., Fryxall, G.A., Phytoplankton quantitative and qualitative assessments, in *Foundations for Ecosystem Research in the Western Antarctic Peninsula Region. Antarctic Research Series 70*, Ross, A., Hofmann, E.H., Quetin, L.B., Eds., American Geophysical Union, Washington, DC, 1995, 173–178.

Bienati, N.L., Gomes, R.A., Spiedo, H., Primary production in Antarctic waters: seasonal variation and production in fertilized samples during the summer cycle, in *Polar Oceans*, Dunbar, M.T., Ed., Arctic Institute of North Amarica, Calgary, 1977, 377–390.

Bienfang, P.K., Phytoplankton sinking rates in oligotrophic water off Hawaii, *Mar. Biol.*, 61, 69–77, 1980.

Bienfang, P.K., Sinking rates of heterogeneous temperate phytoplankton populations, *J. Plankton Res.*, 3, 235–253, 1981.

Bienfang, P.K., Size, structure, and sedimentation of biogenic microparticulates in a subarctic ecosystem, *J. Plankton Res.*, 6, 983–994, 1984.

Bienfang, P.K., Size, structure, and sinking rates of various microparticulate constituents in oligotrophic Hawaiian waters, *Mar. Ecol. Prog. Ser.*, 23, 143–151, 1985.

Bienfang, P.K., Harrison, P.J., Sinking rate response of natural assemblages of temperate and subtropical phytoplankton to nutrient depletion, *Mar. Biol.*, 83, 293–300, 1994.

Biggs, D.C., Zooplankton excretion and NH_4 cycling in near-surface waters of the Southern Ocean, I: Ross Sea, austral summer 1977–1978, *Polar Biol.*, 1, 55–67, 1982.

Biggs, D.C., Johnson, M.A., Bigidare, R.R., Guffy, J.D., Holm-Hansen, O., Shipboard autoanalyzer studies of nutrient chemistry, 0–200 m, in the eastern Scotia Sea during FIBEX, *Technical Report 82-11-T*, Department of Oceanography, Texas A&M University, College Station, TX, 1983.

Billen, G., Heterotrophic utilization and regeneration of nitrogen, in *Heterotrophic Activity in the Sea*, Hobbie, J.E., Williams, P.L.leB., Eds., Plenum Press, New York, 1984, 313–356.

Billen, G., Becquevort, S., Phytoplankton-bacterial relationship in the Antarctic marine ecosystem, *Polar Biol.*, 10, 245, 1991.

Billen, G., Fontigny, A., Dynamics of a *Phaeocystis* spring bloom in Belgian coastal waters. II. Bacterioplankton dynamics, *Mar. Ecol. Prog. Ser.*, 37, 249–257, 1987.

Billen, G., Joiris, C., Wijnant, J., Gillain, G., Concentration and microbial utilization of small organic molecules in the Scheldt Estuary, the Belgian coastal zone of the North Sea, and the English Channel, *Estuar. Coast. Mar. Sci.*, 11, 279–294, 1980.

Binnerup, S.J., Jensen, K., Revsheck, N.P., Jensen, M.H., Sorenson, J., Denitrification, dissimilatory reduction in nitrate to ammonium, and nitrification in a bioturbated sediment as measured with ^{15}N and microsensor techniques, *Appl. Environ. Microbio.*, 58, 303–313, 1992.

Bird, D.F., Maranger, R., Karl, D.M., Palmer LTER: Aquatic virus abundance near the Antarctic Peninsula, *Antarc. J. U.S.*, 28, 234–235, 1993.

Bird, D.F., Juniper, S.K., Riccardi-Rigault, M., Martine, P., Prarie, Y.T., Calvert, S.E., Subsurface viruses and bacteria in Holocene/Late Pleistocene sediments of Saanich Inlet, B.C.: ODP Holes 1033B and 1034B, leg 1695, *Mar. Geol.*, 174, 227–239, 2001.

Bischof, K., Hanelt, D., Wiencke, C., UV-radiation can affect depth zonation of Antarctic macroalgae, *Mar. Biol.*, 131, 597–601, 1998.

Bjørnsen, P.K., Kuparinen, J., Growth and herbivory by heterotrophic dinoflagellates in the Southern Ocean, studied by microcosm experiments, *Mar. Biol.*, 109, 397–405, 1991.

Blome, D., Riemann, F., Antarctic sea ice nematodes, with description of *Geomonhystera glaciei* sp. nov. (Monhysteridae). *Mitteilungen Hamb. Zool. Mus. Inst.*, 96, 15–20, 1999.

Boak, A.C., Goulder, R., Bacterioplankton in the diet of the calanoid copepod *Eurytemora* sp. in the Humber Estuary, *Mar. Biol.*, 73, 139–149, 1994.

Bo Chen, Distribution and abundance of choanoflagellates in Great Wall Bay, King George Island, Antarctica, in austral summer, *NIPR Symp. Polar Biol.*, 7, 32–42, 1994.

Bocher, P., Cherel, Y., Hobson, K.A., Complete trophic segregation between South Georgian and common diving petrels during breeding at Isles Kerguelen, *Mar. Ecol. Prog. Ser.*, 208, 249–264, 2000.

Boesch, D.F., Species diversity in the macrobenthos of the Virginia area, *Chesapeake Sci.*, 13, 206–211, 1972.

Boesch, I., Beauchamp, K.A., Steele, M.E., Pearse, J.S., Development, metomorphosis, and seasonal abundance of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayeri*, *Biol. Bull.*, 1763, 126–135, 1987.

Bogdanov, M.A., Solyankin, E.V., Radionev, S.N., The distribution of mingled water and secondary frontal zone in the Sea of Scotia and the distribution of krill swarms, in *Biological Resources of Antarctic Krill*, Lubimova, T. G., Ed., VNIRO, Moscow, 1980, 218–231. In Russian.

Bolter, M., Dawson, R., Heterotrophic utilization of biochemical compounds in Antarctic waters, *Neth. J. Sea Res.*, 16, 315–332, 1982.

Boltovosk, D., Alder, V.A., Spinelli, F., Summer Weddell Sea microplankton: Assemblage structure, distribution, and abundance, with special emphasis on the tintinnina, *Polar Biol.*, 9, 447–456, 1980.

Bonner, W.N., Notes on the southern fur seal in South Georgia, *Proc. Zool. Soc. London*, 130, 241–252, 1958.

Bonner, W.N., Population increase in the fur seal, *Arctocephalus tropicalis gazella*, at South Georgia, in *Biologie Antarctique*, Carrick, R., Holdgate, W.M., Prevost, J., Eds., Herman, Paris, 1964, 438–443.

Bonner, W.N., The fur seal of South Georgia, *Sci. Rep. Br. Antarc. Surv.*, 56, 1–81, 1968.

Bonner, W.N., The status of the Antarctic fur seal, *Arctocephalus gazella*. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals, ACMRR/MM/SC/50, 18, 1976.

Bonner, W.N., Southern fur seals: *Arctocephalus* (Geoffrey SaintHilaire and Cuvier, 1926), in *Handbook of Marine Mammals,* Vol. 1, Ridgway, S.R.H., Harrison, R.J., Eds., Academic Press, London, 1981, 161–208.

Bonner, W.N., Conservation and the Antarctic, in *Antarctic Ecology,* Vol. 2, Laws, R.M., Ed., Academic Press, London, 1984, 821.

Bonner, W.N., Birds and mammals—Antarctic seals, in *Key Environments—Antarctica*, Bonner, W.N., Walton, D.W.H., Eds., Pergamon Press, London, 1985a, 202–222.

Bonner, W.N., Impact of fur seals on the terrestrial environment at South Georgia, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985b, 640–641.

Bonner, W.N., Laws, R.M., Seals and sealing, in *Antarctic Research*, Priestly, R., Adie, R.J., deQ. Robin, G., Eds., Butterworth, London, 1964, 163–190.

Bonner, W.N., Watson, D.W.H., Marine habitats—introduction, in *Key Environments—Antarctica*, Bonner, W.N., Ed., Pergamon Press, Oxford, 1985, 133–142.

Bonner, W.N., Everson, I., Prince, P.A., A shortage of krill, *Euphausia superba*, around South Georgia, *International Council for the Exploration of the Sea, Series C, CM, 1978, L/22.*

Boone, R.J., Manthey, M., The anatomical distribution of fluoride within various body segments and organs of Antarctic krill, *Archiv für Fischereiwissenschaft*, 34, 81–85, 1983.

Boronin, A.V., Frolkina, Zh.A., Age determination in green notothenia (*Notothenia gibberifrons*) from the Southwest Atlantic, *Trudy Atlantic NIRO*, 70, 29–37, 1976. In Russian.

Boucher, N.P., Prezelin, B.B., An *in situ* biological weighting function for UV inhibition of phytoplankton carbon fixation in the Southern Ocean, *Mar. Ecol. Prog. Ser.*, 146, 223–236, 1996.

Bouvey, M., Soyer, J., Benthic seasonality in an intertidal mud flat at Kerguelen Islands (Austral Ocean). The relationship between meiofaunal abundance and their potential microbial food, *Polar Biol.*, 10, 19–27, 1989.

Bowen, S.H., Evidence of a detritus food chain based on the consumption of organic precipitates, *Bull. Mar. Sci.*, 35, 440–448, 1984.

Bowman, J.P., Brown, M.V., Nichols, D.S., Biodiversity and ecophysiology of bacteria associated with Antarctic sea ice, *Antarc. Sci.*, 9, 134–142, 1997.

Boyd, I.L., Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia, *Antarc. Sci.*, 5, 17–25, 1993.

Boyd, I.L., Croxall, J.P., *Preliminary estimates of krill consumption by Antarctic fur seals and macaroni penguins at South Georgia*, Document WG-Emm-96/96, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1996.

Boyd, P.W., Law, C.S., The Southern Ocean Iron Release Experiment (SOIREE)—Introduction and summary, *Deep-Sea Res. II*, 48, 2425–2438, 2001.

Boyd, J.C., Sladen, J.L., Telemetry studies of the internal body temperatures of Adélie and emperor penguins at Cape Crozier, Ross Island, Antarctica, *The Auk*, 88, 366–391, 1971.

Boyd, C.M., Heyraud, M., Boyd, C.N., Feeding of Antarctic krill, Euphausia superba, *J. Crustacean Biol.*, 4 (Special Issue No.1), 123–141, 1984.

Boyd, P.W., Watson, A.J., Law, C.S., Abraham, E.R., Trull, T., Murdoch, R., Bakker, D.C.E., Bowie, A.R., Buesseler, K.O., Chang, H. et al., A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization, *Nature (Lond.)*, 407, 695–702, 2000.

Boyle, P.R., Ed, *Cephalopod Life Cycles,* Vol. 1, Academic Press, London, 1983.

Boyle, P.W., Pumping iron makes thinner diatoms, *Nature (Lond.)*, 393, 733–734, 1998.

Boysen-Ennen, E., Piatkowski, U., Meso- and nanozooplankton communities in the Weddell Sea, *Polar Biol.*, 9, 17–35, 1988.

Boysen-Ennen, E., Hagen, W., Hubold, G., Piatkowski, U., Zooplankton biomass in the ice-covered Weddell Sea, Antarctica, *Mar. Biol.*, 111, 227–235, 1991.

Bracher, A., Photoacclimation of phytoplankton in different biogeochemical provinces of the Southern Ocean and its significance for estimating primary production, *Berichte zur Polarforscherung*, 341, 1–88, 1999.

Bracher, A.W., Wiencke, C., Simulation of the effects of naturally-enhanced UV radiation on photosynthesis of Antarctic phytoplankton, *Mar. Ecol. Prog. Ser.*, 196, 127–141, 2000.

Bracher, A., Kroon, B.M.A., Lucas, M.I., Primary production and physiological state of the phytoplankton in the Atlantic sector of the Southern Ocean, *Mar. Ecol. Prog. Ser.*, 190, 1–16, 1999.

Bradfield, P., The ecology of *Trematomus borchgrevinki* in McMurdo Sound, Antarctica. BSc. (Hons) Project in Zoology, University of Canterbury, Christchurch, 1980.

Bradford, J.M., The fauna of the Ross Sea, 8: Pelagic Copepoda, *Bull.—NZ Depart. Sci. Ind. Res.*, 206, 9–31, 1971.

Bradford, J.M., Sea-ice organisms and their importance in the Antarctic ecosystem, *NZ Antarc. Rec.*, 1, 43–50, 1978.

Bragg, J.R., Prince, R.C., Harner, E.J., Atlas, R.M., Effectiveness of bioremediation for the Exxon-Valdez oil spill, *Nature*, 308, 413–418, 1994.

Brandini, F.P., Phytoplankton biomass in an Antarctic coastal environment during stable water conditions—implications for the iron limitation theory, *Mar. Ecol. Prog. Ser.*, 93, 267–275, 1993.

Brandini, F.P., Kutner, M.B.B., Phytoplankton and nutrient distribution off the northern South Shetland Islands (summer 1984 BIOMASS/SIBEX), *La Mer*, 25, 93–99, 1997.

Brandt, A., The deep-sea isopod genus *Echinozone* Sars and its occurrence on the continental shelf of Antarctica, *Antarc. Sci.*, 2, 215–219, 1990.

Brandt, A., Evolution of Antarctic biodiversity in the context of the past: the importance of the Southern Ocean deep sea. Abstracts Scar Open Science Conference, Bremen, 2004, 83, 2004.

Bratbak, G., Thingstad, T.F., Phytoplankton-bacteria interactions: an apparent paradox? Analysis from a model system with both competition and commensalism, *Mar. Ecol. Prog. Ser.*, 25, 23–30, 1985.

Bregazzi, P.K., Life cycles and seasonal movements of *Cheriimedon femoratus* (Pfeffer) and *Tryphosella kergueleni* (Miers) (Crustacea:Amphipoda), *Br. Antarc. Surv. Bull.*, 30, 1–34, 1972.

Brenner, M., Buck, B.H., Cordes, S., Dietrich, L., Jacob, U., Mintenbeck, K., Schroder, A., Brey, T., Knust, R., Antz, W., The role of iceberg scours in niche separation within the Antarctic fish genus *Trematomus*, *Polar Biol.*, 24, 502–507, 2001.

Brey, T., Temperature and reproductive metabolism in macrobenthic populations, *Mar. Ecol. Prog. Ser.*, 125, 87–93, 1995.

Brey, T., Clarke, A., Population dynamics of marine benthic invertebrates in Antarctic and sub-Antarctic environments: are there unique adaptations?, *Antarc. Sci.*, 5, 253–266, 1993.

Brey, T., Gerdes, D., Is Antarctic benthos really higher than elsewhere?, *Antarc. Sci.*, 1, 266–267, 1997.

Brey, T., Gerdes, D., High Antarctic macrobenthic production, *J. Exp. Mar. Biol. Ecol.*, 231, 191–200, 1998.

Brieley, A.S., Watkins, J.L., Effects of sea ice cover on the swarming behaviour of Antarctic krill, *Euphausia superba*, *Canadian J. Fish. Aquatic Sci.*, 51(S3), 24–30, 2000.

Brierley, A.S., Goss, C., Acoustic estimates of krill density at South Georgia, December-January 1989/90. CCAMLR Scientific Abstracts WG-EMM, 1999.

Brierley, A.S., Thomas, D.N., Ecology of Southern Ocean pack ice, *Adv. Mar. Biol.*, 43, 171–276, 2002.

Brieley, A.S., Watkins, J.L., Goss, C., Wilkinson, M.T., Everson, I., Acoustic estimates of krill density at South Georgia, 1981–1998, *CCAMLR Sci.*, 6, 47–57, 1999.

Brierley, A.S., Fernandes, P.G., Brandon, M.A., Armstrong, F., Millard, N.W., McPhail, S.D., Stevenson, P., Pebody, M., Perrett, J., Squires, M., Bone, D.G., Griffiths, G., Antarctic krill under sea ice: elevated abundance in a narrow band just south of the ice edge, *Science*, 295, 1890–1892, 2002.

Briggs, K.T., Tyler, W.B., Lewis, D.B., Carlson, D.P., Bird communities at sea off California, *Stud. Avian Biol.*, 16, 1–74, 1987.

Brightman, R.I., Smith, W.O., Jr., Photosynthesis-irradiance relationships of Antarctic phytoplankton during the austral winter, *Mar. Ecol. Prog. Ser.*, 53, 143–151, 1989.

Brinton, E., Observations of plankton organisms obtained by bongo nets during the November–December iceedge investigations, *Antarc. J. U.S.*, 19, 113–115, 1984.

Brinton, E., The oceanographic structure of the eastern Scotia Sea, III: Distribution of euphausiid species and their development stages in in relation to hydrography, *Deep-Sea Res.*, 32, 1153–1180, 1985.

Brinton, E., Antezana, T., Structure of swarming and dispersed populations of krill (*Euphausia superba*) in Scotia Sea and South Shetland waters during January–March, determined by bongo nets, *J. Crustacean Biol.*, 4(Special Issue No.1), 45–60, 1984.

Brinton, E., Townsend, A.W., Regional relationships between development and growth in larvae of Antarctic krill *Euphausia superba*, from field samples, *J. Crustacean Biol.*, 4(Special Issue No.1), 224–246, 1984.

Brock, V.E., Riffenberg, R.H, Fish schooling: a possible factor in reducing predation, *Journal du Conseil Council International pour l'Exploration de la Mer*, 25, 307–317, 1960.

Brodie, J., Oceanography, in *Antarctica*, Hatherton, T., Ed., Methuen&Co. Ltd, London, 1965, 101–127.

Brodie, P.F., Cetacean energetics: an overview of intraspecific size variation, *Ecology*, 56, 152–161, 1975.

Broecker, W.S., Comment on "Iron deficiency limits phytoplankton growth in Antarctic waters" by John H. Martin, et al., *Global Biogeochem. Cycles* 4, 5–12, 1990.

Bromwich, D., Liu, Z., Rogers, A.N., Winter atmosphere forcing of the Ross Sea polyna. in *Ocean, Ice, and Atmosphere Interactions of the Antarctic Continental Margin*, Jacobs, S.S., Weller, R.F., Eds., *Antarctic Research Series* 75, 1998, 103–133.

Brooke, M.deL., Prince, P.A., Nocturnality in seabirds, *Acta XX Congressus Internationalis Ornithologici*, 1113–1121, 1991.

Brown, K.G., The leopard seal at Heard Island, 1951–54, *Aust. Natl Antarc. Res. Exped. Interim Rep.*, 16, 1–34, 1957.

Brown, S.G., The movements of fin and blue whales within the Antarctic zone, *Discov. Rep.*, 33, 1–54, 1962a.

Brown, S.G., A note on the migration of fin whales, *Norsk Hvalfangsttid*, 50, 13–16, 1962b.

Brown, S.G., Whale marking—progress report, 1970, *Int. Whaling Committee Rep.*, 21, 31–55, 1971.

Brown, S.G., Some results of sei marking in the Southern Hemisphere, *Int. Whaling Committee Rep. Spec. Issue*, 1, 39–43, 1977.

Brown, R.G.B., Seabirds as marine animals, in *Behaviour of Marine Animals, Vol. 4: Marine Birds*, Berger, J., Olla, B.L., Winn, H.E., Eds., Plenum Press, New York, 1980, 80.

Brown, S.G., Lockyer, G.H., Whales, in *Antarctic Ecology,* Vol. 2, Laws, R.M., Ed., Academic Press, London, 1984, 717–782.

Brown, R.G.B., Nettleship, D.N., The biological significance of polynas to Arctic colonial seabirds, *Can. Wildlife Ser. Occas. Papers*, 45, 59–63, 1981.

Brown, R.G.B., Cooke, F., Kinner, P.K., Mills, E.L., Summer seabird distributions in the Drake Passage, Chilean fjords, and off Southern South America, *Ibis*, 117, 339–356, 1975.

Brown, K.M., Keiron, P.P.F., Barnes, D.K.A., Peck, L.S., Links between the structure of an Antarctic shallow-water community and ice scour frequency, *Oecologia*, 146, 121–129, 2004.

Brownell, R.L., Jr*., Small odontocetes in the Antarctic*, Antarctic Map Folio Series, Vol. 18, American Geographical Society, Washington, DC, 1974, PP. 13–19.

Broyer, C., Jazdzewski, K., Contribution to the marine biodiversity inventory: a checklist of the Amphipoda (Crustacea) of the Southern Ocean, *Bet. Inst. Naturwiss, Brussels*, 73, 1–114, 1993.

Bruckhausen, P.M., Raymond, J.A., Jacobs, S.S., DeVries, A.L., Thorndike, E.M., Dewitt, H.H., Fish, crustaceans, and the sea floor under the Ross Ice Shelf, *Science*, 203(4379), 449–451, 1979.

Bryden, M.M., Kirkwood, G.P., Slade, R.W., Humpback whales, Area V: An increase in numbers off Australia's east coast, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin, 1990, 271–277.

Buchholz, F., Drach's moult staging system, adapted for euphausiids, *Mar. Biol.*, 66, 301–305, 1982.

Buchholz, F., Moulting and moult physiology in krill, *Berichte zur Polarforschung*, 4, 81–88, 1983.

Buchholz, F., Moult and growth in euphausiids, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, W.R., Eds., Springer, Berlin, 1985, 339–345.

Buck, K.R., A study of choanoflagellates (Acanthoecidae) from the Weddell Sea, including a description of *Diaphanoeca multiannulata* n.sp, *J. Protozool.*, 28, 47–54, 1981.

Buck, K.R., Garrison, D.L., Protists from the ice-edge region of the Weddell Sea, *Deep-Sea Res.*, 30, 1261–1278, 1983.

Buck, K.R., Garrison, D.L, Distribution and abundance of choanoflagellates (Acanthoecidae) across the ice-edge zone in the Weddell Sea, Antarctica, *Mar. Biol.*, 98, 263–269, 1988.

Buck, K.R., Garrison, D.L., Hopkins, T.L., Abundance and distribution of tintinnids in an ice-edge zone: An AMERIEZ study, *EOS*, 68, 1773, 1987.

Buck, K.R., Bolt, P.A., Garrison, D.L., Phagotrophy and fecal pellet production by an athecate dinoflagellate in Antarctic sea ice, *Mar. Ecol. Prog. Ser.*, 60, 75–84, 1990.

Buck, K.R., Garrison, D.L., Hopkins, T.L., Abundance and distribution of tintinnid ciliates in an ice-edge zone during the austral summer, *Antarc. Sci.*, 4, 3–8, 1992.

Buckley, R.G., Trodahl, H.J., Scattering and absorption of visible light by sea ice, *Nature (Lond.)*, 326, 867–869, 1987.

Buckley, R.G., Trodahl, H.J., Radiation risk, *Nature (Lond.)*, 346, 24–31, 1990.

Buckley, J.R., Gammelsrod, T., Johannesson, J.A., Johannesson, O.M., Roed, L.P., Upwelling: Oceanic structure at the edge of the Arctic ice pack in winter, *Science*, 203, 165–167, 1979.

Budd, W.F., Antarctic glaciation and global change, *Climate Change*, 18, 271, 1991.

Budkoviskiy, T.V., Yaragov, B.A., Studying the Antarctic krill for the purpose of organizing krill fisheries, in *Soviet Fishery on Antarctic Krill*, Burukovsky, R.N., Ed., U.S. Department of Commerce (TT-67-32683), Washington, DC.

Budylenko, G.A., Distribution and migration of sei whales in the Southern Hemisphere, *Int. Whaling Committee Rep.*, 28, 373–377, 1978.

Budzinski, E., Bykowski, P., Dutkiewicz, D. Possibilities of processing and marketing of products made from Antarctic krill, FAO Fisheries Technical Paper 268, Rome, 1985.

Buma, A.G.J., De Baar, H.J.W., Nöthig, R.F., van Bennekom, A.J., Metal enrichment experiment in the Weddell-Scotia Seas: effects of iron and magnesium in various plankton communities, *Limnol. Oceanogr.*, 36(8), 1865–1878, 1991.

Buma, A.G.J., Gieskes, W.W.C., Thomson, H.A., Abundance of Cryptophyceae and chlorophyll *b*-containing organisms in the Weddell-Scotia Confluence in the spring of 1988, *Polar Biol.*, 12, 43–52, 1992.

Bunt, J.S., Introductory studies: Hydrology and plankton at Mawson, June to February 1957, *ANARE Rep.*, 56, 1–135, 1960.

Bunt, J.S., Diatoms in Antarctic sea ice as agents of primary production, *Nature (Lond.)*, 199, 1255–1257, 1963.

Bunt, J.S., Primary productivity under sea ice in Antarctic waters, 1: Concentrations and photosynthetic activities of Antarctic marine microalgae, *Antarc. Res. Ser.*, 1, 13–26, 1964a.

Bunt, J.S., Primary productivity under the sea ice in Antarctic waters. Influence of light and other factors on photosynthetic activities of Antarctic marine microalgae, *Antarc. Res. Ser.*, 1, 27–31, 1964b.

Bunt, J.S., Some characteristics of microalgae isolated from Antarctic sea ice, *Antarc. Res. Ser.*, 11, 1–14, 1967.

Bunt, J.S., Microalgae of the Antarctic pack ice zone, in *Symposium on Antarctic Oceanography*, Currie, R.I., Ed., Scott Polar Research Institute, Cambridge, UK, 1968a, 198–218.

Bunt, J.S., Influence of light and other factors on the photosynthetic activities of Antarctic marine microalgae, *Antarc. Res. Ser.*, 11, 27–31, 1968b.

Bunt, J.S., Microbiology of sea ice, *Antarc. J. U.S.*, 4, 193–197, 1969.

Bunt, J.S., Lee, C.C., Seasonal primary production in Antarctic sea ice at McMurdo Sound in 1967, *J. Mar. Res.*, 28, 304–320, 1970.

Bunt, J.S., Wood, E.J.F., Microalgae and Antarctic sea ice, *Nature (Lond.)*, 199, 1254–1255, 1963.

Bunt, J.S., Lee, C.C., Boggs, W.J., Jr., Microalgae and Protozoa of Antarctic pack ice, *Antarc. J. U.S.*, 3, 87–90, 1968.

Burchett, M.S., The ecology of some coastal fish populations at South Georgia, *Prog. Underwater Sci.*, 7, 15–20, 1982.

Burchett, M.S., Food, feeding, and behaviour of *Notothenia rossii* nearshore at South Georgia, *Br. Antarc. Surv. Bull.*, 61, 45–51, 1983a.

Burchett, M.S., Age and growth of the Antarctic fish *Notothenia rossii* Fisher (1885) from South Georgia, *Br. Antarc. Surv. Bull.*, 60, 45–61, 1983b.

Burchett, M.S., Life cycle of *Notothenia rossii* from South Georgia, *Br. Antarc. Surv. Bull.*, 61, 71, 1983c.

Burchett, M.S., Sayers, P.J., North, A.W., White, G.M., Some biological aspects of the nearshore fish populations at South Georgia, *Br. Antarc. Surv. Bull.*, 59, 63–74, 1983.

Burchett, M.S., DeVries, A., Briggs, A.J., Age determination and growth of *Dissothicus mawsoni* (Norman, 1937) (Pisces, Nototheniidae) from McMurdo Sound (Antarctica), *Cybium*, 8, 27–31, 1984.

Burger, A.E., Breeding biology, moult, and survival of lesser sheathbills (*Chionis minor*) at Marion Island, *Ardea*, 67, 1–14, 1979.

Burger, A.E., Lindeboom, H.J., Williams, A.J., Mineral and energy contribution of guano of selected species of seabirds in the Marion Island terrestrial ecosystem, *S. Afr. J. Antarc. Res.*, 8, 59–65, 1978.

Burkholder, P.R., Mandelli, E.F., Productivity of microalgae in Antarctic sea ice, *Science*, 149, 972–974, 1965.

Burkholder, P.R., Mandelli, E.F., Productivity of microalgae in Antarctic sea ice, *Nature (Lond.)*, 199, 972–984, 1965.

Burkill, P.H., Ciliates and other microplankton components of a nearshore food web: Standing stocks and production processes, *Annu. Rep. Natl Inst. Oceanogr.*, 58(Suppl.), 335–350, 1982.

Burkill, P.H., Edwards, E.S., Sleigh, M.A., Microzooplankton and their role in controlling phytoplankton growth in a marginal ice zone of the Bellinghausen Sea, *Deep-Sea Res. II*, 42, 1277–1290, 1995.

Burns, J.M., Trumble, S.J., Castellini, M.A., Testa, J.W., The diet of Weddell seals in McMurdo Sound, Antarctica, as determined from scat collections and stable isotope analysis, *Polar Biol.*, 19, 272–282, 1998.

Butterworth, D.S., Antarctic ecosystem management, in *Selected Papers Presented to the Scientific Committee of CCAMLR 1982–1984, Part II*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 15–42, 1985.

Butterworth, D.S., Antarctic marine ecosystem management, *Polar Rec.*, 23, 37–47, 1986.

Butterworth, D.S., Punt, A.E., Basson, M., A simple approach to calculating the potential yield of krill from biomass survey results, in *Selected Scientific Papers, 1991* (SC-CAMLR,-SSR/8), Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 207–217, 1991.

Butterworth, D.S., Gluckman, G.R., Thompson, R.B., Chalis, S., Hiramatsu, K., Agnew, D., Further computations of the consequences of settling the annual catch limit to a fixed fraction of the estimate of krill biomass from a survey, *CCAMLR Sci.*, 1, 81–106, 1994.

Bykova, V.P., Radakova, T.N., Changes in the properties of precooked frozen krill flesh during storage, in *Krill Processing Technology*, Bykov, V.P. Ed., VNIRO, Moscow, 1981, 7–16. In Russian with English summary.

Cadee, G.C., Gonzales, H., Schnack-Schiel, S.B., Krill diet affects faecal string settling, *Polar Biol.*, 12, 75–80, 1992.

Calhaem, I., Christoffel, D.A., Some observations of the feeding habits of a Weddell seal and measurements of its prey, *NZ J. Mar. Freshwater Res.*, 3, 181–190, 1969.

Capriulo, G.M., Feeding-related ecology of marine protozoa, in *Ecology of Marine Protozoa*, Carpenter, G.M., Ed., Oxford University Press, New York, 1992, 186–259.

Capriulo, G.M., Sherr, E.B., Sherr, B. F., Trophic behaviour and related community feeding activities of heterotrophic marine protists, in *Protozoa and Their Role in Marine Processes, Nato ASI Series G Ecological Sciences*, Vol. 25, Springer, Heidelberg, 219–265, 1991.

Car, M., Codspoti, L.A., Oceanographic cruise summary, Ross Sea, Antarctica, February 1968. Informal Report No. 68–64, Naval Oceanographic Office, Washington, DC, 1968.

Carey, A.G., Jr., Marine ice fauna: Arctic, in *Sea Ice Biota*, Horner, R.A., Ed., CRC Press, Boca Raton, FL, 1985, 173–190.

Carlson, C.A., Hansell, P.A., The contribution of DOM to the biogeochemistry of the Ross Sea, in *Biogeochemical Cycles in the Ross Sea*, DiTullio, G.R., Dunbar, R.B., Eds., American Geophysical Union, Washington, DC, 2002.

Carlson, C.A., Ducklow, H.W., Hansell, D.A., Smith, W.O., Jr., Organic carbon partitioning during spring phytoplankton blooms in the Ross Sea polyna and the Sargasso Sea, *Limnol. Oceanogr.*, 43, 375–386, 1998.

Carlucci, A.F., Cuhel, R.L., Vitamins in the South Polar Seas: Distribution and significance of dissolved and particulate Vitamin B_{12}, thymine, and biotin in the Southern Indian Ocean, in *Adaptations Within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 115–123.

Carmack, E.C., Circulation and mixing in ice-covered waters, in *The Geophysics of Sea Ice*, Untershiner, N., Ed., Plenum Press, New York, 1986, 646–712.

Carmack, E.C., Large-scale physical oceanography of polar oceans, in *Polar Oceanography, Part A: Physical Sciences*, Smith, W.O., Jr., Ed., 1992, 171–222.

Carmack, E.C., Forster, T.D., On the flow of water out of the Weddell Sea, *Deep-Sea Res.*, 22, 711–724, 1975.

Caron, D.A., Grazing of attached bacteria by heterotrophic microflagellates, *Microb. Ecol.*, 13, 203–218, 1987.

Caron, D.A., Heterotrophic flagellates associated with sedimentary detritus, in *The Biology of Free-living Heterotrophic Flagellates*, Patterson, D.J., Larsen, J., Eds., Clarendon Press, Oxford, 1996, 77–92.

Caron, J.McN., Davis, P.G., Madin, L.P., Siebruth, J.McN., Heterotrophic bacteria and bacterivorous Protozoa in oceanic macroaggregates, *Science*, 218, 795–797, 1982.

Caron, D.A., Madin, I.D., Cole, J.J., Composition and degradation of salp fecal pellets: Implications for vertical flux in oceanic systems, *J. Mar. Res.*, 47, 829–856, 1989.

Carpenter, E.J., Capone, D.G., Eds., *Nitrogen in the Marine Environment*, Academic Press, New York, 1983.

Carrada, G.C., Mangoni, O., Russo, G.F., Saggioma, V., Phytoplankton size fractionated biomass in the Ross Sea: Spatial and temporal variations during the austral spring, in *Ross Sea Ecology*, Farando, F.M., Guglielmo, L., Ianora, A., Eds., Springer-Verlag, New York, 1999, 205–216.

Carrick, R., Southern seals as subjects of ecological research, in *Biologie Antarctique*, Carrick, R., Holdgate, W.M., Prévost, J., Eds., Herman, Paris, 1964, 421–432.

Carrick, R., Population ecology of the Australian black-backed magpie, royal penguin, and silver gull, in *Population Ecology of Migratory Birds: A Symposium*, U.S. Department of the Interior Wildlife Research Report No. 2, U.S. Department of the Interior, Washington, DC, 41–49, 1972.

Carrick, R., Ingham, S.E., Studies on the southern elephant seal, *Mirounga leonina* (L.), IV: Breeding and development, *CSIRO Wildlife Res.*, 7, 161–197, 1962.

Casaux, R., Baroni, A., Corlini, A., The diet of the Weddell Seal *Leptonychotes weddelli* at Harmony Point, South Shetland Islands, *Polar Biol.*, 18, 371–375, 1997.

Cassie, I., The distribution of surface phytoplankton between New Zealand and Antarctica December, 1957, *Transa-Atarc. Exped.—Sci. Rep.*, 7, 1–11, 1963.

Castellanos, Z.J.A., Perez, J.C.L., Algunos aspectos bioecologicos de la zona intercotidal de Carbo Primavera (Costa de Danco, Peninsula Antártica), *Contribución Instituto Antártico Argentino*, 50, 1–29, 1963.

Castellini, M.A., Davis, R.W., Davis, M., Horning, M., Antarctic marine life under the McMurdo Ice Shelf at White Island: A link between nutrient flux and seal population, *Polar Biol.*, 2, 229–231, 1984.

Castilla, J.C., Rozbaczylo, N., Rocky intertidal assemblages and predation on the gastropod *Nacella (Patinigera) concinna* at Robert Island, South Shetlands, Antarctica, *Serie Científica Instituto Antártico Chileno*, 32, 65–74, 1985.

Catalano, G., Povero, P., Fabiano, M., Benedetti, F., Goffart, A., Nutrient utilization and particulate organic mater changes during summer in the upper mixed layer (Ross Sea, Antarctica), *Deep-Sea Res.*, 44, 97–112, 1997.

Catry, P., Phillips, R.A., Phalan, B., Silk, J.R.D., Croxall, J.P. et al., Foraging strategies of grey-headed albatross, Thalassarche chrysotomaInteraction of movements, activity, and feeding events, *Mar. Ecol. Prog. Ser.*, 280, 261–273, 2004.

Cattaneo-Viette, R., Bavestrello, G., Cerrano, C., Gano, E., Manzella, L., Pansivi, M., Sara, M., The role of sponges in the Terra Nova Bay ecosystem, in *Ross Sea Ecology*, Farmando, F.M., Guglielmo, L., Ianora, A., Eds., Springer, Berlin, 1998, 539–549.

Cauwet, G., Non-living particulate matter, in *Marine Organic Chemistry*, Dursma, E.K., Dawson, R., Eds., Elsevier, Amsterdam, 1981, 71–89.

Cavender-Bares, K.K., Karl, D.M., Chisholm, S.W., Nutrient gradients in the western North Atlantic Ocean: Relationships to microbial community structure and to patterns in the Pacific Ocean, *Deep-Sea Res. I.*, 48, 2373–2395, 2001.

Cawthron, M.W., Whale research in New Zealand, *Int. Whaling Committee Rep.*, 28, 109–113, 1978.

CCAMLR Standard Methods for Monitoring Parameters of Predatory Species, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1988.

CCAMLR Ecosystem Monitoring Program: Standard Methods for Monitoring Studies, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 2003.

Cerri, R.D., Fraser, D.F., Predation and risk in foraging minnows: Balancing conflicting demands, *Am. Nat.*, 121, 552–561, 1983.

Chang, F.H., The ultrastructure of *Phaeocystis pouchetii* (Prymnesiophyceae) vegetative colonies, with special reference to the production of new gelatinous envelope, *NZ J. Mar. Freshwater Res.*, 18, 303–308, 1984.

Chaolum, L., Zhang, S.G., Peng, J.I., Summer feeding activities of zooplankton in Prydz Bay, Antarctica, *Polar Biol.*, 24, 892–900, 2001.

Chapman, D.G., Re-analysis of Antarctic fin whale population data, *Rep. Int. Whal. Commun.*, 20, 510–559, 1970.

Chapman, D.G., Management of international whaling and North Pacific fur seals: implications for fisheries management, *J. Fish Res. Board Can.*, 30, 24198–24260, 1972.

Chapman, D.G., Whales, *Oceanus*, 31, 64–70, 1988.

Charnov, E.L., Orians, G.H., Hyatt, K., The ecological implications of resources depression, *Am. Nat.*, 110, 247–259, 1970.

Charrassin, J.-B., Bost, C.-A., Putz, K., Zora, T., Le Maho, Y., Foraging strategy of incubating and brooding king penguins, *Aptenodytes Patagonicus*, *Oecologia*, 114, 194–201, 1998.

Charrassin, J-B., Kato, A., Handrich, Y., Sato, K., Naito, Y., Ancel, A., Bost, C.-A., Gauthier-Clerc, M., Ropert-Coudert, Y., Le Maho, Y., Feeding behaviour of free-ranging penguins determined by oesophageal temperatures, *Proc. R. Soc. Lond., Ser. B: Biol. Sci.*, 2, 151–157, 2001.

Charassin, J.-B., Le Maho, Y., Bost, C.-A., Seasonal changes in the diving parameters of king penguins (*Aptenodytes Patagonicus*), *Mar. Biol.*, 141, 581, 2002.

Chavez, F.P., Barker, R.T., An estimate of new production in the equatorial Pacific, *Deep-Sea Res.*, 34, 1229–1243, 1987.

Chechun, I.S., Feeding and food interrelationships of some subantarctic fishes of the Indian Ocean. *Proceedings of the Zoological Institute of Leningrad*, 127, 38–68, 1984. In Russian.

Chekunova, V.I., Naumov, A.G., Energy metabolism and food requirements of the marbled Notothenia, *Notothenia rossii mammorata* (Nototheniidae), *Journal of Ichthyology*, 22, Translated from Vorosy Ikhtiologii, 112–121, 1972

Chekunova, V.I., Rynkova, T.I., Energy requirements of the Antarctic crustacean, *Euphausia superba*, *Oceanology*, 14, 434–440, 1974.

Chen, Bo, Distribution and abundance of choanoflagellates in Great Wall Bay, King George Island, Antarctica, in austral summer, *NIPR Symp. Polar Biol.*, 7, 32–44, 1994.

Cheng, C.C., DeVries, A.L., The role of antifreeze glycopeptides and peptides in the freezing avoidance of cold-water fish, in *Life Under Extreme Conditions: Biochemical Adaptation*, di Prisco, G., Ed., Springer, Berlin and Heidelberg, 1991, 1–14.

Cherel, Y., Duhamel, G., Diet of the squid Moroteuthis ingens (Teuthoidea: Onychoteuthidae) in the upper slope waters of the Kerguelen Islands, *Mar. Ecol. Prog. Ser.*, 250, 197–203, 2003.

Cherel, Y., Klages, N., A review of the food of albatrosses, in *Albatross Biology and Conservation*, Robertson, G., Gales, R., Eds., Beaty and Sons, Chipping Norton, Surrey, 1998, 113–136.

Cherel, Y., Kooyman, G.L., Food of emperor penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica, *Mar. Biol.*, 130, 335–344, 1998.

Cherel, Y., Wiemerskirch, H., Seabirds as indicators of marine resources: Black-browed albatrosses feeding on ommastrephid squids in Kerguelen waters, *Mar. Ecol. Prog. Ser.*, 129, 295–300, 1995.

Cherel, Y., Weimerskirch, H., Duhamel, G., Interactions between longline vessels and seabirds in Kerguelen waters and a method to reduce seabird mortality, *Conservation Biology*, 75, 63–70, 1996.

Chiba, S., Ishimani, T., Hosie, G.W., Fukuchi, M., Spatio-temporal variability of zooplankton community structure off east Antarctica (90° to 160° E), *Mar. Ecol. Prog. Ser.*, 216, 95–108, 2001.

Chisholm, S.W., Morel, F.M.M., What controls phytoplankton production in nutrient-rich areas of the open sea?, *Papers from the Symposium of the American Society of Limnology and Oceanography*, 36(8), 1507–1565, 1991.

Chittleborough, R.G., Determination of the age in humpback whale, *Megaptera nodosa* (Bonnaterre), *Australian Journal of Marine and Freshwater Research*, 9, 1–10, 1959.

Chittleborough, R.G., Marked humpback whale of known age, *Nature (Lond.)*, 187, 164, 1960.

Chittleborough, R.G., Australian catches of humpback whales, 1961, *Reports of the Division of Fisheries and Oceanography, CSIRO, Australia*, 34, 1–13, 1962.

Chittleborough, R.G., Dynamics of two populations of humpback whales, *Megaptera novaeangliae* (Borowski), *Australian Journal of Marine and Freshwater Research*, 16, 33–128, 1965.

Choi, C., Primary production and release of dissolved organic carbon from phytoplankton in the Western North Atlantic, *Deep-Sea Res.*, 19, 731–735, 1972.

Chojancki, J., Wegelenska, T., Periodicity of composition, abundance, and vertical distribution of summer zooplankton (1977/1978) in Ezcurra Inlet, Admiralty Bay (King George Island, South Shetland), *J. Plankton Res.*, 6, 997, 1984.

Chown, S.L., Kelp degradation by *Paractora trichosterma* (Thompson) (Diptera: Helcomyzidae) at subantarctic South Georgia, *Polar Biol.*, 16, 171–178, 1996.

Christaki, U., Dolan, J.R., Pelegri, S., Rassoulzadegan, F., Consumption of picoplankton-size particles by marine ciliates: Effects of physiological state of the ciliate and particle quality, *Limnol. Oceanogr.*, 43, 458–464, 1998.

Christians, O., Leinemann, M., Untersuchungen über Fluor im Krill, *Informationer für Fischwirtschaft*, 27, 254–260, 1980.

Christians, O., Leinemann, M., Mahanty, M., Neue Ertentnisse uber den Flouridgehalt im krill, *Informationer fur Fischwirtschaft*, 28, 70–72, 1981.

Clarke, G.L., Dynamics of production in a marine area, *Ecological Monographs*, 16(4), 321–337, 1946.

Clarke, M.R., Sperm whales of the Azores, *Discovery Reports*, 28, 237–298, 1956.

Clarke, M.R., New technique for the study of sperm whale migrations, *Nature (Lond.)*, 238, 405–406, 1972.

Clarke, A., Some observations on krill (*Euphausia superba* Dana) maintained in the laboratory, *Br. Antarc. Surv. Bull.*, 43, 111–118, 1976.

Clarke, M.R., Beaks, nets, and numbers, *Symp. Zool. Soc. Lond.*, 38, 89–126, 1977.

Clarke, A., On living in cold water: Kstrategies in AntarcticAntarctic benthos, *Mar. Biol.*, 7, 111–119, 1979.

Clarke, A., The biochemical composition of krill, *Euphausia superba* Dana, from South Georgia, *J. Exp. Mar. Biol. Ecol.*, 43, 221–236, 1980.

Clarke, M.R., Squids and whales, *NERC News J.*, 9, 4–6, 1980a.

Clarke, M.R., Cephalopoda in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology, *Discov. Rep.*, 37, 1–324, 1980b.

Clarke, M.R., Cephalopod biomass estimation from predation, *Memoirs of the National Museum of Victoria*, 44, 95–107, 1983.

Clarke, W.G., Antarctic fin whale, *Balaenoptera physalus*, recruitment rates inferred from cohort analysis, *Int. Whaling Committee Rep. Spec. Issue*, 198–203, 1983.

Clarke, A., Life in cold water: The physiological ecology of polar marine ectotherms, *Oceanography and Marine Biology: An Annual Review*, 21, 341–453, 1983.

Clarke, A., Lipid content and composition of Antarctic krill, *Euphausia superba* Dana, *J. Crustacean Biol.*, 4(Special Issue No.1), 285–294, 1984.

Clarke, A., Energy flow in the Southern Ocean food web, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 571–580.

Clarke, M.R., Marine habitats—Antarctic cephalopods, in *Key Environments—Antarctica*, Bonner, W.N., Walton, D.W.H., Eds., Pergamon Press, Oxford, 1985, 191–200.

Clarke, A., The adaptation of aquatic animals to low temperatures, in *The Effects of Low Temperatures on Biological Systems*, Grout, B.W.W., Morris, G.J., Eds., Edward Arnold, London, 1987, 313–348.

Clarke, A., Seasonality in the Antarctic marine environment, *Comp. Biochem. Physiol.*, 90B, 461–473, 1988.

Clarke, A., A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates, *Biol. J. Linnean Soc.*, 14, 77–92, 1989.

Clarke, A., Is there a latitudinal diversity gradient in the sea?, *Trends Ecol. Evol.*, 7, 286–287, 1990a.

Clarke, A., Temperature and evolution: Southern Ocean cooling and the Antarctic marine fauna, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin, 1990b, 9–22.

Clarke, A., What is cold adaptation and how should we measure it?, *Am. Zoologist*, 3, 81–92, 1991.

Clarke, A., Temperature and extinction in the sea—a physiologist's view, *Palaeobiology*, 19, 499–518, 1993.

Clarke, A., The distribution of Antartic benthic marine communities, *Antarc. Res. Ser.*, 70, 219, 1996.

Clarke, D.B., Ackley, S.F., Physical, chemical and biological properties of winter sea ice in the Weddell Sea, *Antarct. J. U.S.*, 17, 107–109, 1981.

Clarke, D.B., Ackley, S.F., Sea ice structure and biological activity in the marginal ice zone, *J. Geophys. Res.*, 89, 2087–2095, 1981.

Clarke, A., Crame, J.A., The origins of the Southern Ocean marine fauna, in *Macroecology: Reconciling Divergent Views*, Ormons, R.F.C., Ed., Cambridge University Press, Cambridge, UK, 1997a, 253–268.

Clarke, A., Crame, J.A., Diversity, latitude, and time patterns in the shallow sea, in *Macroecology: Reconciling Divergent Views*, Ormons, R.F.C., Ed., Cambridge University Press, Cambridge, UK, 1997b, 122–147.

Clarke, A., Johnston, N.M., Antarctic marine benthic diversity, *Oceanography and Marine Biology: Annual Reviews*, 41, 47–114, 2003.

Clarke, A., Lakhami, K.H., Measures of biomass, moulting behaviour and the pattern of early growth in *Chorismus antarcticus* (Pfeffer), *Br. Antarct. Surv. Bull.*, 47, 61–88, 1979.

Clarke, A., Lakani, K.H., Measures of biomass, moulting behaviour, and the pattern of early growth in *Chorismus antarcticus* (Pfeffer), *British Antarctic Survey Bulletin*, 47, 61–68, 1996.

Clarke, A., Leakey, R.J., Seasonal cycle of phytoplankton, macronutrients, and the microbial community in nearshore Antarctic marine sediments, *Limnol. Oceanogr.*, 41, 1281–1294, 1996.

Clarke, M.R., MacLeod, N., Cephalopods in the diet of elephant seals at Signy Island, South Orkney Islands, *Br. Antarc. Surv. Bull.*, 57, 22–31, 1982a.

Clarke, M.R., MacLeod, N., Cephalopod remains in the stomachs of eight Weddell seals, *Br. Antarc. Surv. Bull.*, 57, 33–40, 1982b.

Clarke, A., Morris, D.J., Development of an energy budget for *Euphausia superba*, *Berichte zur Polarforschung*, 4, 102–110, 1983a.

Clarke, A., Morris, D.J., Towards an energy budget for krill: The physiology and biochemistry of *Euphausia superba* Dana, *Polar Biol.*, 2, 69–86, 1983b.

Clarke, A., Peck, L.S., The physiology of polar marine zooplankton, *Proc. Pro Mare Symp. Polar Mar. Ecol.*, 355–369, 1991.

Clarke, A., Prince, P.A., Chemical composition and calorific value of food fed to Mollymawk chicks (*Diomedea melanophris and D. crysostoma*) at Bird Island, South Georgia, *Ibis*, 122, 488–494, 1980.

Clarke, M.R., Croxall, J.P., Prince, P.A., Cephalopod remains in regurgitations of the wandering albatross at South Georgia, *Br. Antarc. Surv. Sci. Rep.*, 75, 1, 1981.

Clarke, A., Holmes, L.J., White, M.G., The annual cycle of temperature, chlorophyll, and minor nutrients at Signy Island, South Orkney Islands, *Br. Antarc. Surv. Bull.*, 80, 65–90, 1988a.

Clarke, A., Quetin, L.B., Ross, R.M., Laboratory and field estimates of faecal pellet production by Antarctic krill, *Euphausia superba*, *Mar. Biol.*, 98, 557–563, 1988b.

Clarke, J., Manly, B., Kerry, K., Gardner, H., Franchi, E., Corsolini, S., Focardi, S., Sex differences in Adélie Penguins (*Eudyptes*), in *Penguin biology*, Davis, L.S., Darby, J.T., Eds., Academic Press, San Diego, CA, 1998, 131–196.

Claustre, H., Poulet, S.A., Williams, R., Marley, J.-C., Coombs, S., Ben Mlih, F., Hapette, A.M., Martin-Jezequel, V., A biochemical investigation of a *Phaeocystis* sp. bloom in the Irish Sea, *J. Mar. Biol. Assoc. UK*, 70, 197–207, 1990.

Clementson, L.A., Parsluo, J.S., Griffiths, F.B., Lyne, V.D., Mackey, D.J., Harris, G.P., McKenzie, D.C., Bomham, P.L., Rathbone, C.A., Rintoul, S., Controls on phytoplankton production in the Australian sector of the Subtropical Convergence, *Deep-Sea Res.*, 45, 1627–1661, 1998.

Clowes, A.J., Phosphate and silicate in the Southern Ocean, *Discov. Rep.*, 19, 1–170, 1938.

Cobley, N.D., Shears, J.R., Breeding performance of gentoo penguins (*Pygoscelis papua*) at a colony exposed to high levels of human disturbance, *Polar Biol.*, 21, 335–360, 1999.

Cole, Y., Findlay, S., Pace, M.L., Bacterial production in fresh and saltwater systems: a cross-system overview, *Mar. Ecol. Prog. Ser.*, 43, 1–10, 1988.

Colos, Y., Slawyk, G., C13 and N14 uptake by marine phytoplankton, 4: Uptake ratios and the contribution of nitrate to the productivity of Antarctic waters (Indian Ocean sector), *Deep-Sea Res.*, 33(8A), 1039–1051, 1986.

Comiso, J.C., Gordon, A.L., Recurring polynas over the Cosmonaut Sea and Maud Rise, *J. Geophys. Res.*, 92, 2819–2833, 1987.

Comiso, J.C., Gordon, A.L., Cosmonaut polyna in the Southern Ocean: Structure and variability, *J. Geophys. Res.*, 101, 19297–19313, 1996.

Comiso, J.C., Sullivan, C.W., Satellite microwave and *in situ* observations of Weddell Sea ice cover and its marginal ice zone, *J. Geophys. Res.*, 91, 9663–9681, 1986.

Comiso, J.C., Zwally, H.T., Concentration gradients and growth and decay characteristics of seasonal sea ice cover, *J. Geophys. Res.*, 89(C5), 8081–8103, 1984.

Comiso, J.C., Maynard, N.G., Smith, W.O., Jr., Sullivan, C.W., Satellite ocean colour studies of Antarctic ice edges in summer and autumn, *J. Geophys. Res.*, 95(C6), 9481–9496, 1990.

Condy, P.R., Results of the third seal survey in the Haakon VII Sea, Antarctica, *S. Afr. J. Antarc. Res.*, 6, 2–8, 1976.

Condy, P.R., Annual cycle of the elephant seal, *Mirounga leonina* (Linn.), at Marion Island, *S. Afr. J. Antarc. Res.*, 14, 95–102, 1977a.

Condy, P.R., Results of the fourth seal survey in the KingHaakonVII Sea, Antarctica, *S. Afr. J. Antarc. Res.*, 6, 2–8, 1977b.

Condy, P.R., Annual food consumption and seasonal fluctuations in biomass of seals at Marion Island, *Mammalia*, 45, 21–30, 1981.

Condy, P.R., van Aarde, R.J., Bester, M.V., The seasonal occurrence and behaviour of killer whales (*Orcinus orca*) at Marion Island, *J. Zool. (Lond.)*, 184, 449–464, 1978.

Conlon, K.E., Rau, G., McFeters, G.A., Kvitek, R., Influence of the McMurdo Station sewage outfall on coastal marine fauna, in *Antarctic Ecosystems: Models for Wider Understanding*, Davidson, W., Howard-Williams, C., Broady, P., Eds., New Zealand Natural Sciences, Christchurch, 2000, 315–318.

Conlon, K.E., Kim, S.I., Hunter, S., Lenihan, S., Oliver, J.S., Benthic community changes at McMurdo Station: A response to sewage abatement?, in *Antarctic Biology in a Global Context*, Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backhuys Publishers, Leiden, The Netherlands, 2003, 264–270.

Conover, R.J., Huntley, M., Copepods in an ice-covered sea—Distribution, adaptations to seasonally-limited food, metabolism, growth pattern, and life cycle, *J. Mar. Syst.*, 2, 1–41, 1991.

Conroy, J.W.H., Recent increases in penguin populations in the Antarctic and sub-Antarctic, in *The Biology of Penguins*, Stonehouse, B., Ed., MacMillan, London, 1975, 321–370.

Conroy, J.W.H., Twelves, E.L., Diving depths of the Gentoo Penguin (*Pygoscelis papua*) and Blue-eyed Shag (*Phalacrocorax atriceps*) from the South Orkney Islands, *Br. Antarc. Surv. Bull.*, 30, 106–108, 1972.

Conroy, J.W.H., White, M.G., The breeding status of the King Penguin (*Aptenodytes patagonica*), *Br. Antarc. Surv. Bull.*, 32, 31–40, 1973.

Conroy, J.W.H., Darling, O.W.H., Smith, H.G., The annual cycle of the chinstrap penguin (*Pygoscelis antarctica*) on Signy Island, South Orkney Islands, in *The Biology of Penguins*, Stonehouse, B., Ed., Macmillan, London, 1975, 353–363.

Constable, A.J., CCAMLR ecosystem monitoring and management: Future work, *CCAMLR*, 9, 233–253, 2002.

Constable, A.J., CCAMLR ecosystem monitoring and management framework. WG-EMM-01 Presentation Paper, *CCAMLR Science*, 9, 235, 2004.

Constable, A.J., de la Mare, W.Y., Agnew, D.J., Everson, I., Miller, D.G.M., Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) ICES, *Mar. Sci.*, 57, 778–791, 2000.

Cooke, J.C., Beddington, J.R., Further development of an assessment technique for male sperm whales based on length data from the catches, *Rep. Int. Whal. Commun.*, 32, 239–241, 1982.

Cooke, J.G., de la Mare, W.K., The effects of variability in age data on the estimation of biological parameters in minke whales (*Balaenoptera acutorostratus*), *Int. Whaling Committee Rep.*, 33, 333–338, 1983.

Cooper, J., Berruti, A., The conservation status of South Africa's continental and oceanic islands, in *Biotic Diversity in South Africa: Concepts and Conservation*, Huntley, B.J., Ed., Oxford University Press, Cape Town, 1989, 239–253.

Cooper, J., Woehler, E.J., Consumption of Antarctic krill (*Euphausia superba*) by seabirds during the summer in the Prydz Bay region, Antarctica, in *Southern Ocean Ecology: The BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, UK, 1994, 247–260.

Cooper, J., Brown, C.R., Gales, R.P., Hindell, M.A. et al., Diets and dietary segregation of crested penguins (*Eudyptes*), in *Penguin Biology*, Davis, L.S., Darby, J.T., Eds., Academic Press, London, 1990, 131–156.

Copping, A.E., Lorenzen, C.J., Carbon budget of a marine phytoplankton-herbivore system with carbon-14 as a tracer, *Limnology and Oceanography*, 25, 873–882, 1980.

Corless, J.O., Snyder, R.A., A preliminary description of several new ciliates from the Antarctica, including *Cohnilembus grassei* n. sp., *Protistologica*, 22, 39–46, 1986.

Cormaci, M., Funari, G., Scammacca, B., The benthic algal flora of Terra Nova Bay (Ross Sea, Antarctica), *Botanica Marina*, 35(6), 541–552, 1992.

Cormaci, M., Funari, G., Scammacca, B., The macrophytobenthos of Terra Nova Bay, in *Ross Sea Ecology*, Farando, F.M., Guglielmo, L., Ianora, A., Eds., Springer, Berlin, 1998, 493–502.

Corner, R.W.M., Observations on a small crabeater seal breeding group, *Br. Antarc. Surv. Bull.*, 30, 104–106, 1972.

Corsolini, S., Focardi, S., Bioconcentration of polychlorinated biphenyls in the pelagic food chain of the Ross Sea, in *Ross Sea Ecology*, Farando, F.M., Guglielmo, L., Ianora, A., Eds., Springer, Berlin, 1998, 575–584.

Costa, D.P., Reproductive and foraging energetics of pinnipeds: Implications for life history patterns, *Am. Zoologist*, 31, 111–130, 1991.

Costa, D.P., Reproductive and foraging energetics of pinnipeds: Implications for life history patterns, in *Pinniped Behaviour*, Renouf, D., Ed., Chapman Hall, London, 1991, 300–344.

Costa, D.P., The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia, in *Recent Advances in Marine Mammal Science*, Boyd, I., Ed., Oxford University Press, Oxford, 1993, 293–314.

Costa, D.P., Crocker, D.E., Marine mammals in the Southern Ocean, *Antarc. Res. Ser.*, 70, 287–301, 1996.

Costa, D.P., Croxall, J., Duck, C., Foraging energetics of Antarctic fur seals in relation to changes in prey availability, *Ecology*, 70, 596–606, 1989.

Cota, G.F., Photoadaptation in high Arctic ice algae, *Nature (Lond.)*, 315, 219–222, 1985.

Cota, G.F., Kottmeier, S.T., Robinson, D.H., Smith, W.O., Jr., Sullivan, W.C., Bacterioplankton in the marginal ice zone of the Weddell Sea: Biomass, production and metabolic activities during the austral autumn, *Deep-Sea Res.*, 37, 1145–1167, 1990.

Cota, G.F., Smith, W.O., Jr., Nelson, D.M., Nutrient and biogenic particulate distributions, primary production, and nitrogen uptake in the Weddell-Scotia Sea marginal ice zone during winter, *J. Mar. Res.*, 50, 155–181, 1992.

Court, G.S., Dacis, L.S., Focardi, S., Bargargli, R., Fossi, C., Leonizu, C., Marili, L., Chlorinated hydrocarbons in the tissues of South Polar skuas (*Catharacta maccormicki*) and Adélie Penguins (*Pygoscelis adeliae*) from Ross Sea, Antarctica, *Environ. Pollut.*, 97, 295–301, 1997.

Cox, G.F.N., Weeks, W.F., Equations for determining the gas and brine volumes in sea ice samples, *J. Glaciol.*, 29(102), 306–316, 1983.

Crafford, J.E., Life cycle and kelp consumption of *Paractora dreuxi mirabilis* (Diptera: Helcomzidae) a primary decomposer of stranded kelp on Marion Island, *S. Afr. J. Antarc. Res.*, 14(1), 18–22, 1984.

Crafford, J.E., Scholtz, C.H., Phenology of stranded kelp degradation by the kelp fly *Paractora dreuxi mirabilis* (Helcomyzidae) at Marion Island, *Polar Biol.*, 7(2), 289–294, 1987.

Cram, D.L., Agenbag, J.J., Hampton, I., Robertson, A.A., SAS Protea Cruise, The general results of the acoustics and remote sensing study, with recommendations for estimating the abundance of krill (*Euphausia superba* Dana), *S. Afr. J. Antarc. Res.*, 9, 3, 1979.

Crawford, R.M., The role of sea ice in the sedimentation of a diatom bloom, *Limnol. Oceanogr.*, 40, 200–204, 1995.

Crawford, C.C., Hobbie, J.E., Webb, K.L., The utilization of dissolved free amino acids by estuarine microorganisms, *Ecology*, 55, 331–363, 1974.

Crisafi, E., Assaro, F., La Ferla, R., Monticelli, S., Microbial biomass and respiratory activity related to the ice-melting upper layers in the Ross Sea (Antarctica), in *Ross Sea Ecology*, Faranda, F.M., Guglielmo, L., Ianora, A., Eds., Springer, Berlin, 1998, 171–180.

Crocker, K.M., Ondrusek, M.E., Petty, R.L., Smith, R.C., Dimethylsulphide, algal pigments, and light in an Antarctic *Phaeocystis* sp. bloom, *Mar. Biol.*, 124, 335–340, 1995.

Croll, D.A., Tersky, B.R., Penguins, fur seals, and fishing: Prey requirements and potential competition in the South Shetland Islands, Antarctica, *Polar Biol.*, 19, 365–374, 1998.

Croxall, J.P., Seabirds, in *Antarctic Ecology,* Vol. 2, Laws, R.M., Ed., Academic Press, London, 1984, 533–619.

Croxall, J.P., Use of indices of predation status and performance in CCAMLR fishery management, *CCAMLR Selected Scientific Papers SC-CCAMLR SSP16*, 333–336, 1989.

Croxall, J.P., Southern Ocean environmental changes: Effects on seabird, seal, and whale populations, in *Antarctic and Environmental Change*, Drewry, D.J., Laws, R.M., Pyle, J.A., Eds., Oxford University Press, Oxford, 1992, 319–328.

Croxall, J.P., Southern Ocean environmental changes: Effects on seabird, seal, and whale populations, *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 338, 319–328, 1992.

Croxall, J.P., Davis, R.W., Metabolic rate and foraging behaviour of *Pygoscelis* and *Eudyptes* penguins at sea, in *Penguin Biology*, Davis, L.S., Darby, J.T., Eds., Academic Press, San Diego, CA, 1990, 207–228.

Croxall, J.P., Furse, J.R., Food of the chinstrap penguin, *Pygoscelis antarctica*, and macaroni penguin, *Eudyptes chrysolophus*, at the Elephant Island group, South Shetland Islands, *Ibis*, 122, 237–245, 1980.

Croxall, J.P., Hiby, L., Fecundity, survival, and site fidelity in Weddell seals, *Leptonychotes weddelli*, *J. Appl. Ecol.*, 20, 19–32, 1983.

Croxall, J.P., Kirkwood, E.D., The breeding distribution of penguins on the Antarctic peninsula and the islands of the Scotia Sea, *British Antarctic Survey*, Cambridge, UK, 1979.

Croxall, J.P., North, A.W., Fish prey of Wilson's storm petrel (*Oceanites oceanicus*) at South Georgia, *Br. Antarc. Surv. Bull.*, 78, 37–42, 1988.

Croxall, J.P., Prince, P.A., Antarctic seabird and seal monitoring studies, *Polar Rec.*, 19, 573–595, 1979.

Croxall, J.P., Prince, P.A., Food feeding, and ecological segregation of seabirds at South Georgia, *Biol. J. Linnean Soc.*, 14, 103–131, 1980a.

Croxall, J.P., Prince, P.A., The food of gentoo penguins (*Pygoscelis papua*) and macaroni penguins (*Eudyptes chrysolophus*) at South Georgia, *Ibis*, 122, 245–253, 1980b.

Croxall, J.P., Prince, P.A., Calorific value of squid (Mollusca: Cephalopoda), *Br. Antarc. Surv. Bull.* , 55, 27–31, 1982.

Croxall, J.P., Prince, P.A., Seabirds as predators in marine resources, especially krill, at South Georgia, in *Seabirds: Feeding Ecology and Role in Marine Ecosystems*, Croxall, J.P., Ed., Cambridge University Press, Cambridge, UK, 1987, 345–368.

Croxall, J.P., Rothery, P., Population regulation of seabirds: Implications of their demography for conservation, in *Bird Population Studies: Relevance to Conservation and Management*, Perrins, C.M., LeBreton, J.D., Hirons, G.M., Eds., Oxford University Press, Oxford, 1991, 272–296.

Croxall, J.P., Prince, P.A., Hunter, I., McInnes, S.J., Copestake, P.G., The seabirds of the Antarctic Peninsula, islands of the Scotia Sea, and Antarctic Continent between 80° W and 20° W: their status and conservation, in *The Status and Conservation of the World's Seabirds*, Technical Publication No. 2, 637–666, 1984.

Croxall, J.P., Ricketts, C., Prince, P.A., Impact of seabirds on marine resources, especially krill, of South Georgia waters, in *Seabird Energetics*, Waters, G.C., Rahn, H., Eds., Plenum Press, New York, 1984, 285–318.

Croxall, J.P., Prince, P.A., Ricketts, C., Relationships between prey life-cycles and the extent, nature, and timing of seal and seabird predation in the Scotia Sea, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 516–533.

Croxall, J.P., Davis, R.W., O'Connell, M.J., Diving patterns in relation to diet of gentoo and macaroni penguins at South Georgia, *Condor*, 90, 157–167, 1988a.

Croxall, J.P., Davis, R.W., O'Connell, M.J., Diving patterns in relation to diet of gentoo and macaroni penguins at South Georgia, *Condor*, 96, 157–167, 1988b.

Croxall, J.P., McCann, T.S., Prince, P.A., Rothery, P., Reproductive performance of seabirds and seals at Georgia Signy Island, South Orkney Islands, 1976–1987: Some implications for Southern Ocean monitoring studies, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin, 1988, 261–285.

Croxall, J.P., Ricketts, C., Wood, A.G., Food consumption by predators in a CCAMLR Integrated Study Region, in *Selected Scientific Papers 1990 (SC-CAMLR-SSD/7)*, *Commission for the Conservation of Antarctic Marine Living Resources*, Hobart, 1990, 489–579.

Croxall, J.P., Rothery, P., Pickering, S.P.C., Prince, P.A., Reproductive performance, recruitment, and survival of wandering albatrosses (*Diomedea exulans*) at Bird Island, South Georgia, *J. Anim. Ecol.*, 59, 775–796, 1990.

Croxall, J.P., Reid, K., Prince, P.A., Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill, *Mar. Ecol. Prog. Ser.*, 177, 115–131, 1999.

Culik, B., Flouride turnover in Adélie Penguin (*Pygoscelkis adeliae*) and other bird species, *Polar Biol.*, 7, 179–187, 1987.

Culik, B.M., Wilson, P.R., Penguins crowded out?, *Nature (Lond.)*, 351, 331–340, 1991.

Culik, B.M., Woakes, A.J., Adelung, D., Wilson, R.P., Coria, N.R., Spairani, H.J., Energy requirements of Adélie Penguins (*Pygoscelis adeliae*) chicks, *J. Compar. Physiol. B: Biochem.*, 160, 61–70, 1990.

Cullen, J.J., Hypothesis to explain high-nutrient conditions in the open sea, *Limnol. Oceanogr.*, 36, 1578–1599, 1991.

Cullen, J.J., Lesser, M.P., Inhibition of photosynthesis by ultraviolet radiation as a function of dose and dosage rates: Results for a marine diatom, *Mar. Biol.*, 111, 183–190, 1991.

Currie, R., Environmental features in the ecology of Antarctic sea, in *Biologie Antarctique*, Holdgate, M.W., Prévost, J., Eds., Herman, Paris, 1964, 87–94.

Cushing, D.H., Temporal variation in production system, in *Analysis of Marine Ecosystems*, Longhurst, A.R., Ed., Academic Press, London, 1981, 443–471.

Cuzin-Roudy, J., Gonad history of the Antarctic krill *Euphausia superba* Dana during its breeding season, *Polar Biol.*, 7, 237–244, 1987.

Cuzin-Roudy, J., Schalk, P.H., Macrozooplankton—biomass, development and activity, *Berichte zur Polarforschung*, 66, 146–159, 1989.

Cziko, P., Cheng, C.-H., DeVries, A.L., Ice active protein in Antarctic echinoderms: Do isosmotic marine organisms risk freezing in freezing seawater? *IX SCAR Biology Symposium* Abstracts, p. 67, 2005.

Dahlback, A., Recent changes in the surface UV radiation and atmospheric ozone in a high Arctic site, in *Radiation and the Arctic System*, Hesson, D.O., Ed., Springer, Berlin, 2002, 3–22.

Dahms, H.U., Bergmans, S.M., Schminke, H.R., Distribution and adaptations of sea ice-inhabiting Harpacticoida (Crustacea: Copepoda) of the Weddell Sea, Antarctica, PSNZI, *Mar. Ecol.*, 11, 207–226, 1990a.

Dahms, H.U., Bergmans, S.M., Schminke, H.R., Distribution adaptations of sea ice-inhabiting Harpacticoida (Crustacea: Copepoda), *Limnol. Oceanogr.*, 35, 1569–1576, 1990b.

Daly, K.L., Overwintering development, growth, and feeding of larval *Euphausia superba* in the Antarctic marginal zone, *Limnol. Oceanogra.*, 35, 1564–1576, 1990.

Daly, K.L., Macaulay, M.C., Influence of physical and biological mesoscale dynamics on the seasonal distribution and behaviour of *Euphausia superba* in the marginal ice zone, *Mar. Ecol. Prog. Ser.*, 79, 37–66, 1991.

Daly, K.L., Macaulay, M.C., Abundance and distribution of krill in the ice edge zone of the Weddell Sea, austral spring1983, *Deep-Sea Res.*, 35, 21–41, 1998.

Daniels, R.A., Nesting behaviour of *Harpagifer bispinis* in Arthur Harbour, Antarctic Peninsula, *J. Fish Biol.*, 12, 465–474, 1979.

Daniels, R.A., Feeding ecology of some fishes of the Antarctic Peninsula, *Fish. Bull. US Natl Mar. Fish. Serv.*, 80, 575–588, 1979.

Daniels, R.A., Feeding ecology of some fishes of the Antarctic Peninsula, *Fish. Bull. US Natl Mar. Fish. Serv.*, 12, 575–588, 1982.

Danovaro, R., Puseddy, S., Mirto, S., Fabio, M., Meiofaunal assemblages associated with scallop beds (*Adamussium colbecki*) in the coastal sediments of Terra Nova Bay (Ross Sea, Antarctica), *Antarc. Sci.*, 11, 415–418, 1999.

Darnell, R.M., The organic detritus problem, in *Estuaries*, Publication No. 83 of the American Association for the Advancement of Science, Lauff, G.H., Ed., American Association for the Advancement of Science, Washington, DC, 1967a, 374–375.

Darnell, R.M., Organic detritus in relation to the estuarine system, in *Estuaries*, Publication No. 83 of the American Association for the Advancement of Science, Lauff, G.H., Ed., American Association for the Advancement of Science, Washington, DC, 1967b, 376–382.

David, P.M., The distribution of *Sagitta gazellae* Ritter-Zahoney, *Discov. Rep.*, 27, 235–278, 1955.

David, P.M., The distribution of chaetognaths in the Southern Ocean, *Discov. Rep.*, 29, 199–228, 1958.

David, P.M., The chaetognatha of the Southern Ocean, in *Biogeography and Ecology of Antarctica*, van Meighem, J., van Oye, P., Eds., Dr. W. Junk., The Hague, 1965, 296–303.

Davidson, K., Modelling microbial food webs, *Mar. Ecol. Prog. Ser.*, 145, 279–296, 1996.

Davidson, W., Lowe, C.L., How stenothermal are Antarctic marine animals, *Abstracts, Final Symposium on Ecology of the Antarctic Sea Ice Zone, Korcula, Croatia*, 05, 2002.

Davidson, A.T., Marchant, H.J., Binding of manganese by Antarctic *Phaeocystis pouchetii* and the role of bacteria in its release, *Mar. Biol.*, 95, 481–487, 1987.

Davidson, A.T., Marchant, H.J., Protist abundance and carbon concentration during a *Phaeocystis*-dominated bloom at an Antarctic coastal site, *Polar Biol.*, 12, 387–395, 1992.

Davidson, A.T., Marchant, H.J., Comparative impact of in situ UV exposure on productivity, growth, and survival of Antarctic *Phaeocystis* and diatoms, *Proc. NIPR Symp. Polar Biol.*, 4, 53–69, 1994.

Davidson, A.T., Bramich, D., Marchant, H.J., McMinn, A., Effects of UV-B irradiation on growth and survival of Antarctic marine diatoms, *Mar. Biol.*, 119, 507–515, 1994.

Davies, J.L., The southern form of the pilot whale, *J. Mammal.*, 41, 29–34, 1960.

Davis, R.W., Kooyman, G.L., Free-ranging energetics of penguins, in *Seabird Energetics*, Whitlow, G.C., Rahn, H., Eds., Plenum Press, New York, 1984, 245–253.

Davis, P.G., Siebruth, J.McN., Estuarine and microflagellate predation of actively-growing bacteria: Estimates by frequency of dividing-divided bacteria, *Mar. Ecol. Prog. Ser.*, 19, 237–246, 1984.

Davis, R.W., Castellini, M., Horning, M., Davis, M.P., Kooyman, G.L., Maue, R., Winter ecology of Weddell seals at White Island, *Antarc. J. U.S.*, 17, 183–184, 1982.

Davis, R.W., Kooyman, G.L., Croxall, J.P., Water flux and estimated metabolism of free-ranging gentoo and macaroni penguins at South Georgia, *Polar Biol.*, 2, 41–46, 1983.

Davis, L.S., Boersma, P.D., Court, G.S., Satellite telemetry of the winter migration of Adélie Penguin (*Pygoscelis adeliae*), *Polar Biol.*, 16, 221–225, 1996.

Davis, L.S., Harcourt, R.G., Bradshaw, C.J.A., The winter migration of Adélie Penguins breeding in the Ross Sea sector of Antarctica, *Polar Biol.*, 24, 593–597, 2002.

Dawbin, W.H., The seasonal migratory cycle of humpback whales, in *Whales, Dolphins, and Porpoises*, Norris, K.S., Ed., University of California Press, Berkeley, CA, 1966, 145–170.

Dayton, P.K., Observations on the growth, dispersal and population dynamics of some sponges in McMurdo Sound, Antarctica, in *Biologie des Spongaires*, Vol. 391, Levi, C., Bouvy-Esnant, N., Eds., 1979, 271–282.

Dayton, P.K., Polar benthos, in *Polar Oceanography Part B: Chemistry, Biology and Geology*, Smith, W.O., Jr., Ed., Academic Press, San Diego, CA, 1990, 631–685.

Dayton, P.K., Hessler, R.R., Role of biological disturbance in maintaining diversity in the deep sea, *Deep-Sea Res.*, 19, 199–208, 1972.

Dayton, P.K., Martin, S., Observations on ice stalactites in McMurdo Sound, Antarctica, *J. Geophys. Res.*, 76, 1595–1599, 1971.

Dayton, P.K., Oliver, S., Antarctic soft-bottom benthos in oligotrophic and eutrophic environments, *Science*, 197, 55–58, 1977.

Dayton, P.K., Robilliard, G.A., Notes on the biology of the Chaenichthyid fish *Pagetopsis macropterus* from McMurdo Sound, Antarctica, *Antarc. J. U.S.*, 4(6), 304–305, 1969.

Dayton, P.K., Robilliard, G.A., DeVries, A.L., Anchor ice formation in McMurdo Sound, Antarctica, and its biological significance, *Science*, 163, 273–274, 1969.

Dayton, P.K., Robilliard, G.A., Paine, R.T., Benthic faunal zonation as a result of anchor ice formation at McMurdo Sound, Antarctica, in *Antarctic Ecology,* Vol. I, Holdgate, M.W., Ed., Academic Press, London, 1970, 244–258.

Dayton, P.K., Robilliard, G.A., Paine, R.T., Dayton, L.B., Biological accommodation in the benthic community at McMurdo Sound, Antarctica, *Ecol. Monogr.*, 44, 105–128, 1974.

Dayton, P.K., Watson, D., Palmisano, A.C., Barry, J.P., Oliver, J.S., Rivera, D., Distribution patterns of benthic microalgal standing stock at McMurdo Sound, Antarctica, *Polar Biol.*, 6, 207–213, 1986.

Deacon, G.E.R., A general account of the hydrology of the Southern Ocean, *Discov. Rep.*, 15, 177–238, 1937.

Deacon, G.E.R., The Southern Ocean, in *The Sea, Volume 2: The Composition of Sea-Water, Comparative and Descriptive Oceanography*, Hill, M.N., Ed., Interscience Publishers, New York, 1963, 281–296.

Deacon, G.E.R., The Southern Ocean, in *Antarctic Research*, Priestley, R., Ed., Herman, Paris, 1964a, 292–307.

Deacon, G.E.R., Antarctic oceanography: The physical environment, in *Biologie Antarctique*, Carrick, R., Holdgate, M.W., Prévost, J., Eds., Herman, Paris, 1964b, 81–86.

Deacon, G.E.R., Antarctic Ocean, *Interdisciplinary Science Review*, 2, 109–123, 1977.

Deacon, G.E.R., Physical and biological zonation in the Southern Ocean, *Deep-Sea Res.*, 29, 1–15, 1982.

Deacon, G.E.R. *The Antarctic Circumpolar Ocean*, Cambridge University Press, Cambridge, UK, 1984.

Dearborn, J.H., Reproduction in the Nototheniid fish *Trematomus bernacchii* Boulenger at McMurdo Sound, Antarctica, *Copeia*, 3, 302–308, 1965a.

Dearborn, J.H., Food of Weddell seals at McMurdo Sound, Antarctica, *J. Mammal.*, 106, 37–43, 1965b.

Dearborn, J.H., Food and reproduction of *Glyptonotus antarcticus* (Crustacea: Isopoda) at McMurdo Sound, Antarctica, *Transactions of the Royal Society of New Zealand*, 8, 163–168, 1967.

Dearborn, J.H., Benthic invertebrates, *Aust. Nat. Hist.*, 16, 134–139, 1968.

De Broyer, C., Analysis of gigantism and dwarfness of Antarctic and Sub-Antarctic Gammaridean Amphipoda, in *Adaptations Within Antarctic Ecosystems*, Llano, G., Ed., Smithsonian Institution, Washington, DC, 1977, 327–334.

De Broyer, C., Jazdzewski, K., Dauby, P., Biodiversity pattern in the Southern Ocean: Lessons from Crustacea, in *Antarctic Biology in a Global Context*, Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backhuys Publishing, Leiden, The Netherlands, 2003, 201–204.

Decho, A.W., Microbial exopolymer secretions in ocean environments: their role(s) in food webs and marine processes, *Oceanography and Marine Biology: Annual Reviews*, 28, 73–153, 1990.

Deflandre, G., Sur la presence de *Pavicorbicula* n.g. *socialis* dans le plankton de l'Antarctique (Terre Adélie), *Reviews in Algology*, 5, 183–188, 1960.

Deflandre, G., Deflandre-Rigand, M., Nanofossils siliceux, I: Archaeomonadacae, *Fichier Micropaleontologique*, 19, 4173–4400, 1970.

Dehairs, F., Goeyens, L., Stroobants, N., Mathot, S., Elemental composition of suspended matter in the Scotia–Weddell Confluence area during spring and summer (EPOS Leg 2), in *Weddell Sea Ecology*, Hempel, G. Ed., Springer, Berlin, 1995, 25–34.

de la Mare, W.K., Some principles for fisheries regulation from an ecosystem perspective. in *Selected Scientific Papers, 1986 (SC-CAMLR-SSP/3)*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1986, 323–339.

de la Mare, W.K., Preliminary consideration of performance criteria for the evaluation of conservation strategies, *Document WG-CSD 88/9*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1988.

de la Mare, W.K., Some recent developments in the management of marine living resources, in *Frontiers of Ecology*, Floyd, R.R., Sheppard, A.W., Barro, P.J.D., Eds., CSIRO Publishing, Melbourne, 1996, 559–616.

de la Mare, K.W., Tidier fisheries management requires a new MOP (management-orientated paradigm, *Rev. Fish. Biol. Fish*, 8, 349–356, 1998.

de la Mare, W.K., Abrupt mid-twentieth century decline in Antarctic sea ice extent from whaling records, *Nature (Lond.)*, 389, 87–90, 1997.

Delepine, R., La vegetation marine dans l'Antarctique de l'Ouest comparée a cell des Îles Australes Françaises: Consequences biogeographiques, *Compte rendu sommaire des séances. Société Biogéographique de Paris*, 374, 52–68, 1966.

Delepine, R., Hureau, J.C., Comparative study of the vertical distribution of marine vegetation of Archipel de Kerguelen and Isles Crozet, in *Symposium on Antarctic Oceanography*, Scott Polar Research Institute, Cambridge, UK, 1968, 164–165.

Delepine, R., Loamb, I.M., Zimmerman, M.H., Preliminary report on the marine vegetation of Archipel de Kerguelen and Isles Crozet, in *Proceedings of the 5th International Seaweed Symposium, Halifax*, Vol. 107, Plenum Press, London, 1965, 116.

Delille, D., Seasonal changes in the abundance and composition of the marine heterotrophic bacterial community in an Antarctic coastal area, *Polar Biol.*, 13, 463–470, 1993.

Delille, D., Marine bacterioplankton at the Weddell Sea ice edge: Distribution of psychrophilic and psychrotrophic populations, in *Weddell Sea Ecology*, Hempel, G., Ed., Springer, Berlin, 1995, 205–210.

Delille, D., Rosiers, C., Seasonal changes of Antarctic marine bacterioplankton and sea ice bacterial assemblages, *Polar Biol.*, 16, 27–34, 1995a.

Delille, D., Fiala, M., Rosiers, C., Seasonal changes in phytoplankton and bacterioplankton in an ice-water interface in the Antarctic neritic ice, *Mar. Ecol. Prog. Ser.*, 123, 225–233, 1995b.

Dell, R.K., Marine biology, in *Antarctica*, Hatherton, T., Ed., A.W. Reed, Wellington, 1965, 129–157.

Dell, R.K., Antarctic benthos, *Adv. Mar. Biol.*, 10, 1–126, 1972.

Dell, R.K., Fleming, C.A., Oligocene-Miocene bivalve Mollusca and other macrofossils from sites 270 and 272 (Ross Sea), DSDP, Leg 8, *Initial Reports of the Deep Sea Drilling Project*, 28, 693–703, 1975.

Delord, K., Gasco, N., Weimerskirch, H., Barbraud, C., Nicol, T., Seabird mortality in the Patagonian toothfish longline fishery at Crozet and Kerguelen Islands, *CCAMLR Science*, 12, 53–60, 2005.

DeMaster, D.P., The supply and accumulation of silica in the marine environment, *Geochimica et Cosmochimica Acta*, 45, 1715–1732, 1981.

Demers, S., Legendre, L.J., Therriault, C., Ingram, R.G., Biological production at the ice-water ergocline, in *Marine Interfaces Ecohydrodynamics*, Elsevier Oceanography Series, Nihoul, J.C.J., Ed., Vol. 42, Elsevier, Amsterdam, 1985, 31–44.

Deming, J.W., Psychophiles and polar regions, *Curr. Opin. Microbiol.*, 5, 301–309, 2000.

Denham, K.L., Powell, T.M., Effects of physical processes on planktonic ecosystems in the coastal oceans, *Oceanogr. Mar. Biol.: Annu. Rev.*, 22, 125–168, 1984.

Denys, C.J., McWhinnie, M.A., Fecundity and ovarian and preliminary assessment of contaminated sites at Casey Station, Wilkes Land, Antarctica, *Polar Biol.*, 35, 299–306, 1999.

Deprez, P.P., Arens, M., Locher, H., Identification and preliminary assessment of contaminated sites at Casey Station, Wilkes Land, Antarctica, *Polar Rec.*, 35, 299–316, 1999.

Desbruyeres, D., Benthic bionomy of the continental shelf of the Kerguelen Archipelago, Macrofauna, 2: Diversity of benthic annelid population in a Fjord close to the Morbihan Gulf, in *Adaptations Within Antarctic Ecosystems*, Llano, G., Ed., Smithsonian Institution, Washington, DC, 1977, 227–238.

Desbruyeres, D., Guile, A., La faune benthic de l'archipel de Kerguelen: Premiéres données quantitatives, *Comptes-rendus de l'Académie des Sciences Paris*, 276, 633–636, 1973.

Desperin, B., Note preliminaire sur la manchot papou (*Pygoscelis papua*) de l'île de la Possession (archipel Crozet), *L'Oiseau et la RFO*, 42, 69–83, 1972.

De Villiers, A.F., Littoral ecology of Marion and Prince Edward Islands (Southern Ocean), *S. Afr. J. Antarc. Res.* (Suppl. 1), 1–40, 1976.

DeVries, A.L., Survival at freezing temperatures, in *Biochemical and Biophysical Perspectives in Marine Biology,* Vol. 1, Mallins, D.W., Sargent, J.R., Eds., Academic Press, London, 1974, 289–330.

DeVries, A.L., The physiology of cold adaptations in polar marine poikilotherms, in *Polar Oceans*, Dunbar, J.M., Ed., Arctic Institute of North America, Calgary, 1977, 409–420.

DeVries, A.L., The physiology and biochemistry of low temperature adaptations in polar marine ecosystems, in *Polar Research: To the Present and the Future*, AAAS Selected Symposium No. 7, McWhinnie, M.A., Ed., Westview Press, Boulder, 1978, 175–202.

DeVries, A.L., Biological antifreezes and survival in freezing environments, in *Animals and environmental fitness*, Gilles, R., Ed., Pergamon Press, Oxford, 1980, 583–607.

DeVries, A.L., Antifreeze peptides and glycopeptides in cold—water fishes, *Annu. Rev. Physiol.*, 45, 245–260, 1983.

DeVries, A.L., The role of antifreeze glycoproteins and peptides in the freezing avoidance of Antarctic fishes, *Comp. Biochem. Physiol.*, 90B, 611–621, 1988.

DeVries, A.L., The role of antifreeze proteins in survival of Antarctic fishes in freezing environments, in *Antarctic Communities: Species, Structure and Survival*, Valencia, J., Walton, D.W.H., Eds., Cambridge University Press, Cambridge, UK, 1997, 202–208.

DeVries, A.L., Lin, Y., The role of glycoprotein antifreezes in the survival of Antarctic fishes, in *Adaptations Within Antarctic Ecosystems*, Llano, G.A., Ed., Gulf Publishing Company, Houston, TX, 1977, 439–457.

DeWitt, H.H., The character of the midwater fish fauna of the Ross Sea, Antarctica, in *Antarctic Ecology,* Vol. 1, Holdgate, M.W., Ed., Academic Press, London, 1970, 305–314.

DeWitt, H.H., *Coastal and deep-water benthic fishes of the Antarctic*, Antarctic Map Folio Series, Vol. 15, American Geographical Society, Washington, DC, 1971.

DeWitt, H.H., Hopkins, T.L., Aspects of the diet of the Antarctic silverfish, *Pleurogramma antarcticum*, in *Adaptations Within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 557–567.

DeWitt, H.H., Tyler, J.C., Fishes of the Stanford Antarctic Biological Research Programme, 1958–1959, *Stanford Ichthyol. Bull.*, 7, 162–199, 1960.

Dichie, L.M., Perspective on fisheries biology and implications for management, *J. Fish Res. Board Can.*, 36, 838–844, 1979.

Dickie, L.M., Problems in predation, *Oceanus*, 18, 30–35, 1975.

Dickinson, A.B., Tagging elephant seals for life-history studies, *Polar Rec.*, 13, 443–446, 1967.

Dieckmann, G.S., Arrigo, K., Sullivan, C.W., A high-resolution sampler for nutrient and chlorophyll *a* profiles of the sea ice platelet layer and underlying water column below the fist ice in polar oceans: Preliminary results, *Mar. Ecol. Prog. Ser.*, 80, 291, 1992.

Dieckmann, G., Reicharalt, W., Zielinski, K., Growth and production of the seaweed *Himanothalia grandifolius* at King George Island, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 105–108.

Dieckmann, G.S., Rohart, G., Hellmer, H., Kipfskuhi, J., The occurrence of ice platelets at 150m depth near the Filchner Ice Shelf and its significance for sea ice biology, *Deep-Sea Res.*, 33, 141–148, 1986.

Dieckmann, G.S., Lange, M., Spindler, M., Ackley, S.F., The foraminifer *Neogloboquadrina pachyderma* in sea ice of the Weddell Sea, *Eos*, 69, 1267–1270, 1988.

Dieckmann, C.S., Lange, M.A., Ackley, S.F., Jennings, J.C., The nutrient status of sea ice of the Weddell Sea during winter: Effects of sea ice texture and algae, *Polar Biol.*, 11, 449–456, 1991.

Dieckmann, G.S., Eicken, H., Haas, C. et al., A compilation of data on sea ice algal standing crop from the Bellinghausen, Amundsen, and Weddell Seas from 1983 to 1994, *Antarc. Res. Ser.*, 73, 85–92, 1998.

di Prisco, G.D., Physiological and biochemical adaptation in fish to a cold marine environment, in *Antarctic Communities: Species, Structure and Survival*, Battaglia, B., Valencia, J., Walton, D.W.H., Eds., Cambridge University Press, Cambridge, UK, 1997, 251–260.

di Prisco, G.D., Arino, R., Molecular adaptation of the blood of Antarctic teleosts to environmental conditions, *Antarc. Sci.*, 1, 119–124, 1989.

Di Tuillo, G.R., Geesey, M.E., Jones, D.R., Daly, K.L., Campbell, L., Smith, W.O., Jr., Phytoplankton assemblage structure and primary productivity along 170° W in the South Pacific Ocean, *Mar. Ecol. Prog. Ser.*, 255, 55–80, 2003.

Divorky, G.J., Sea ice as a factor in seabird distribution and ecology in the Beaufort, Chukchi, and Bering Seas, in *Conservation of Marine Birds of Northern North America*, U.S. Fish and Wildlife Service, Wildlife Research Report No. 11, Bartonek, J.C., Nettleship, D.N., Eds., U.S. Fish and Wildlife Service, Washington, DC, 9–17, 1977.

Doake, C.S.M., Vaughan, D.G, Rapid disintegration of the Wordie Ice Shelf in response to atmospheric warming, *Nature (Lond.)*, 350, 328–330, 1991.

Dohler, G., Effect of ultraviolet radiation on pigmentation and nitrogen metabolism of Antarctic phytoplankton and ice algae, *J. Plant Physiol.*, 153, 603–609, 1998.

Doi, T., Ohsumi, S., Nemoto, T., Population assessment of sei whales in the Antarctic, *Norsk Hvafangsttd*, 56, 25–41, 1967.

Doidge, D.W., McCann, T.S., Croxall, J.P., Attendance behaviour of Antarctic fur seals, *Arctocephalus gazella*, in *Fur Seals: Maternal Strategies at Land and at Sea*, Gentry, R.L., Kooyman, G.L., Eds., Princeton University Press, Princeton, NJ, 1986, 102–114.

Doige, D.W., Croxall, J.P., Breeding density, pup mortality, and mother-pup behaviour in Antarctic fur seals at South Georgia, in *Proceedings of the Fourth Biennial Conference on the Biology of Marine Mammals, San Francisco, December 14–18, 1981*, 1983.

Doige, D.W., Croxall, J.P., Diet and energy budget of the Antarctic fur seal (*Arctocephalus gazella*) at South Georgia, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 460–465.

Dolzhenkov, V.N., Peculiarities of the distribution of *Euphausia superba* Dana in the Western part of the Pacific sector of Antarctica. Abstracts of papers, AllUnion Conference on Macroplankton, AllUnion Research Institute of Marine Fisheries and Oceanography, Moscow, 10–12, 1973. In Russian.

Domach, E.W., McClennen, C.E., Accumulation of glacial marine sediments in fjords of the Antarctic Peninsula and their use as Holocene palaeoenviromental indicators, *Antarct. Res. Ser.*, 70, 735–754, 1996.

Domach, E.W., McDenney, C.E., Accumulation of glacial marine sediments of the Antarctic Peninsula and their use as Holocene paleoenvironmental indicators, *Antarc. Res. Ser.*, 70, 135–154, 1996.

Domanov, M.M., Lipiski, M., Annual cycle of chlorophyll a and primary production of phytoplankton in Admiralty Bay (Antarctica), *Polskie Archiwum Hydrobiologii*, 37, 471–478, 1990.

Donnelly, B.G., Further observations on the southern right whale, *Eubalena australis*, in South African waters, *J. Reprod. Fertil. (Suppl.)*, 6, 347–352, 1969.

Dore, J.E., Tien, G., Letelier, R., Parrish, G., Szyper, J., Burgett, J., Karl, D., RACER: Distribution of nitrogenous nutrients near receding pack ice in Marguerite Bay, *Antarc. J. U.S.*, 27, 177–179, 1992.

Doroshenko, N.V., Populations of minke whales in the Southern Hemisphere, *Int. Whaling Committee Rep.*, 29, 361–364, 1979.

Douglas, D.P., Novitzky, J.A., Fournier, R.O., Microaudiography-based enumeration of bacteria with estimates of thymidine-specific growth and reproduction rates, *Mar. Ecol. Prog. Ser.*, 26, 91–99, 1987.

Dower, K.M., Lucas, M.I., Photosynthesis-irradiance relationships and production associated with a warm-core ring shed from the Agulhas Retrofection, South Africa, *Mar. Ecol. Prog. Ser.*, 95, 141–154, 1993.

Dower, K.M., Lucas, M.I., Phillips, R., Diechmann, G., Robinson, D.H., Phytoplankton biomass, P-I relationships and primary production in the Weddell Sea, Antarctica, during the austral summer, *Polar Biol.*, 16, 41–52, 1996.

Drew, E.A., Hastings, R.M., A year-round ecophysiological study of *Himentothallus grandifolius* (Desmarestiales: Phaeophyta) at Signy Island, Antarctica, *Phycologia*, 31, 262–277, 1992.

Drewery, D.J., Morris, E.M., The response of large ice sheets to climate change, *Philos. Trans. R. Soc. Lond., Ser. B*, 338, 235–342, 1992.

Dring, M.J., Jewson, D.H., What does ^{14}C-uptake by phytoplankton really measure? A fresh approach using a theoretical model, *Br. Phycol. J.*, 14, 122–123, 1979.

Drits, A.N., Pasternak, A.F., Feeding of mass species of Antarctic zooplankton in summer, in *Pelagic Ecosystems of the Southern Ocean*, Voronina, N.M., Ed., Nauka, Heyka, 1993, 250–259.

Droop, M.R., Heterotrophy of carbon, in *Physiology and Biochemistry of Algae*, Stewart, W.D.P., Ed., University of California Press, Berkeley, CA, 1974, 530–559.

Dubischer, C.D., Bathmann, U.V., Grazing impact of copepods and salps on phytoplankton in the Atlantic sector of the Southern Ocean, *Deep-Sea Res. II*, 44, 415–433, 1997.

Dubreuil, C., Denis, M., Conan, P., Ray, S., Spatial-temporal variability of ultraplankton vertical distribution in Atlantic frontal zones 60–66° E, 43–46° S, *Polar Biol.*, 26(11), 734–745, 2003.

Ducklow, H., Production and fate of bacteria in oceans, *BioScience*, 33, 494–501, 1983.

Dugdale, R.C., Goering, J.J., Uptake of new and regenerated forms of nitrogen in primary productivity, *Limnol. Oceanogr.*, 12, 196–206, 1967.

Dugdale, R.C., Wilkerson, F.P., Iron addition experiments in the Antarctic: a reanalysis, *Global Biogeochem. Cycles*, 4, 13–19, 1990.

Duhamel, G., Biology and population dynamics of *Notothenia rossii rossii* from the Kerguelen Islands (Indian Sector of the Southern Ocean), *Polar Biol.*, 1, 141–151, 1982.

Duhamel, G., Reproduction des Nototheniidae et Channichthyidae des Isles Kerguelen. In Antes du colloquer sur l'ecologie marine îles subantartiques, *Comité Nacional Français des Recherches Antarctiques*, 57, 91–108, 1987.

Duhamel, G., Hureau, J.C., La situation de la peche aux îles Kerguelen en 1981, *La Peche Maritime*, 5, 1–8, 1981.

Duhamel, G., Hureau, J.-C., The role of zooplankton in the diet of certain sub-Antarctic marine fishes, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 422–429.

Duhamel, G., Hureau, J.-C., Changes in fish populations and fisheries around the Kerguelen Islands during the last decade, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin, 1990, 323–333.

Duhamel, G., Pletikowsic, M., Données biologiques sur les Nototheniidae de Îles Crozets, *Cybium*, 7, 43–57, 1983.

Dunbar, M.J., Physical causes and biological significance of polynas and other open water, in *Polynas and the Canadian Arctic*, Canadian Wildlife Service Occasional Paper, Ottawa, 1981, 29–41.

Dunbar, R.B., Sediment trap experiments on the Antarctic continental margin, *Antarct. J. U.S.*, 19, 71–74, 1983.

Dunbar, R.B., Anderson, J.B., Domack, E.W., Oceanographic influences on sedimentation along the Antarctic continental shelf, in *Oceanology of the Antarctic Continental Shelf, Antarctic Research Series* 43, Jacobs, S.S., Ed., 1985, 291–312.

Dungan, M.L., Miller, T.E., Thompson, D.A., Catastrophic decline of a top carnivore in the Gulf of California rocky intertidal zone, *Science*, 215, 989–991, 1982.

Eastman, J.T., Evolutionary divergence in McMurdo Sound fishes, *Antarc. J. U.S.*, 15, 151–153, 1980.

Eastman, J.T., The evolution of neutrally-buoyant nothothenoid fishes: their specializations and potential interactions in the Antarctic food web, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985a, 430–436.

Eastman, J.T., *Pleurogramma antarcticum* (Pisces: Nototheniidae) as food for other fishes in McMurdo Sound, *Polar Biol.*, 4, 155–160, 1985b.

Eastman, J.T., Evolution and diversification of Antarctic notothenioid fishes, *Am. Zoologist*, 31, 93–109, 1991.

Eastman, J.T. Antarctic Fish Biology: Evolution in a Unique Environment, Academic Press, San Diego, CA, 1993.

Eastman, J.T., DeVries, A.L., Lipid sacs as a buoyancy adaptation in Antarctic fish, *Nature (Lond.)*, 271, 352–353, 1978.

Eastman, J.T., DeVries, A.L., Buoyancy adaptations in a swim-bladder-less Antarctic fish, *J. Morphol.*, 167, 91–102, 1981.

Eastman, J.T., DeVries, A.L., Buoyancy studies of notothenioid fishes in McMurdo Sound, Antarctica, *Copeia*, 2, 385–393, 1982.

Eastman, J.T., DeVries, A.L., Adaptations for cryopelagic life in the Antarctic notothenioid fish *Pagothenia borchgrevinki*, *Polar Biol.*, 4, 45–52, 1985.

Eastman, J.T., DeVries, A.L., Antarctic fishes, *Sci. Am.*, 254, 106–114, 1986.

Eastman, J.T., Hubold, G., The fish fauna of the Ross Sea, Antarctica, *Antart. Sci.*, 11, 293–304, 1999.

Eberhart, L.L., Optimal policies for conservation of large mammals, *Environ. Conserv.*, 4, 205–212, 1977.

Eberhart, L.L., Siniff, D.B., Population dynamics and marine management policies, *J. Fish. Res. Board Canada*, 34, 183, 1977.

Eberlein, K., Leal, M.T., Hammer, K.D., Hickel, W., Dissolved organic substances during *Phaeocystis* blooms in the German Bight (North Sea), *Mar. Biol.*, 89, 311–316, 1985.

Eddie, G.C., The harvesting of krill, FAO, GLO/SO/77/2, Southern Ocean Fisheries Survey Programme, Rome, 1977.

Edwards, D.M., Heap, J.A., Convention on the conservation of Antarctic Marine Living Resources: A commentary, *Polar Rec.*, 20 (127), 353–362, 1981.

Edwards, R., Hennemuth, R., Maximum yield: Assessment and attainment, *Oceanus*, 18(2), 3–9, 1975.

Edwards, D.D., McFeters, G.A., Venkatsan, M.I., Distribution of *Clostridium perfringens* and fecal sterols in a benthic coastal marine environment influenced by the sewage outfall from McMurdo Station, Antarctica, *Appl. Environ. Microbiol.*, 64, 2596–2600, 1998.

Efremenko, V.N., Atlas of the fish larvae of the Southern Ocean, *Cybium*, 7, 1–74, 1983.

Efremenko, V.N., Distribution of eggs and larvae of Myctophidae in the southern Atlantic. *Voporsykittiologii* 20:620. In Russian; reproduced in English in *J. Ichthyol.*, 26, 141–147, 1986.

Ehrenberg, C.G., Einige vorlanffge Desultale der Untersuchungen der von der Südpoleise des Capitain Ross, so wie von den Herren Schayer und Darwin zugehommenen Materialen, *Meber Preussiche Academie der Wissenschaften*, 182–187, 1844.

Ehrenberg, C.G., Uber neue Anschauungen des Kleinsten nordlicher Polarlebens, *Monaistker der Berlin Akademie*, 522–529, 1853.

Eicken, H., The role of sea ice in structuring Antarctic ecosystems, *Polar Biol.*, 12, 3–13, 1992.

Eicken, H., Lange, M., Development and properties of sea ice in the coastal region of the southeastern Weddell Sea, *J. Geophys. Res.*, 98, 8193–8206, 1989.

Eicken, H. et al., The underice water layer. In "The winter expedition of the RV Polarstern to the Antarctic" (SNT V/13), *Berichte zur Polarforschung* 39, 102–183, 1987.

Ekau, W., Okmorphologie natotheniidae Fische aus dem Weddellmeer, Antarktis, *Berichte zur Polarforscherung*, 51, 1–140, 1988.

Ekau, W., Demersal fish fauna of the Weddell Sea, *Antarc. Sci.*, 2, 129–137, 1990.

Ekman, V.K., A survey of some theoretical investigations in ocean current, *Journal du Conseil, Conseil Permanent International pour l'Exploration de la Mer*, 3, 295–297, 1928.

Ekman, V.K., Zoogeography of the Sea, Sidgwick and Jackson, London, 1953.

Eldred, G.E., Miller, G.V., Stark, W.S., Feeney-Burns, L., Lipofuscin: Resolution of discrepant fluorescence data, *Science*, 216, 757–759, 1982.

Elizarov, A.A., Peculiarities of water dynamics in places of krill concentrations (*Euphausia superba* Dana), *Trudy Vsesoiuznogo Naucho-issledovatel'skii Morskogo Rybnogo Khoziaistva i Okeanographii*, 79, 31–40, 1971. In Russian with English summary.

Elliot, D.H., Physical geography–geological evolution, in *Antarctica (IUCN Key Environment Series)*, Bonner, W.N., Walton, D.W.H., Eds., Pergamon Press, Oxford, 1985, 39–61.

El-Sayed, S.Z., Primary productivity of the Antarctic and subantarctic, in *Biology of the Antarctic Seas II*, Schmidt, W., Llano, G., Eds., American Geophysical Union, Washington, DC, 1967, 15–47.

El-Sayed, S.Z., Prospects of primary productivity studies in Antarctic waters, in *Symposium on Antarctic oceanography, Santiago, Chile, 1966*, Currie, R.I., Ed., Scott Polar Research Institute/SCAR, Cambridge, UK, 1968a, 227–239.

El-Sayed, S.Z., On the productivity of the southwest Atlantic Ocean and the waters west of the Antarctic Peninsula, in *Biology of the Antarctic Seas III*, Schmidt, W., Llano, G., Eds., American Geophysical Union, Washington, DC, 1968b, 15–47.

El-Sayed, S.Z., Primary productivity of the Antarctic and subAntarctic, in *Antarctic Map Folio Series 10*, Bushnell, V., Ed., American Geographical Society, New York, 1968c, 1–6.

El-Sayed, S.Z., On the productivity of the Southern Ocean, in *Antarctic Ecology,* Vol. 1, Holdgate, M.W., Ed., Academic Press, London, 1970a, 119–135.

El-Sayed, S.Z., Phytoplankton production in the South Pacific sector of Antarctica, in *Scientific Exploration of the South Pacific*, Worster, W.S., Ed., National Academy of Sciences, Washington, DC, 1970a, 193–210.

El-Sayed, S.Z., Biological aspects of the pack ice ecosystem, in *Symposium on Antarctic Water Masses, Tokyo, Japan, Sept. 19, 1970*, Scientific Committee on Antarctic Research, Cambridge, UK, 35–54 pp, 1971a.

El-Sayed, S.Z., Observations on a phytoplankton bloom in the Weddell Sea, in *Biology of the Antarctic Seas 17*, Llano, G., Wallen, I.E., Eds., American Geophysical Union, Washington, DC, 1971b, 301–312.

El-Sayed, S.Z., Dynamics of trophic relationships in the Southern Ocean, in *Research in the Antarctic*, Quam, L.O., Ed., American Association for the Advancement of Science, Washington, DC, 1971c, 73–91.

El-Sayed, S.Z., Ed., *Biological investigations of marine Antarctic systems and stocks,* Vol. 1: Research proposals, Scientific Committee on Antarctic Research, Cambridge, UK, 1977.

El-Sayed, S.Z., Primary productivity and estimates of potential yields on the Southern Ocean, in *Polar Research: To the Present and the Future*, AAAS Selected Symposia 7, Whinnie, M.A., Ed., American Association for the Advancement of Science, Washington, DC, 1978, 141–160.

El-Sayed, S.Z., Biological Investigations of Antarctic Systems and Stocks (BIOMASS), II: Selected Contributions to the Woods Hole Conference on Living Resources of the Southern Ocean, Scott Polar Research Institute/SCAR, Cambridge, UK, 1981.

El-Sayed, S.Z., Productivity of Antarctic waters—a reappraisal, in *Marine Phytoplankton and Productivity*, HolmHansen, O., Bolis, L., Gilles, R., Eds., Springer, Berlin, 1984, 19–34.

El-Sayed, S.Z., Plankton of the Antarctic seas, in *Key Environments—Antarctica*, Bonner, W.N., Walton, D.W.H., Eds., Pergamon Press, Oxford, 1985, 135–154.

El-Sayed, S.Z., Biological productivity of Antarctic waters: Present paradoxes and emerging paradigms, in *Antarctic Aquatic Biology, BIOMASS Scientific Series 7*, El-Sayed, S.Z., Tomo, A.P., Eds., SCAR Scott Polar Research Institute, Cambridge, UK, 1987, 1–21.

El-Sayed, S.Z., Seasonal and interannual variabilities in Antarctic phytoplankton, with reference to krill distribution, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin, 1988a, 101–119.

El-Sayed, S.Z., Productivity of the Southern Ocean: a closer look, *Comp. Biochem. Physiol.*, 90B, 489–498, 1988b.

El-Sayed, S.Z. Southern Ocean ecology: The BIOMASS perspective, Cambridge University Press, Cambridge, UK, 1996.

El-Sayed, S.Z., Jitts, H.R., Phytoplankton production in the southeastern Indian Ocean, in *Biology of the Indian Ocean*, Zeitzschel, B., Ed., Chapman and Hall, London, 1973, 131–134.

El-Sayed, S.Z., Mandelli, E.F., Primary production and standing crop of phytoplankton in the Weddell Sea and Drake Passage, in *Biology of the Antarctic Seas II*, Llano, G.A., Ed., American Geophysical Society, Washington, DC, 1965, 87–106.

El-Sayed, S.Z., McWhinnie, M.A., Protein of the last frontier, *Oceanus*, 22(1), 13–20, 1979.

El-Sayed, S.Z., Taguchi, S., Primary production and standing crop of phytoplankton along the iceedge in the Weddell Sea, *Deep-Sea Res.*, 28(A), 1017–1032, 1981.

El-Sayed, S.Z., Turner, J.T., Productivity of the Antarctic and tropical-subtropical regions: a comparative study, in *Polar Oceans*, Dunbar, M.J., Ed., Arctic Institute of North America, Calgary, 1977, 463–504.

El-Sayed, S.Z., Weber, L.H., Spatial and temporal variation in phytoplankton biomass and primary productivity in the southwest Atlantic and Scotia Sea, *Polar Biol.*, 1, 83–90, 1982.

El-Sayed, S.Z., Weber, L.H., Size fractionation of Atlantic phytoplankton, *Antarc. J. U.S.*, 19, 141–143, 1986.

El-Sayed, S.Z., Stockwell, P.A., Reheim, H.A., Taguchi, S., Meyer, M.A., On the productivity of the southwestern Indian Ocean, *CNFRA*, 44, 1–43, 1979.

El-Sayed, S.Z., HolmHansen, O., Biggs, D.C., Phytoplankton standing crop, primary productivity, and nearsurface nitrogenous nutrient fields of the Ross Sea, Antarctica, *Deep-Sea Res.*, 30(8), 871–886, 1983.

El-Sayed, S.Z., Stephens, F.C., Bidigare, R.R., Ondrusek, M.E., Effects of ultraviolet radiation on Antarctic marine phytoplankton, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin, 1990a, 379–385.

El-Sayed, S.Z., Stephens, F.C., Bidigare, R.R., Ondrusek, M.E., Potential effects of solar ultraviolet radiation on Antarctic phytoplankton in *Effects of Solar Ultraviolet Radiation on Biochemical Dynamics in Aquatic Environments*, Woods Hole Oceanographic Institution Technical Report WHOI-90-09, Blough, N.V., Zepp, R.G., Eds., Woods Hole Oceanographic Institution, Woods Hole, MA, 141–142, 1990b.

Emerson, W.B., Feeding preferences of the Adélie Penguin at Cape Crozier, Ross Island, in *Antarctic Bird studies, Antarctic Research Series 12*, Austin, O.L., Ed., American Geophysical Society, Washington, DC, 1968, 191–212.

Emslie, S.D., McDonald, J.D., Adélie Penguin diet and climate change during the middle to late Holocene in northern Marguerite Bay, Antarctic Peninsula, *Polar Biol.*, 25, 222–229, 2002.

Emslie, S.D., Fraser, W., Smith, R.C., Walker, W., Abandoned penguin rookeries and environmental change in the Palmer Station area, Anvers Island, Antarctic Peninsula, *Antarc. Sci.*, 10, 257–268, 1998.

Endo, Y., Asari, H., Watanuki, Y., Biological characteristics of euphausiids preyed upon by Adélie Penguins, *Pygoscelis adeliae*, breeding at Hukuro Cove, Lützow-Holm Bay, in 1995/96, *Polar Biosci.*, 13, 66–73, 2000.

Enzenbacher, D., Antarctic tourism and environmental concerns, *Mar. Poll. Bull.*, 25, 258–265, 1992.

Eppley, R.W., Temperature and phytoplankton growth in the sea, *Fish. Bull. Natl Ocean. Atmos. Adm.*, 70, 1063, 1972.

Eppley, R.W., Estimating phytoplankton growth rates in oligotrophic oceans, in *Primary Productivity in the Sea*, Falkowski, P.K., Ed., Plenum Press, New York, 1980, 231–242.

Eppley, Z.A., Assessing indirect effects of oil in the presence of natural variation: The problem of reproductive failure of South Polar skuas during *Bahia Paraiso* oil spill, *Marine Pollution Bulletin*, 25, 307–312, 1992.

Eppley, Z.A., Rubega, M.A., Indirect effects of an oil spill: Reproductive failure of a population of South Polar skuas following the *Bahia Paraiso* oil spill in Antarctica, *Mar. Ecol. Prog. Ser.*, 67, 1–6, 1990.

Eppley, R.W., Horrigan, S.G., Fuhrman, J.A., Brooks, E.R., Price, C., Sellner, K., Origins of dissolved organic matter in Southern California coastal waters: Experiments on the role of zooplankton, *Mar. Ecol. Prog. Ser.*, 6, 149–159, 1981.

Erickson, A.W., Aerial census of seals, whales, and penguins in the pack ice of the northwestern Weddell Sea, November 1983, *Antarc. J. U.S.*, 19, 121–124, 1984.

Erickson, A.W., Hofman, R.J., Antarctic seals, *Antarctic Map Folio Series*, Vol. 18, American Geographical Society, Washington, DC, 4–12, 1974.

Erickson, A.W., Siniff, D.B., Cline, D.R., Hofman, R.J., Distributional ecology of Antarctic seals, in *Symposium on Antarctic Ice and Water Masses*, Deacon, G., Ed., Scientific Committee on Antarctic Research, Cambridge, UK, 1971, 55–76.

Estep, K.W., Davis, P.G., Keller, M.D., Siebruth, J.McN., How important are oceanic algal nanoflagellates in bacterivory?, *Limnology and Oceanography*, 31, 646–650, 1986.

Estep, K.W., Nejstgaard, J.C., Skjoldal, R.H., Rey, F., Predation by copepods upon natural populations of *Phaeocystis pouchettii* as a function of the physiological state of the prey, *Mar. Ecol. Prog. Ser.*, 67, 235–249, 1990.

Estrada, M., Delgado, M., Summer phytoplankton distribution in the Weddell Sea, *Polar Biol.*, 10, 413–422, 1990.

Estrup, K.W., Nejsgaard, J.C., Skjoldal, R.H., Rey, I., Predation by copepods on natural populations of *Phaeocystis pouchetti* as a function of the physiological state of the prey, *Mar. Ecol. Prog. Ser.*, 67, 235–249, 1986.

Ettershank, G., A new look at the age structure of the Antarctic krill, *Euphausia superba*, *BIOMASS Newsletter*, 4, 5–9, 1982.

Ettershank, G., Age structure and cyclical annual size changes in Antarctic krill (*Euphausia superba*), *Polar Biol.*, 2, 189–193, 1983.

Ettershank, G., A new approach to the assessment of longevity in the Antarctic krill *Euphausia superba*, *J. Crustacean Biol.*, 4(Special issue No.1), 295–305, 1984.

Ettershank, G., MacDonald, I., Croft, R., The estimation of age in the flesh fly (*Sarcophaga bullata*) using the age pigment lipofuscin, *Aust. J. Z.*, 31, 131–138, 1982.

Evans, R.H. Unpublished manuscript. Current observations and lead line soundings McMurdo Sound, Antarctica, U.S. Naval Oceanographic Office. IMR No. 0-18-65.

Everitt, D.A., Thomas, D.P., Observations on the seasonal change in diatoms at inshore localities near Davis Station, East Antarctica, *Hydrobiologica*, 139, 3–12, 1986.

Everson, I., The population dynamics and energy budget of *Notothenia neglecta* Nybelin at Signy Island, South Orkney Islands, *Br. Antarc. Surv. Bull.*, 23, 25–50, 1970a.

Everson, I., Reproduction in *Notothenia neglecta* Nybelin, *Br. Antarc. Surv. Bull.*, 23, 81–92, 1970b.

Everson, I., Antarctic krill: A reappraisal of its distribution, *Polar Rec.*, 112, 15–23, 1976.

Everson, I., Antarctic marine secondary production and the phenomenon of cold adaptation, *Philos. Trans. R. Soc. Lond., Ser. B*, 279, 55–66, 1977a.

Everson, I. The Living Resources of the Southern Ocean FAO, Southern Ocean Fisheries Survey Programme, Rome, GLO/SO/77/1, 1–156, 1977.

Everson, I., Antarctic fisheries, *Polar Rec.*, 19, 233–251, 1978.

Everson, I., Antarctic krill, in *Biological Investigations of Marine Antarctic Systems and Stocks.* Vol. II: Selected Contributions to the Woods Hole Conference on the Living Resources of the Southern Ocean, El-Sayed, S.Z., Ed., Scott Polar Research Institute/SCAR, Cambridge, UK, 1981, 31–46.

Everson, I., Diurnal variations in mean volume backscattering strength of an Antarctic krill (*Euphausia superba*) patch, *J. Plankton Res.*, 4, 155–162, 1982.

Everson, I., Estimation of krill abundance, *Berichte zur Polarforschung*, 4, 156–158, 1983.

Everson, I., Zooplankton, in *Antarctic Ecology,* Vol. 2, Laws, R.M., Ed., Academic Press, London, 1984a, 463–490.

Everson, I., Fish biology, in *Antarctic Ecology,* Vol. 2, Laws, R.M., Ed., Academic Press, London, 1984b, 491–492.

Everson, I., Marine interactions, in *Antarctic Ecology,* Vol. 2, Laws, R.M., Ed., Academic Press, London, 1984c, 783–819.

Everson, I., Can we satisfactorily estimate krill abundance?, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin, 1988, 199–208.

Everson, I., Managing Southern Ocean krill and fish stocks in a changing environment, *Philos. Trans. R. Soc. Lond., Ser. B*, 338, 311–317, 1992.

Everson, I., Consideration of the major issues in ecosystem monitoring and management, *CCAMLR Sci.*, 9, 213–232, 2002.

Everson, I., Goss, C., Krill fishing activity in the southwest Atlantic, *Antarct. Sci.*, 3, 351–358, 1991.

Everson, I., Miller, D.G.M., Krill mesoscale distribution and abundance: Results and implications of research during the BIOMASS Program, in *Southern Ocean Ecology: The BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, UK, 1996, 129–144.

Everson, I., Ralph, R., Respiratory metabolism of *Chaenocephalus aceratus*, in *Antarctic Ecology* Vol. I, Holdgate, M.W., Ed., Academic Press, London, 1970, 315–319.

Everson, I., Ward, P., Aspects of Scotia Sea zooplankton, *Biol. J. Linnean Soc.*, 14, 93–101, 1980.

Fabiano, M., Danovaro, R., Meiofauna distribution and mesoscale variability in two sites of the Ross Sea (Antarctica) with contrasting food supply, *Polar Biol.*, 22, 115–123, 1999.

Falkowski, P.G., Raven, J.A. Aquatic Photosynthesis, Blackwell Scientific Publishers, Oxford, MA, 1997.

Falkowski, P.G., Rosenthal, Y., Biological diversity and resource plunder in the geological record: Causal correlations or causal relationships?, *Proc. Natl Acad. Sci. USA*, 98, 4290–4292, 2002.

Falkowski, P.G., Winick, C.D., A simulation model of the effects of vertical mixing on primary production, *Mar. Biol.*, 65, 69–75, 1981.

Falkowski, P.G., Scholes, R.J., Boyle, E., Canadell, J., Canfield, D., Elser, J., Gruber, N., Hibbard, K., Högberg, P., Linder, S., Mackenzie, F.T., Moore, B. III, Pedersen, T., Rosenthal, Y., Seitzinger, S., Smetacek, V., Steffen, W., The global carbon cycle: A test for our knowledge of the earth as a system, *Science*, 290(5490), 291–296, 2000.

FAO, Mammals of the Sea, Vol. 3. FAO Fisheries Series No. 5. (1981), Food and Agricultural Organization of the United Nations, Rome, 1981.

FAO, Southern Ocean CCAMLR Convention Area. Fishing Areas 48, 58 and 88. FAO Species Identification Sheets for Fishery Purposes Volume II, Food and Agricultural Organization of the United Nations/Commission for the Conservation of Antarctic Marine Living Resources, Rome, 233–471, 1985.

Fay, R.R., Significance of nanoplankton in primary production of the Ross Sea, Antarctica, during the 1972 austral summer. Ph.D. Thesis, Texas A&M University, College Station, TX., 1973.

Fell, H.B., Dawsey, S., Asteroidea, *Antarctic Map Folio Series*, Vol. 11, American Geographical Society, Washington, DC, 41, 1969.

Fell, H.B., Holzinger, T., Sherraden, M., Ophiuroidea, *Antarctic Map Folio Series*, Vol. 11, American Geographical Society, Washington, DC, 42–43, 1969.

Fenchel, T., The ecology of heterotrophic microflagellates, I: Some important forms and their functional morphology, *Mar. Ecol. Prog. Ser.*, 8, 211–223, 1982a.

Fenchel, T., The ecology of heterotrophic flagellates, II: Quantitative occurrence and importance as consumers of bacteria, *Mar. Ecol. Prog. Ser.*, 9, 35–42, 1982b.

Fenchel, T., Marine plankton food chains, *Annual Review of Ecology and Systematics*, 19, 19–38, 1988.

Fenchel, T., Harrison, D., The significance of bacterial grazing and mineral cycling for the decomposition of particulate detritus, in *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*, Anderson, J.M., Macfadyen, A., Eds., Blackwell, Oxford, 1976, 285–299.

Fenchel, T., Lee, C.C., Studies on ciliates associated with sea ice from Antarctica, I: The nature of the fauna, *Archiv für Protistenkunde*, 114, 231–236, 1972.

Ferguson, R.L., Rublee, P., Contributions of bacteria to the standing crop of phytoplankton, *Limnology and Oceanography*, 21, 141–145, 1976.

Fevolden, S.E., Investigations of krill (Euphausiacea) sampled during the Norwegian Antarctic Research Expedition, *Sarsia*, 64, 189–198, 1979.

Fevolden, S.E., Genetic variation of *Euphausia superba* in the Antarctic Peninsula waters, *Sarsia*, 66, 169–175, 1986.

Fevolden, S.E., Ayala, F.J., Enzyme polymorphism in Antarctic krill (Euphausiacea); genetic variation between populations and species, *Sarsia*, 66, 167–181, 1987.

Fevolden, S.E., Schneppenheim, R., Genetic structure of *Euphausia superba* Dana in the Atlantic sector of the Southern Ocean as demonstrated by different electrophoretic techniques, *Polar Biol.*, 9, 15–298, 1988.

Fiala, M., Delille, D., Annual changes of microalgae biomass in Antarctic sea ice contaminated by crude oil and diesel fuel, *Polar Biol.*, 21, 391–396, 1999.

Fiala, M., Semerich, M., Oriol, L., Size-fractionated phytoplankton biomass and species composition in the Indian sector of the Southern Ocean during austral summer, *J. Mar. Syst.*, 17, 179–197, 1998.

Fiala, M., Delille, B., Debreuil, C., Kopczynska, E., Leblanc, K., Morvan, J., Quéguiner, B., Blain, S., Cailliau, C., Conan, P., Corvaisier, R., Denis, M., Frankignoulle, M., Oriol, L., Roy, S., Mesoscale surface distribution of biogeochemical characteristics associated with a frontal system in the Crozet Basin (southern Indian Ocean) during austral summer, 1999, *Mar. Ecol. Prog. Ser.*, 249, 1–14, 2003.

Figuerias, F.G., Estrada, M., Lopez, O., Arbores, B., Photosynthetic parameters and primary production in the Bransfield Strait: Relationships with mesoscale hydrographic structures, *J. Mar. Syst.*, 17, 129–141, 1998.

Filin, A.A., Gorchusky, K.V., Kischeva, V.M., Biomass of myctophids in the Atlantic sector of the Southern Ocean estimated by acoustic surveys, *SC-CCAMLR Selected Scientific Papers 1990*, 417–429, 1990.

Filipova, J.A., New data on the squids (Cephalopoda, Oegosida) from the Scotia Sea, *Malacologia*, 11, 391–406, 1972.

Fischer, G., Fütterer, D., Gersonde, R., Honjo, S., Ostertman, D., Wefer, G., Seasonal variability of particle flux in the Weddell Sea and its relation to ice cover, *Nature (Lond.)*, 335, 426–428, 1988.

Floodgate, G.D., Some environmental aspects of marine hydrocarbon bacteriology, *Aqua. Microbial Ecol.*, 9, 3–11, 1995.

Focardi, S., Bargagli, R., Cotsolini, S., Isomer-specific analysis and toxic potential evaluation of the polychlorinated biphenyls in Antarctic fish, seabirds, and Weddell seals from Terra Nova Bay (Ross Sea), *Antarc. Sci.*, 7, 31–35, 1995.

Fogg, G.E., The extracellular products of algae, *Oceanogr. Mar. Biol.: Annu. Rev.*, 4, 195–212, 1966.

Fogg, G.E., Aquatic primary production in Antarctica, *Philosophical Transactions of the Royal Society of London, Series B*, 279, 27–38, 1977.

Fogg, G.E., Nitrogen cycling in sea waters, *Philosophical Transactions of the Royal Society of London, Series B*, 296, 511–520, 1982.

Fogg, G.E., Nalewajko, C., Watt, W.D., Extracellular products of phytoplankton phorosynthesis, *Proceedings of the Royal Society of London, Series B*, 162, 517–534, 1965.

Foldvik, A., Gammelsrad, T., Notes on Southern Ocean sea-ice and bottom water formation, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 67, 3–17, 1988.

Forster, T.D., The temperature and salinity fields under the Ross Ice Shelf, Antarctica, *Antarc. J. U.S.*, 13, 81–82, 1978.

Forster, T.D., The physical oceanography of the Southern Ocean, *BIOMASS Scientific Series*, 2, 9–22, 1981.

Forster, T.D., The marine environment, in *Antarctic Ecology,* Vol. 2, Laws, R.M., Ed., Academic Press, London, 1984, 345–371.

Forster, B.A., Composition and abundance of zooplankton under the spring sea-ice of McMurdo Sound, Antarctica, *Polar Biol.*, 8, 41–48, 1989.

Forster, B.A., Time and depth comparison of sub-ice zooplankton in McMurdo Sound, Antarctica, *Polar Biol.*, 9, 431–435, 1989.

Forster, T.D., Carmack, E.C., Frontal zone mixing and Antarctic bottom water formation in the southern Weddell Sea, *Deep-Sea Res.*, 23, 301–317, 1976.

Forster, M.E., Franklin, C.E., Taylor, H.H., Davidson, W., The aerobic scope of an Antarctic fish, *Pagothenia borchgrevinki*, and its significance for cold adaptation, *Polar Biol.*, 8, 155–159, 1987.

Forster, B.A., Cargill, J.M., Montgomery, J.C., Planktivory in *Pagothenia borchgrevinki* (Pisces: Nototheniidae) in McMurdo Sound, Antarctica, *Polar Biol.*, 8, 49–54, 1989.

Fortier, L., Le Fevre, S., Legendre, L., Export of biogenic carbon to fish and to the deep ocean: The role of large planktonic microphages, *J. Plankton Res.*, 7, 809–839, 1994.

Fowler, C.W., Indices of population status, in *A Search for Management Criteria*, Fowler, C.W., Bunderson, M.B., Cherry, M.B., Ryel, R.J., Steele, B.B., Eds., United States Marine Mammal Commission, Washington, DC, 1980, 283–295.

Fowler, G.S., Field studies, tourism, and stress responses in Magellanic penguins, in *Report: Workshop on Researcher-Seabird Interactions*, Fraser, W.R., Trivelpiece, W.Z., Eds., Montana, MN, 1993, 44–55.

Fowler, S.W., Knauer, G.A., Role of large particles in the transport of elements and organic compounds through the oceanic water column, *Prog. Oceanogr.*, 16, 147–194, 1986.

Fowler, C.W., Smith, T.D., *Dynamics of Large Mammal Populations*, Wiley, New York, 1981.

Foxton, P., The distribution of the standing crop of zooplankton in the Southern Ocean, *Discovery Reports*, 28, 191–236, 1956.

Foxton, P., Seasonal variation in the plankton of Antarctic waters, in *Biologie Antarctique*, Carrick, R., Holdgate, W.M., Prevost, J., Eds., Herman, Paris, 1964, 311–318.

Foxton, P., The distribution and life history of *Salpa thompsoni* Foxton with observations on a related species, *Salpa gerlachii* Foxton, *Discov. Rep.*, 34, 1–116, 1966.

Foxton, P., Roe, R.S.J., Observations on the nocturnal feeding of some mesopelagic crustaceans, *Mar. Biol.*, 28, 37–49, 1974.

Fradet, G., Evaluation of chitosan as a thermostatic agent, in *Proceedings of the Third International Conference on Chitan/Chitosan*, Seregallia, Italy, 1985.

Frakes, L., Kemp, E.M., Influence of continental positions on early tertiary climates, *Nature (Lond.)*, 240, 97–100, 1972.

Franks, P.J.S., Sink or swim: Accumulation of biomass at fronts, *Mar. Ecol. Prog. Ser.*, 82, 1–12, 1992.

Franz, G., Hagen, W., Hempel, I., Marshall, H.-P., Marshall, S., Mizdal Shi, E., Die Winter-Expedition mit FS *Polarstern* in die Antarktkis (ANT VII-3), *Berichte zur Polarforschung*, 39, 197–204, 1987.

Fraser, F.C., On the development and distribution of the young stages of krill (*Euphausia superba*), *Discov. Rep.*, 14, 1–192, 1936.

Fraser, W.R., Ainley, D.G., Ice edges and seabird occurrence in Antarctica, *BioScience*, 36, 258–263, 1986.

Fraser, W.R., Patterson, D.L., Human disturbance and long-term changes in Adélie Penguin populations: A natural experiment at Palmer Station, Antarctic Peninsula, in *Antarctic Communities: Species, Structure and Survival*, Battaglia, B., Valencia, J., Walton, D.W.H., Eds., Cambridge University Press, Cambridge, UK, 1997, 445–452.

Fraser, W.R., Trivelpiece, W.Z., Ainley, D.G., Trivelpiecer, S.G., Increases in Antarctic penguin populations: Reduced competition with whales or a loss of sea ice due to environmental warming, *Polar Biol.*, 11, 525–531, 1992.

Fraser, T.H., Quetin, L.B., Ross, R.M., Energetic demands of larval krill, *Euphausia superba*, in winter, *J. Exp. Mar. Biol. Ecol.*, 277, 157–171, 2002a.

Fraser, T.H., Quetin, L.B., Ross, R.M., Abundance, sizes and development stages of larval krill, *Euphausia superba*, during winter in ice-covered seas west of the Antarctic Peninsula, *J. Plankton Res.*, 24, 1067–1077, 2002b.

Friedberg, E.C., DNA Repair, W.H., Freeman, New York, 1985, 614.

Freyer, G., The food of some fresh-water cyclopoid copepods and its ecological significance, *J. Anim. Ecol.*, 26, 263–286, 1957.

Freytag, C.E., Betrage zur Biologie von *Notothenia rossii mamorata* Fischer. MS thesis, University of Keil, 1977.

Fritzen, C.H., Sullivan, C.W., Distribution and dynamics of microbial communities in the pack ice of the western Weddell Sea, Antarctica, in *Antarctic Communities: Species, Structure and Survival*, Battaglia, B., Valencia, J., Walton, D.W.H., Eds., Cambridge University Press, Cambridge, UK, 1999, 101–108.

Fritzen, C.H., Lythe, V.I., Ackley, S.F., Sullivan, C.W., *American Zoologist*, 32, 17–33, 1994.

Froneman, P.W., Balarin, M.S., Structure and grazing impact of the protozooplankton community in the waters surrounding the sub-Antarctic Prince Edward Islands, *Polar Biol.*, 20, 198–205, 1998.

Froneman, P.W., Bernard, K.S., Trophic cascading in the Polar Frontal Zone of the Southern Ocean during austral autumn 2002, *Polar Biol.*, 26, 268–275, 2004.

Froneman, P.W., Pakhomov, E.A., Perissinotto, R., Meaton, V., Feeding and predation impact of two chaetognath species, *Euchronia hamata* and *Sagitta gazellae*, in the vicinity of Marion Island (Southern Ocean), *Mar. Biol.*, 131, 95–101, 1992.

Froneman, P.W., Perissinotto, R., Pakhomov, E.A., Biogeographical structure of the micro-phytoplankton assemblage in the region of the Subtropical Convergence and across the warm core eddy during the austral winter, *J. Plankton Res.*, 19, 519–531, 1997.

Froneman, P.W., Pakhomov, E.A., Perissinotto, R., McQuaid, C.D., Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in the late austral summer 1973, Part 2: Biochemical zonation, *Deep-Sea Res.*, 147, 1687–1692, 2000.

Frost, G.W., McCrone, L.E., Vertical distribution and abundance of some mesopelagic fishes in the eastern subarctic Pacific Ocean in summer, *Fish. Bull.*, 76, 751–770, 1979.

Fry, B., Sherr, E.B., ^{13}C measurements as indicators of carbon flow in marine and freshwater ecosystems, in *Stable Isotopes in Ecological Research*, Rundell, P.W., Ehleringer, J.R., Nagy, K.A., Eds., Springer, New York, 1988, 169–229.

Fryxell, G.A., Marine phytoplankton at the Weddell Sea ice edge: Seasonal changes at the specific level, *Polar Biol.*, 10, 1–18, 1989.

Fryxell, G.A., Hasle, G.R., The genus *Thalassiosira: T.trifuta* sp. nov., and other species with tricolumnar support on strutted processes, *Beihefte zur Nova Hedwiga*, 64, 13–31, 1979.

Fryxell, G.A., Kendrick, G.A., Austral spring microalgae across the Weddell Sea ice edge: Spatial relationships found along a northernward transect during AMERIEZ 83, *Deep-Sea Res.*, 35, 1–20, 1988.

Fryxell, G.A., Theriot, E.C., Buck, K.B., Phytoplankton, ice algae and choanoflagellates from AMERIEZ, the Southern Atlantic, and Indian Ocean, *Antarc. J. U.S.*, 19, 107–109, 1984.

Fuhrman, J.A., Close coupling between release and uptake of dissolved free amino acids in seawater studied by isotope dilution approach, *Mar. Ecol. Prog. Ser.*, 37, 45–55, 1987.

Fuhrman, J.A., Marine viruses and their biogeochemical and ecological effects, *Nature (Lond.)*, 399, 541–548, 1999.

Fuhrman, J.A., Azam, F., Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica, and California, *Appl. Environ. Microbiol.*, 39, 1085–1095, 1980.

Fuhrman, J.A., Azam, F., Thymidine incorporation as a measure of heterotrophic bacterioplankton in marine surface waters: Evaluation and field results, *Mar. Biol.*, 73, 79–89, 1982.

Fuhrman, J.A., McManus, G.B., Do bacteria-sized eucaryotes consume significant bacterial production?, *Science*, 224, 1257–1260, 1984.

Fukami, K., Simidu, O., Taga, N., Microbial decomposition of phyto- and zooplankton in seawater, 1: Changes in organic matter, *Mar. Ecol. Prog. Ser.*, 21, 1–5, 1985a.

Fukami, K., Simidu, O., Taga, N., Microbial decomposition of phyto- and zooplankton, 2: Changes in the bacterial community, *Mar. Ecol. Prog. Ser.*, 21, 7–23, 1985b.

Fukuchi, M., Chlorophyll a content in surface waters along the course of the *Fuji* to and from Antarctica in 1976–77, *Antarc. Rec.*, 60, 57–69, 1977.

Fukuchi, M., Phytoplankton chlorophyll stocks in the Antarctic Ocean, *J. Oceanogr. Soc. Jpn*, 36, 73–84, 1980.

Fukuchi, M., Sasaki, H., Phytoplankton and zooplankton stocks and downward flux of particulate matter around the fast ice edge of Lützow-Holm Bay, Antarctica, *Memoirs Natl Inst. Polar Res.*, 34, 52–59, 1981.

Fukuchi, M., Tanimura, S., A preliminary note on the occurrence of copepods under the sea ice near Syowa Station, Antarctica, *Memoirs Nat. Inst. Polar Res., Special Issue*, 52, 51–59, 1981.

Fukuchi, M., Tanimura, S., Chlorophyll a distribution in the Indian sector of the Southern Ocean in 1978–1979, *Antarc. Rec.*, 74, 143–162, 1982.

Fukuchi, M., Tanimura, S., Ohtsuka, H., Seasonal change of chlorophyll a under fast ice in Lützow-Holm Bay, Antarctica, *Memoirs Natl Inst. Polar Res., Spec. Issue*, 32, 51–59, 1984.

Fukuchi, M., Tanimura, S., Ohtsuka, H., Marine biological and oceanographical investigations in Lützow-Holm Bay, Antarctica, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985a, 52–59.

Fukuchi, M., Tanimura, S., Ohtsuka, H., Zooplankton community conditions under the sea ice near Syowa Station, Antarctica, *Bulletin of Marine Science*, 37, 518–528, 1985b.

Fukuchi, M., Fukuda, Y., Ohno, M., Hattori, H., Surface phytoplankton chlorophyll distributions continuously observed in the JARE-26 cruise (1984/85) to Syowa Station, Antarctica (SIBEX II), *Memoirs Natl Inst. Polar Res.*, 44, 15–23, 1986.

Fukuchi, M., Hattori, H., Sasaki, H., Hoshiai, T., A phytoplankton bloom and associated processes observed with a long-term moored system in Antarctic waters, *Mar. Ecol. Prog. Ser.*, 45, 279–288, 1988.

Fukuda, Y., Ohno, M., Fukuchi, M., Surface chlorophyll *a* distribution in the marginal ice zone in Antarctica in 1984/85, *Memoirs Natl Inst. Polar Res.*, 44, 15–23, 1985.

Fukui, F., Otomo, K., Okabe, S., Nutrient depression in a blooming area in Prydz Bay, Antarctica, *Memoirs Natl Inst. for Polar Res.*, 44, 43–54, 1986.

Furness, R.W., Estimating the food requirements of seabird and seal populations and interactions with commercial fisheries and fish stocks, in *Proceedings of the Symposium on Sea and Shore Birds, African Seabird Group, Capetown*, Cooper, J., Ed., 1982, 1–14.

Gain, L, La flore algaloique et subantarcticques, *Seconde Expedition Antarctiques Francaise*, Science naturalle Documentation Scientifique, Paris, 1912.

Galeron, J., Herman, R.L., Arnaud, P.M., Antz, W.E., Hain, S., Klages, M., Macrofaunal communities on the continental shelf and slope of the southeastern Weddell Sea, Antarctica, *Polar Biol.*, 12(2), 283–290, 1992.

Gales, N.J., Klages, N.T.W., Williams, R., Woehler, E.J., The diet of emperor penguins, *Aptenodytes forsteri*, in Admiralty Bay, Princess Elizabeth Land, Antarctica, *Antarc. Sci.*, 2, 185–186, 1990.

Gallardo, V.A., The sublittoral benthos of the Antarctic shelf, *Environ. Intl.*, 13, 71–81, 1988.

Gallardo, V.A., Castilla, J.G., Quantitative observations on the benthic infauna of Chile Bay (Greenwich Island, South Shetland Islands), *Gayana (Zoología)*, 16, 3–18, 1969.

Gallardo, V.A., Castilla, J.G., Quantitative observations on the benthic macrofauna of Port Foster (Deception Island) and Chile Bay (Greenwich Island), in *Antarctic Ecology,* Vol. 1, Holdgate, M.W., Ed., Academic Press, London, 1970, 242–243.

Gallardo, V.A., Castilla, J.G., Retamel, M., Yanez, A., Moyana, H.I., Hermosilla, H.G., Quantitative studies on the soft-bottom macrobenthic communities of shallow Antarctic bays, in *Adaptations within Antarctic Ecosystems*, Llano, G., Ed., Smithsonian Institution, Washington, DC, 1977, 361–387.

Gambell, R., Seasonal cycles and reproduction in sei whales of the southern hemisphere, *Discov. Rep.*, 35, 31–134, 1968.

Gambell, R., Seasonal cycles and reproduction in sei whales of the southern hemisphere, *Discov. Rep.*, 35, 35–133, 1972.

Gambell, R., Some effects of exploitation on reproduction in whales, *Journal of Reproduction and Fertility (Supplement)*, 19, 531–551, 1973.

Gambell, R., Variations in reproductive parameters associated with whale stock size, *Intl. Whaling Committee Rep.*, 25, 182–189, 1975.

Gambell, R. in *Population Biology and the Management of Whales*, Croker, T.H., Ed., *Applied Biology*, Vol. 1, Academic Press, London, 1976, 247–343.

Gambell, R., Dentinal layer formation in sperm whale teeth, in *A Voyage of Discovery*, Angel, M., Ed., Pergamon Press, London, 1977, 583–590.

Gambell, J.C., Copepod grazing during a declining spring phytoplankton bloom in the North Sea, *Mar. Biol.*, 49, 303–315, 1978.

Gambell, R., Birds and mammals: Antarctic whales, in *Key Environments*, Bonner, W.N., Walton, D.W.H., Eds., Pergamon Press, Oxford, 1985, 223–241.

Gambell, R., How many great whales in Antarctica?, *BIOMASS Newsletter*, 10, 4, 1989.

Gambi, M.C., Bussott, S., Composition, abundance and stratification of soft-bottom macrobenthos for selected areas of the Ross Sea (Antarctica), *Polar Biol.*, 21, 347–354, 1999.

Gambi, M.C., Lorenzi, M., Russo, G.F., Scipione, M.B., Benthic associations of the shallow hard bottoms off Terra Nova Bay, Ross Sea: Zonation, biomass, and population structure, *Antarc. Sci.*, 5, 449–462, 1994.

Gammie, F., Breakaway ‘iceberg’ due to warming, *Nature (Lond.)*, 374(6518), 108, 1995.

Garrison, D.L., Marine planktonic diatoms, in *Significance of Planktonic Life Cycles in Population Survival*, Steidinger, K.A., Walker, L.M., Eds., CRC Press, Boca Raton, FL, 1984, 1–17.

Garrison, D.L., Antarctic sea ice biota, *Am. Zoologist*, 31, 17–34, 1991a.

Garrison, D.L., An overview of the abundance and role of protozooplankton in Antarctic waters, *J. Mar. Syst.*, 2, 317–331, 1991b.

Garrison, D.L., Buck, K.R., Microheterotrophs in the ice edge zone: An AMERIEZ study, *Antarc. J. U.S.*, 21, 169–171, 1985a.

Garrison, D.L., Buck, K.R., Sea-ice algal communities in the Weddell Sea: Species composition in ice and plankton assemblage, in *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*, Grey, J.S., Christiansen, M.E., Eds., Wiley, New York, 1985b, 103–122.

Garrison, D.L., Buck, K.R., Organism losses during ice melting: A serious loss in sea ice community studies, *Polar Biol.*, 6, 237–239, 1986.

Garrison, D.L., Buck, K.R., The biota of the Antarctic pack ice in the Weddell Sea and Antarctic Peninsula region, *Polar Biol.*, 10, 211–219, 1989a.

Garrison, D.L., Buck, K.R., Protozooplankton in the Weddell Sea, Antarctica: Abundance and distribution in the ice edge zone, *Polar Biol.*, 8, 341–351, 1989b.

Garrison, D.L., Buck, K.R., Surface layer assemblages in Antarctic pack ice during austral spring: Environmental conditions, primary production and community structure, *Mar. Ecol. Prog. Ser.*, 75, 161–172, 1991.

Garrison, D.L., Close, A.I., Winter ecology of the sea ice biota in the Weddell Sea pack ice, *Mar. Ecol. Prog. Ser.*, 96, 17–31, 1993.

Garrison, D.L., Gowing, M.M., Protozooplankton, in *Antarctic Microbiology*, Friedman, E.I.F., Ed., Wiley-Liss, New York, 1992, 123–165.

Garrison, D.L., Mathot, S., Pelagic and sea ice microbial communities, *Antarc. Res. Ser.*, 70, 155–172, 1996.

Garrison, D.L., van Scoy, K., Wilkes Land Expedition 1985: Biological observations in the ice-edge zone, *Antarc. J. U.S.*, 19, 123–124, 1985.

Garrison, D.L., Ackley, S.F., Buck, H.R., A physical mechanism for establishing ice algal populations in frazil ice, *Nature (Lond.)*, 306, 363–365, 1983.

Garrison, D.L., Buck, K.R., Silver, M.W., Microheterotrophs in the ice edge zone, *Antarc. J. U.S.*, 19, 109–111, 1984.

Garrison, D.L., Sullivan, C.W., Ackley, S.F., Sea ice microbial communities in the ice-edge zone, *Antarc. J. U.S.*, 19, 10–13, 1986a.

Garrison, D.L., Sullivan, C.W., Ackley, S.F., Sea ice microbial communities in Antarctica, *BioScience*, 36, 243–250, 1986b.

Garrison, D.L., Buck, K.R., Fryxell, G.A., Algal assemblages in Antarctic pack ice and ice edge plankton, *J. Phycol.*, 23, 564–572, 1987.

Garrison, D.L., Close, A.I., Gordon, L.I., in *Sea Ice Processes and Properties*, Army Cold Regions Research and Engineering Laboratory (CRREL) Monograph 90-1, Ackley, S.F., Weeks, W.F., Eds., 35–59, 1989.

Garrison, D.L., Buck, K.R., Gowing, M.M., Plankton assemblage in the ice edge zone in the Weddell Sea during the austral winter, *J. Mar. Syst.*, 2, 123–130, 1991.

Garrison, D.L., Buck, K.R., Gowing, M.M., Winter plankton assemblage in the ice edge zone of the Weddell and Scotia Seas: Composition, biomass and spatial distributions, *Deep-Sea Res.*, 40, 311–338, 1993.

Garside, C., Garside, J.C., The '*f-ratio*' on 20° W during the North Atlantic Bloom Experiment, *Deep-Sea Res.*, 40, 75–90, 1993.

Gartshore, N.A., Steele, W.K., Klages, N.T.W., Summer diet of the Salvin's prion at sub-Antarctic Marion Island, *S. Afr. J. Zool.*, 23, 309–313, 1988.

Gaskin, D.E., The evolution, zoogeography, and ecology of Cetacea, *Oceanogr. Mar. Biol: Annu. Rev.*, 14, 247–346, 1976.

Gaskin, D.E., The Ecology of Whales and Dolphins, Heinman, London, 1982.

Geesey, G.G., Microbial exopolymers: Ecological and economic considerations, *Am. Soc. Microbiol. News*, 48, 9–14, 1982.

George, R.W., Biology of Antarctic krill, *Euphausia superba*, *J. Crustacean Biol.*, 4(Special Issue No.1), 1984a, 537pp.

George, R.W., Ontogenetic adaptations in growth and respiration of *Euphausia superba* in relation to temperature and pressure, *J. Crustacean Biol.*, 4(Special Issue No.1), 252–262, 1984b.

Geraci, J.R., Pinniped nutrition, *Rapports et Proces-Verbaux des Reunion Conseil Interntional Pour l'Exploration de la Mer*, 169, 312, 1975.

Gerdes, D., Klages, M., Antz, W.E., Herman, R.L., Galeron, J., Hain, S., Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea based on multibox corer samples, *Polar Biol.*, 12, 291–301, 1992.

Gerdes, D., Hilbeg, B., Montiel, A., Impact of iceberg scouring on macrobenthic communities in the high-Antarctic Weddell Sea, *Polar Biol.*, 26, 295–301, 2003.

Gersonde, R., Wefer, G., Sedimentation of biogenic siliceous particles in Antarctic waters (Atlantic Sector), *Mar. Micropaleontol.*, 11, 311–332, 1987.

Gibson, J.A.E., Garrick, R.C., Burton, H.R., McTaggert, A.R., Dimethylsulphide and the alga *Phaeocystis pouchetti* in AntarcticAntarctic coastal waters, *Mar. Biol.*, 104, 339–346, 1989.

Gibson, J.A.E., Garrick, R.C., Burton, H.R., Seasonal fluctuation of bacterial numbers near the Antarctic continent, *Proc. NIPR Symp. Polar Biol.*, 3, 16–22, 1990.

Giese, M., Effects of human activity on Adélie Penguins *Pygoscelis adeliae* breeding success, *Biological Conservation*, 75, 157–164, 1996.

Gieskes, W.W.C., Elbracher, M., Abundance of nanoplankton-size chlorophyll-containing particles caused by diatom disruption in surface waters of the Southern Ocean (Antarctic Peninsula region), *Neth. J. Sea Res.*, 20, 291–303, 1986.

Gieskes, W.W.C., Kray, G.W., Baars, M.A., Current ^{14}C method for measuring primary production: Gross underestimates in oceanic waters, *Neth. J. Sea Res.*, 13, 58–78, 1979.

Gilbert, N.S., Microphytobenthic seasonality in near-shore marine sediments at Signy Island, South Shetland Islands, Antarctica, *Estuarine, Coast. Shelf Sci.*, 33, 89–104, 1991a.

Gilbert, N.S., Primary production by benthic microalgae in nearshore marine sediments of Signy Island, Antarctica, *Polar Biol.*, 11, 339–346, 1991b.

Gilbert, J.R., Ericksen, A.W., Status of seals in pack ice of the pacific sector of the Southern Ocean, in *Adaptations within Antarctic Ecosystems*, Llano, G., Ed., Smithsonian Institution, Washington, DC, 1977, 703–735.

Gilbert, P.M., Biggs, D.C., McCarthy, J.J., Utilization of ammonium and nitrate during austral summer in the Scotia Sea, *Deep-Sea Res.*, 29, 837–850, 1982.

Gill, A.E., Circulation and bottom water formation in the Weddell Sea, *Deep-Sea Res.*, 20, 111–140, 1973.

Gille, S.T., Warming of the Southern Ocean since the 1950s, *Science*, 295, 1275–1277, 2002.

Gille, S.T., Kelly, K.A., Scales of spatial and temporal variability in the Southern Ocean, *J. Geophys. Res.*, 101, 8759–8773, 1996.

Gillespie, P.A., Morita, R.Y., Jones, L.P., The heterotrophic actvity for amino acids, glucose and acetate in Antarctic waters, *Journal of the Oceanographical Society of Japan*, 32, 4, 1976.

Gilmour, A.E., McMurdo Sound hydrological observations 1972–73, *NZ. J. Mar. Freshwater Res.*, 9, 75–95, 1975.

Gilmour, A.E., Ross Ice Shelf sea temperatures, *Science*, 203, 438–439, 1979.

Gilmour, A.E., MacDonald, W.J.P., van der Hoeven, F.G., Ocean currents in McMurdo Sound, *Nature (Lond.)*, 474, 867–870, 1960.

Gilmour, A.E., MacDonald, W.J.P., van der Hoeven, F.G., Winter measurements of sea currents in McMurdo Sound, *NZ J. Geol. Geophys.*, 5, 778–789, 1962.

Gilstard, M., Effects of photoperiod and irradiance on phytoplankton growth. M.S. thesis, University of Trondheim, Norway, 1987.

Gleitz, M., Kirst, G.O., Photosynthesis irradiance relationships and carbon metabolism of different ice algal assemblages collected from the Weddell Sea pack ice during austral spring, *Polar Biol.*, 11, 385–392, 1991.

Gleitz, M., Thomas, D.N., Variation in phytoplankton standing stock, chemical composition and physiology during sea ice formation in the southeastern Weddell Sea, Antarctica, *J. Exp. Mar. Biol. Ecol.*, 173, 211–230, 1993.

Gleitz, M., Kurtert, H., Riebsell, U., Dieckman, G.S., Carbon acquisition and growth of Antarctic sea ice diatoms in closed-bottle incubations, *Mar. Ecol. Prog. Ser.*, 135, 169–177, 1996.

Glover, H.E., Smith, A.E., Shapiro, L., Diurnal variations in photosynthetic rates: Comparison of ultraphytoplankton with larger phytoplankton size fractions, *J. Plankton Res.*, 7, 519–535, 1985.

Godlewska, M., Vertical migration of krill (*Euphausia superba* Dana), *Polskie Archiwum Hydrobiologii*, 43(1), 9–63, 1996.

Godlewska, M., Klusek, Z., Vertical distribution and diurnal migrations of krill (*Euphausia superba* Dana) from hydroacoustical observations, SIBEX, December 1983/January 1984, *Polar Biol.*, 8, 17–22, 1987.

Goeyens, L., Treguer, P., Lancelot, J., Mathot, S., Becquevort, S., Morvan, J., Dehairs, F., Baeyens, W., Ammonium regeneration in the Scotia-Weddell confluence area during spring 1978, *Mar. Ecol. Prog. Ser.*, 78, 241–252, 1991.

Goeyens, L., Treguer, P., Baumann, M.E.M., Breyens, W., Dehairs, F., The leading role of ammonium in the nitrogen uptake regime of Southern Ocean marginal ice zones, *J. Mar. Syst.*, 6, 345–361, 1995.

Goldman, J.C., Ocean nutrient cycles, in *Flow of Energy and Materials in Marine Ecosystems: Theory and Practice*, Fasham, M.J.R., Ed., Plenum Press, New York, 1984a, 103, 130–176.

Goldman, J.C., Conceptual role for microaggregates in pelagic waters, *Bull. Mar. Sci.*, 35, 462–476, 1984b.

Goldman, J.C., Caron, D.A., Experimental studies on the omnivorous microflagellate: Implications for grazing and nutrient regeneration in the marine microbial food chain, *Deep-Sea Res.*, 32, 899–915, 1985.

Gomez, I., Wiencke, C., Weykam, C., Seasonal photosynthetic characteristics of Ascoseira mirabilis (Ascoscirales: Phaeophyta) from King George Island, Antarctica, *Mar. Biol.*, 123, 167–172, 1997.

Gon, O., Bovichtidae (thornfish), in *Fishes of the Southern Ocean*, Gon, O., Heemstra, P.C.H., Eds., J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa, 1990, 277–278.

Gon, O., Heemstra, P.C. *Fishes of the Southern Ocean*, J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa, 1990.

Gonzales, H.E., Distribution and abundance of minipellets around the Antarctic Peninsula: Implications for protistan feeding behaviour, *Mar. Ecol. Prog. Ser.*, 90, 223–236, 1992a.

Gonzales, H.E., The distribution and abundance of krill fecal material and oval pellets in the Scotia and Weddell Seas (Antarctica) and their role in particle flux, *Polar Biol.*, 12, 81–89, 1992b.

Gonzales, H.E., The distribution and abundance of krill faecal material and oval pellets in the Scotia and Weddell Seas (Antarctica) and their role in particle flux, in *Weddell Sea Ecology*, Hempel, G., Ed., Springer, Berlin, 1995, 81–91.

Gonzales, H.E., Kurbjeweit, F., Bathman, U.V., Occurrence of cyclopoid copepods' faecal material in the Halley Bay region, Antarctica, during January-February 1991, *Polar Biol.*, 14, 331–342, 1994.

Goodall, R.N.P., Report on the small crustaceans stranded on the coast of Tierra del Fuego, *Sci. Rep. Whales Res. Inst. Tokyo*, 30, 197–223, 1978.

Goodall, R.N.P., Galeazzi, A.R., A review of the food habits of the small cetaceans from the Atlantic and Sub-Antarctic, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 566–572.

Gordon, A.L., Structure of Antarctic waters between 20° W and 170° W, *Antarctic Map Folio Series* 6, American Geographical Society, 1967.

Gordon, A.L., Seasonality of the Southern Ocean sea ice, *J. Geophys. Res.*, 86, 4193–4197, 1981.

Gordon, A.L., Polar oceanography, *Rev. Geophys. Space Phys.*, 21, 1124–1131, 1983.

Gordon, A.L., Spatial and temporal variability within the Southern Ocean, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin, 1988, 41–56.

Gordon, A.L., Goldberg, R.D., Circumpolar characteristics of Antarctic waters, *Antarctic Map Folio Series* 13, American Geographical Society, Washington, DC, 1970.

Gordon, A.L., Huber, B.A., Physical oceanography program in the US-USSR Weddell Sea Polyna Expedition—1981, *Antarc. J. US*, 17, 150–152, 1982.

Gordon, A.L., Molinelli, E.M., *The Southern Ocean Atlas: Thermohaline and Chemical Distribution and the Atlas Data Set*, Columbia University Press, New York, 1982.

Gordon, A.L., Owens, W.B., Polar oceans, *Rev. Geophys.*, 25, 227–233, 1987.

Gordon, A.L., George, D.T., Taylor, H.W., Antarctic Polar Front Zone in the western Scotia Sea: Summer 1975, *J. Phys. Oceanogr.*, 7, 309–328, 1977a.

Gordon, A.L., George, D.T., Taylor, H.W., Antarctic oceanographic zonation, in *Polar Oceans*, Dunbar, M.J., Ed., Arctic Institute of North America, Calgary, 1977a, 45–76.

Gordon, A.L., Molinelli, E.M., Baker, T., Large-scale relative dynamic topography of the Southern Ocean, *J. Geophys. Res.*, 83, 3023–3032, 1978.

Gordon, A.L., Martinson, D.G., Taylor, H.W., The wind-driven circulation in the Weddell-Enderby Basin, *Deep-Sea Res.*, 28A, 151–163, 1981.

Gorelova, M., Gerasimchuk, V.V., Data on nutrition and daily consumption of juvenile *Pleurogramma antarcticum* Boulenger, in *Fishes of the Ocean*, Parvin, N.V., Ed., Academy of Sciences, USSR, Moscow, 1981, 103–109.

Gorney, M., Untersuchungen zur Okologie antarktischer Garnelen (Decapoda: Natantia). Ph.D. thesis, University of Bremen, Germany, 1992.

Goss, C., Everson, I., An acoustic survey of Antarctic krill on the South Georgia shelf, CCAMLR Subarea 48.3, in January 1992, *WG-Emm-96/42*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1996.

Goss, C., Bone, D.G., Peck, J.M., Everson, I., Hunt, G.L., Murray, A.W.A., Small-scale interactions between prions (*Pachyptila* spp.) and their zooplankton prey at an inshore site near Bird Island, South Georgia, *Mar. Ecol. Prog. Ser.*, 154, 41–51, 1997.

Gouretski, V., The large-scale thermohaline structure of the Ross Sea Gyre, in *Oceanography of the Ross Sea*, Spezie, G., Mabzella, G.M.R., Eds., Springer, Milan, 1999, 77–100.

Gow, A.J., Ackley, S.F., Weeks, W.F., Gowing, J.W., Physical and structural characteristics of Antarctic sea ice, *Ann. Glaciol.*, 3, 118–124, 1982.

Gow, A.J., Ackley, S.F., Buck, K.R., Golden, K.M., Physical and structural characteristics of Weddell Sea pack ice. *Cold Reg. Res. Eng. Lab. Rep.*, 87-14-R, 1987.

Gowing, M.M., Abundance and feeding ecology of Antarctic phaeodarian radiolarians, *Mar. Biol.*, 103, 107–118, 1989.

Gowing, M.M., Silver, M.W., Minipellets: A new and abundant size class of marine faecal pellets, *J. Mar. Res.*, 43, 395–418, 1985.

Gradinger, R., Integrated abundance and biomass of sympagic meiofauna in Arctic and Antarctic pack ice, *Polar Biol.*, 22, 169–177, 1999.

Gran, H.H., Phytoplankton: Methods and problems, *Journal du Conseil, Conseil Permanent pour l'Exploration de la Mer*, 8, 343–358, 1932.

Granata, A., Guglielmo, L., Greco, S., Vacchi, M., Sidali, O., Zagami, G., Lathesa, M., Spatial distribution and feeding habitats of larval and juvenile *Pleurogramma antarcticum* in the western Ross Sea, in *Ross Sea Ecology*, Farando, F.M., Guglielmo, L., Ianora, A., Eds., Springer, New York, 1998, 369–393.

Graneli, E., Rabbani, M.M., Fransz, G., Granéli, W., Daugbjerg, N., Cuzin-Roudy, J., Alder, V.A., The influence of copepod and krill grazing on the species composition of phytoplankton communities from the Scotia-Weddell Sea: An experimental approach, *Polar Biol.*, 13, 201–213, 1993.

Grant, W.S., Horner, R.A., Growth responses to salinity variations in four Arctic ice diatoms, *J. Phycol.*, 12, 180–185, 1976.

Grantham, G.J., *The Utilization of Krill*, Southern Ocean Fisheries programme, FAO GLO/So/77/3, FAO, Rome, 1977.

Grassle, J.F., Sanders, H.L., Life histories and the role of disturbance, *Deep-Sea Res.* 20, 643, 1973.

Gray, J.S., Antarctic marine benthic biodiversity in a worldwide latitudinal context, *Polar Biol.*, 24, 633–641, 2001.

Green, K.A., Role of krill in the Antarctic marine ecosystem. *Final Report to the Department of State, Division of Ocean Affairs, Contract, 1722-720248*, 1977.

Green, K., Williams, R., Burton, H.R., The diet of Antarctic fur seals during the late autumn and early winter around Heard Island, *Antarc. Sci.*, 3, 359–361, 1991.

Green-Hammond, K.A., Modelling Antarctic ecosystems, in *Biological Investigations of Antarctic Systems and Stiocks, the BIOMASS Perspective*, El-Sayed, S.Z., Ed., SCAR SCOR, Cambridge, 1981, 22–45.

Green-Hammond, K.A., Ainley, D.G., Diniff, D.B., Urquart, N.S., Selection criteria and monitoring requirements for indirect indicators of changes in the availability of Antarctic krill applied to some pinniped and seabird information, *Rep. US. Mar. Mammal Comm.*, 1983.

Grinley, J.R., David, P., Nutrient upwelling and its effect in the lee of Marion Island, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1995, 46–51.

Grinley, J.R., Lane, S.B., Zooplankton around Marion and Prince Edward Islands, *CNFRA*, 44, 111–125, 1979.

Groscholas, R., Study of the moult fasting followed by an experimental forced fasting in the Emperor penguin *Aptenodytes forsteri*: Relationship between feather growth, body weight loss, body temperature, and plasma fluid level, *Comp. Biochem. Physiol.*, 61A, 287–295, 1978.

Groscolas, R., Clement, C., Utilization des reserves energetiques au cours jeline de la reproduction cnez le manchot emperor *Aptenodytes forsteri*, *Comptes-Rendus de l'Académie des Sciences (Paris), Série D*, 282, 297–303, 1976.

Grossi, S. McG., Response of a sea ice microalgal community to a gradient in under ice irradiance, Ph.D Dissertation, University of Southern California, Los Angeles, CA, 1985.

Grossi, S.McG., Sullivan, C.W., Sea ice microbial communities, 5: The vertical zonation of diatoms in an Antarctic fast ice community, *J. Phycol.*, 21, 401–409, 1985.

Grossi, S.McG., Kottmeier, S.T., Sullivan, C.W., Sea ice microbial communities, III: Seasonal abundance of microalgae and associated bacteria, McMurdo Sound, Antarctica, *Microb. Ecol.*, 10, 231–242, 1984.

Grossi, S.McG., Kottmeier, S.T., Moe, R.L., Taylor, G.T., Sullivan, C.W., Sea microbial communities, VI: Growth and primary production in bottom ice under graded snow cover, *Mar. Ecol. Prog. Ser.*, 35, 153–164, 1987.

Grossman, S., Lochte, K., Scharek, R., Algal and bacterial processes in platelet ice during late austral summer, *Polar Biol.*, 16, 623–633, 1996.

Grua, P., Introduction ecologique invertebres de l'infralittoral rocheux dans Archipel de Kerguelen, *CNFRA*, 30, 1–66, 1971.

Gruzov, E.N., Seasonal alterations in coastal communities in the Davis Sea, in *Adaptations within Antarctic Ecosystems*, Llano, G., Ed., Smithsonian Institution, Washington, DC, 1977, 263–278.

Gubsch, G., Investigation of krill (*Euphausia superba* Dana) off South Shetland Islands, *ICES C.M.1979/L*, 34–41, 1979.

Gubsch, G., Zur Verbreitung und Biologie der Eisfische (Chaenichthyidae) im atlantischen Sektor der Antarktis, *Fischereiforschung*, 20, 39–47, 1982.

Guglielmo, L., Granata, A., Greco, S., Distribution and abundance of postlarval and juvenile *Pleurogramma antarcticum* (Pisces: Nototheniidae) off Terra Nova Bay (Ross Sea, Antarctica), *Polar Biol.*, 19, 37–51, 1998.

Guillard, R.R.L., Kilham, P., The ecology of marine planktonic diatoms, in *The Biology of Diatoms*, Werner, D., Ed., University of California Press, Berkeley, CA, 1977, 372–469.

Guinet, C., Cherel, Y., Ridoux, V., Jouventin, P., Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: Changes in relation to consumer biomass, *Antarc. Sci.*, 8, 23–30, 1996.

Gulland, J.A., The development of the resources of the Antarctic seas, in *Antarctic Ecology, Vol. 1*, Holdgate, M.W., Ed., Academic Press, London, 1970, 217–223.

Gulland, J.A., Antarctic baleen whales: History and prospects, *Polar Rec.*, 18, 5–13, 1976.

Gulland, J.A., The development of fisheries and stock assessment of resources in the Southern Ocean, *Mem. Nat. Inst. Polar Res. Spec. Issue*, 27, 233–246, 1983a.

Gulland, J.A., Fish stock assessment: A manual of basic methods, *FAO/Wiley Series on Food and Agriculture*, Vol. 1, Wiley , Chichester, 1983b.

Gulland, J.A., Comments and questions on ecosystem management, *Selected Papers Presented to the Sci. Comm. CCAMLR, Part II*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 179–201, 1985.

Gulland, J.A., Antarctic treaty system as a resource management mechanism—living resources, in *Antarctic Treaty System*, National Academy of Sciences, Washington, DC, 221–234 pp, 1986.

Gunther, E.R., The habits of whales, *Discov. Rep.*, 25, 113–142, 1949.

Günther, S., Dieckmann, G.S., Vertical zonation and community transition of sea-ice diatoms in fast ice and platelet layers in the Weddell Sea, Antarctica, *Antarc. Sci.*, 11, 305–315, 2001.

Günther, S., George, K.H., Gleitz, M., High sympagic metazoan abundance in platelet layers at Drescher Inlet, Weddell Sea, Antarctica, *Polar Biol.*, 22, 82–89, 1999.

Günther, S., Gleitz, M., Dieckmann, G.S., Biogeochemistry of Antarctic sea ice: A case study on platelet ice layers at Drescher Inlet, Weddell Sea, *Mar. Ecol. Prog. Ser.*, 177, 1–13, 1999.

Gustafsen, D.E., Jr., Anderson, M.R., Rivkin, R.B., Bacterioplankton abundance and productivity at the ice-edge zone of McMurdo Sound, Antarctica, *Antarc. J. US*, 25, 191–193, 1990.

Gutt, J., Zur Verbreitung und Okdeg und Okelegie der Seegarken (Holothuroidea: Echinodermata) im Weddellmeer (Antarcktis), *Ber. Polarforsch.*, 41, 1–87, 1988.

Gutt, J., Some 'driving forces' structuring communities of the subtidal Antarctic macrobenthos, *Antarc. Sci.*, 12(3), 297–313, 2000.

Gutt, J., On the distribution and ecology of holothurians in the Weddell Sea (Antarctica), *Polar Biol.*, 11, 312–329, 1991a.

Gutt, J., Investigations on brood protection in *Psolus dubiosus* (Echinodermata: Holothuroidea) from Antarctica in spring and autumn, *Mar. Biol.*, 11, 533–544, 1991b.

Gutt, J., On direct impact of ice on marine benthic communities: A review, *Polar Biol.*, 24, 553–564, 2001.

Gutt, J., Piepenburg, D., Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs, *Mar. Ecol. Prog. Ser.*, 253, 77–83, 2003.

Gutt, J., Starmans, A., Quantification of iceberg impact and benthic recolonization patterns in the Weddell Sea (Antarctica), *Polar Biol.*, 24, 615–619, 2001.

Gutt, J., Starmans, A., Dieckmann, G., Impact of iceberg scouring on polar benthic habitats, *Mar. Ecol. Prog. Ser.*, 137, 311–316, 1996.

Gutt, J., Sirenko, B.I., Smirov, I.S., Arntz, W.E., How many macrobenthic species might inhabit the Antarctic shelf? *Antarc. Sci.*, 16, 11–16, 2004.

Guzman, D., Distribution and abundance of Antarctic krill (*Euphausia superba*) in the Bransfield Strait, *Ber. Polarforsch.*, 4, 169–190, 1983.

Gutzmann, E., Martinez, A.P., Rose, A., Viet-Kohler, G., Meiofauna communities along an abyssal gradient in the Drake Passage, SCAROpen Science Conference, Abstracts, 172 pp, 2004.

Guzman, O., Marin, B., Hydroacoustic and photographic techniques applied to study the behaviour of krill (*Euphausia superba*), *Mem. Nat. Inst. Polar Res. Special Issue*, 17, 129–152, 1983.

Hader, P., Worrest, R.C., Effects of enhanced solar ultraviolet radiation on aquatic ecosystems, *Phytochem. Phytobiol.*, 53, 717–725, 1991.

Hagen, W., On the significance of lipids in Antarctic zooplankton, *Ber. Polarforsch.*, 49, 103–120, 1988.

Hagen, W., Kattner, G., Tergruggen, A., van Vleet, E.S., Lipid metabolism of Antarctic krill (*Euphausia superba*) and its ecological implications, *Mar. Biol.*, 139, 95–104, 2001.

Hain, S., Die beschalten benthischen Mollusken (Gastropoda and Bivalvia) des Weddellmeeres, Antarktis, *Ber. Polarforsch.*, 70, 1–181, 1990.

Hall, J.A., Barre, H., Jaines, M.B., The importance of phytoflagellate, heteroflagellate and ciliate grazing on bacteria and phytoplankton sized prey in a coastal marine environment, *J. Plankton Res.*, 15, 1075–1086, 1993.

Hallegraeff, G.M., Seasonal study of phytoplankton pigments and species composition at a coastal station off Sydney: Importance of diatoms and nanoplankton, *Mar. Biol.*, 61, 107–118, 1984.

Hamada, E., Numanami, H., Naito, Y., Taniguchi, A., Observation of the marine benthic organisms at Syowa Station in Antarctica using a remotely-operated vehicle, *Mem. Nat. Inst. Polar Res. Special Issue*, 40, 289–298, 1986.

Hamilton, J.E., The leopard seal, *Hydrurga leptonyx* (de Blainville), *Discovery Rep.*, 18, 239–264, 1939.

Hamner, W.M., Aspects of schooling in *Euphausia superba*, *J. Crust. Biol.*, 4(Special Issue No.1), 67–74, 1984.

Hamner, W.M., Hamner, P.R., Stroud, S.W., Gilmer, R.W., Behaviour of Antarctic krill, *Euphausia superba*: Chemoreception, feeding, schooling, and molting, *Science*, 220, 433–435, 1983.

Hamner, W.M., Hamner, P.R., Obst, B.S., Carleton, J.H., Field observations on the ontogeny of schooling of *Euphausia superba* furciliae and its relationship to ice in Antarctic waters, *Limnol. Oceanogr.*, 34, 451–456, 1989.

Hampton, I., Preliminary report of the FIBEX acoustic work to estimate the abundance of *Euphausia superba*, *Mem. Nat. Inst. Polar Res. Special Issue*, 27, 165–175, 1983.

Hampton, I., Abundance, distribution, and behaviour of *Euphausia superba* in the Southern Ocean between 15° and 30° during FIBEX, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 294–303.

Hanelt, D., Melchersmann, B., Wiencke, C., Nultscher, W., Effects of high light stress on photosynthesis of polar macroalgae in relation to depth distribution, *Mar. Ecol. Prog. Ser.*, 149, 255–266, 1997.

Haney, T.F., Diel patterns of zooplankton behaviour, *Bull. Mar. Sci.*, 43, 583–603, 1988.

Hanks, J., Characteristics of population conditions, in *Dynamics of Large Mammal Populations*, Fowler, C.W., Smith, T.D., Eds., Wiley, New York, 1981, 47–73.

Hannah, F.J., Boney, A.D., Nanoplankton in the Firth of Clyde, Scotland: Seasonal abundance, carbon fixation and species composition, *J. Exp. Mar. Biol. Ecol.*, 67, 105–147, 1983.

Hanson, R.B., Lowery, H.K., Spatial distribution, structure, biomass, and physiology of microbial assemblages across the Southern Ocean frontal zones during the late austral winter, *Appl. Environ. Microbiol.*, 49(5), 1029–1035, 1985.

Hanson, R.B., Lowery, H.K., Shafer, D., Sorocco, R., Pope, D.H., Microbes in Antarctic waters of the Drake Passage: Vertical patterns of substrate uptake, productivity, and biomass in January 1980, *Polar Biol.*, 2, 179–188, 1983.

Hanson, R.B., Shafer, D., Pole, D.H., Lowery, H.K., Bacterioplankton in Antarctic Ocean waters during the late austral winter: Abundance, frequency of dividing cells, and estimates of production, *Appl. Environ. Microbiol.*, 45(5), 1622–1632, 1983.

Hara, S., Tanoue, E., Zenimata, M., Komaki, Y., Takashi, E., Heperotrophic processes along a transect of 70°E in the Southern Ocean, *Mem. Nat. Inst. Polar Res. (Special Issue)*, 40, 69–80, 1986.

Hardy, A.C., *Great Waters*, Collins, London, 1967.

Hardy, P., Biomass estimates for some shallow-water infaunal communities at Signy Island, South Orkney Islands, *Br. Antarc. Surv. Bull.*, 31, 93–106, 1972.

Hardy, A.C., Günther, E.R., The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927, *Discov. Rep.*, 11, 1–456, 1936.

Hargraves, B.T., The importance of total and mixed-layer depth in the supply of organic material to bottom consumers, *Symp. Biol. Hung.*, 15, 157–165, 1975.

Harper, P.C., Knox, G.A., Spurr, E.B., Taylor, R.H., Wilson, G.J., Young, E.C., The status and conservation of birds in the Ross Sea sector of Antarctica, in *The Status and Conservation of the World's Seabirds*, International Council for Bird Preservation Technical Publication No. 2, 593–608, 1984.

Harris, G.P., The measurement of photosynthesis in natural populations of phytoplankton, in *The Physiological Ecology of Phytoplankton*, Morris, J., Ed., University of California Press, Berkeley, CA, 1980, 129–187.

Harris, G.P., Comparison of the feeding behaviour of *Calanus* and *Pseudocalanus* in experimentally-manipulated enclosed systems, *J. Mar. Biol. Assoc. UK*, 62, 71–91, 1982.

Harrison, R.J., Reproduction and reproductive organs, in *Biology of Marine Mammals*, Anderson, T.H., Ed., Academic Press, New York, 1969, 253–348.

Harrison, W.G., Respiration and its size-dependence in microplankton populations from the surface waters of the Canadian Arctic, *Polar Biol.*, 6, 145–152, 1986.

Harrison, G.R., Observations on the epipelagic gelatinous fauna of McMurdo Sound, *Antarc. J. U.S.*, 23, 135–136, 1988.

Harrison, W.G., Platt, T., Photosynthesis-irradiance relationships in polar and temperate phytoplankton populations, *Polar Biol.*, 5, 153–164, 1986.

Harrison, W.G., Platt, T., Irwin, B., Primary production and nutrient assimilation by natural phytoplankton populations of the eastern Canadian Arctic, *Can. J. Fish. Aquat. Sci.*, 39, 335–345, 1982.

Hart, T.J., On the phytoplankton of the southwest Atlantic and the Bellinghausen Sea, *Discovery Rep.*, 8, 1–268, 1934.

Hart, T.J., Phytoplankton periodicity in Antarctic surface waters, *Discovery Rep.*, 21, 261–356, 1942.

Hartman, O., Larval development of benthic invertebrates in Antarctic seas: Early development of *Nothria notialis* (Monro) and *Paronuphis antarctica* (Monro) in Bransfield Strait, Antarctica Peninsula, *JARE Sci. Rep. Spec. Issue*, 1, 205–208, 1967.

Hasle, G.R., *Nitzschia* and *Fragilariopsis* species studied in the light and electron microscopes, I: Some marine species of the groups *Nitzschiella* and *Lanceolata*, *Skr. Norske Videnskaps-Akademi*, 16, 1–48, 1964.

Hasle, G.R., *Nitzschia* and *Fragilariopsis* species studied in the light and electron microscopes, III: The genus *Fragilariopsis*, *Skr. Norske Videnskaps-Akademi*, 21, 1–49, 1965.

Hasle, G.R., An analysis of the phytoplankton of the Pacific Southern Ocean: Abundance, composition, and distribution during the Brategg Expedition, 1947–48, *Hvalradets Skr.*, 52, 1–168, 1969.

Hay, M.E., Fenical, W., Chemical mediation of seaweed-herbivore interactions, in *Plant-Animal Interactions in the Marine Benthos*, John, D.M., Hawkins, S.J., Price, J.H., Eds., Clarendon press, Oxford, 1992, 319–337.

Hay, C.H., Adams, N., Parsons, N.M., Marine algae of the subantarctic islands of New Zealand, *National Museum of New Zealand Miscellaneous Series* No. 11, 1985.

Hayes, P.K., Whitaker, T.M., Fogg, G.E., Distribution and nutrient status of phytoplankton in the Southern Ocean between 20° and 70° W, *Polar Biol.*, 3, 153–165, 1984.

Hays, J.D., Climatic record of Late Cenozoic Antarctic Ocean sediments related to the record of world climate, in *Paleoecology of Africa and the Surrounding Islands and Antarctica*, van Zinderen Bakker, E.M., Ed., A.A. Balkkema, Capetown, 1969, 139–164.

Heath, G.R., Mineralogy of Cenozoic deep-sea sediments from the equatorial Pacific Ocean, *Geol. Soc. Am. Bull.*, 80(10), 1997–2018, 1969.

Heath, R.A., Circulation and hydrology under the seasonal ice in McMurdo Sound, Antarctica, *N.Z. J. Mar. Freshwat. Res.*, 5, 497–515, 1971.

Heath, G.R., Dissolved silica and deep-sea sediments, in *Studies in Paleooceanography*, Hay, W.W., Ed., Society of Economic Paleontologists and Mineralogists Special Publication 20, 1974, 77–93.

Heath, R.A., Circulation across the ice shelf edge in McMurdo Sound, Antarctica, in *Polar Oceans*, Dunbar, M.J., Ed., Arctic Institute of North America, Calgary, 1977, 129–149.

Hebling, E.W., Marguet, E.R., Villafane, V.E., Holm-Hansen, O., Bacterioplankton viability in Antarctic waters as affected by solar ultraviolet radiation, *Mar. Ecol. Prog. Ser.*, 123, 296–298, 1995.

Hecq, J.H., Brasseur, P., Goffart, A., Lacroix, G., Guglielmo, I., Modelling approach of the planktonic vertical structure in deep Austral Ocean: The example of the Ross Sea ecosystem, in *Belgian Oceanographic Research, Proceedings of the Annual Workshop on Belgian Oceanographic Research*, Academy of Sciences, Brussels, 235–249, 1993.

Hecq, J.H., Guglielmo, L., Goffart, A., Catalano, G., Goosse, H., A modelling approach to the Ross Sea plankton ecosystem, in *Ross Sea Ecology*, Farando, F.M., Guglielmo, L., Ianora, A., Eds., Springer, Berlin, 1998, 395–411.

Hedgpeth, J.W., Introduction to Antarctic zoogeography, *Antarctic Map Folio Series* Vol. 2, American Geographical Society, Washington, DC, 1–9 pp, 1969.

Hedgpeth, J.W., Marine biogeography of the Antarctic regions, in *Antarctic Ecology,* Vol. 1, Holdgate, M.W., Ed., Academic Press, London, 1970, 97–104.

Hedgpeth, J.W., Perspectives of benthic ecology in Antarctica, in *Research in Antarctica*, American Association for the Advancement of Science Publication No. 9, Quasim, L.O., Ed., American Association for the Advancement of Science, Washington, DC, 1977a, 667–684.

Hedgpeth, J.W., The Antarctic marine ecosystem, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977b, 3–10.

Heinbokel, J.F., Beeres, J.R., Studies on the functional role of tintinnids in the Southern California Bight III: Grazing impact on natural assemblages, *Mar. Biol.*, 52, 23–32, 1979.

Heinbokel, J.F., Coats, D.W., Reproductive dynamics of ciliates in the ice-edge zone, *Antarc. J. U.S.*, 19, 111–113, 1984.

Heinbokel, J.F., Coats, D.W., Ciliates and nanoplankton in Arthur Harbor, December 1984 and January 1985, *Antarc. J. U.S.*, 19, 135–136, 1985.

Heinbokel, J.F., Coats, D.W., Patterns of tintinnine abundance and reproduction near the edge of the seasonal pack ice in the Weddell Sea, November 1983, *Mar. Ecol. Prog. Ser.*, 33, 71–80, 1986.

Heine, A.J., Seals at White Island, *Antarctic*, 2, 272–273, 1960.

Heinle, D.R., Flemer, D.A., Carbon requirements of a population of the estuarine copepod *Eurytemora affinis*, *Mar. Biol.*, 31, 235–247, 1975.

Heinle, D.R., Harris, R.P., Ustach, J.F., Flemer, D.A., Detritus as a food for estuarine copepods, *Mar. Biol.*, 40, 341–353, 1977.

Heip, C., Vinex, M., Vranken, G., The ecology of marine nematodes, *Oceanogr. Mar. Biol., Annu. Rev.*, 23, 399–484, 1985.

Helbling, E.W., Villafane, V., Holm-Hansen, O., Effect of iron on productivity and size distribution of Antarctic phytoplankton, *Limnol. Oceanogr.*, 36, 1879–1885, 1991.

Helbling, E.W., Villafane, V., Ferrario, M., Holm-Hansen, O., Impact of natural ultraviolet radiation on rate of photosynthesis and on specific marine phytoplankton species, *Mar. Ecol. Prog. Ser.*, 80, 89–100, 1992.

Helbling, E.W., Villafane, V., Holm-Hansen, O., Effects of ultraviolet radiation on Antarctic marine phytoplankton photosynthesis, with particular attention to the influence of mixing, *Antarc. Res. Ser.*, 62, 207–227, 1994.

Helbling, E.W., Marguet, E.R., Villafane, V., Holm-Hamsen, O., Bacterioplankton viability in Antarctic waters as affected by solar ultraviolet radiation, *Mar. Ecol. Prog. Ser.*, 127, 293–298, 1995.

Hellebust, J.A., Extracellular products, in *Algal Physiology and Biochemistry*, Stewart, W.D.P., Ed., University of California Press, Berkeley, CA, 1974, 838–893.

Hellebust, J.A., Lewin, J., Heterotrophic nutrition, in *The Biology of Diatoms*, Werner, D., Ed., University of California Press, Los Angeles, CA, 1977, 169–178.

Hellmer, H.H., Bersch, M., Augstein, E., Grabmann, I., The Southern Ocean: A survey of oceanographic and marine meterological research work, *Ber. Polarforsch.*, 26, 1–115, 1985.

Hemmingsen, E.A., Douglas, E.L., Respiratory characteristics of the haemoglobin-free fish *Chaenocephalus aceratus*, *Comp. Biochem. Physiol.*, 33, 733–744, 1970.

Hemmingsen, E.A., Douglas, E.L., Respiratory and circulatory adaptations to the absence of haemoglobin in Chaenichthyid fishes, in *Adaptations within Antarctic Ecosystems*, Llano, G., Ed., Gulf Publishing Company, Houston, TX, 1977, 479–487.

Hempel, G., Antarctica, in *Fish Resources of the Ocean*, Gulland, J.A., Ed., FAO, Rome, 1970.

Hempel, I., Vertical distribution of eggs and nauplii of krill (*Euphausia superba*) south of Elephant Island, *Meeresforschung*, 29, 53, 1978.

Hempel, I., Studies on eggs and larvae of *Euphausia superba and Euphausia crystallorophias* in the Atlantic Sector of the Southern Ocean, *Ber. Polarforsch.*, 4, 30–46, 1983.

Hempel, G., On the biology of polar seas, particularly the Southern Ocean, in *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*, Gray, J.S., Christiansen, M.E., Eds., Wiley, Chichester, 1985a, 3–33.

Hempel, G., Antarctic marine food webs, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985b, 266–270.

Hempel, I., Vertical distribution of larvae of Antarctic krill, *Euphausia superba*, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 308–310.

Hempel, I., Variation in geographical distribution and abundance of larvae of Antarctic krill, *Euphausia superba*, in the Southern Atlantic Ocean, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 304–307.

Hempel, G., The krill-dominated pelagic system of the Southern Ocean, *Environ. Int.*, 13, 33–36, 1987.

Hempel, I., Hempel, G., Larval krill (*Euphausia superba*) in the plankton and neuston samples of the German Antarctic Expedition 1975/76, *Meeresforschung*, 26, 206–216, 1978.

Hempel, I., Hempel, G., Field observations on the developmental ascent of larval *Euphausia superba* (Crustacea), *Polar Biol.*, 6, 121–126, 1986.

Hempel, G., Manthey, M., On the fluoride content of larval krill, *Meeresforschung/Rep. Mar. Res.*, 29, 60–63, 1981.

Hempel, I., Hempel, G., Baker, A.deC., Early life history stages of krill (*Euphausia superba*) in Bransfield Strait and Weddell Sea, *Meeresforschung*, 27, 267–268, 1979.

Hense, I., Bathmann, U.K., Timmermann, R., Plankton dynamics in frontal systems of the Southern Ocean, *J. Mar. Syst.*, 27, 235–252, 2000.

Herberg, L.-M., Thomas, P.N., Kennedy, H.H., Dieckmann, G.S., Dissolved carbohydrates in Antarctic sea ice, *Antarc. Sci.*, 13(2), 119–125, 2001.

Herman, R.L., Dahms, H.U., Meiofauna communities along a depth transect off Halley Bay (Weddell Sea, Antarctica), *Polar Biol.*, 12, 313–320, 1992.

Hernandez-Leon, S., Portillo-Hahnefeld, A., Almaida, G., Becongee, R., Moreno, I., Diel feeding behaviour of krill in Gerlache Strait, Antarctica, *Mar. Ecol. Prog. Ser.*, 223, 235–242, 2001.

Herndl, G.J., Peduzzi, P., The ecology of amorphous aggregations (marine snow) in the Northern Adriatic Sea, 1: General considerations, *Mar. Ecol.*, 9, 79i–99, 1988.

Hewes, C.D., Holm-Hansen, O., Sakshaug, E., Nanoplankton and microplankton studies during the Circumnavigation Cruise, *Antarc. J. U.S.*, 18, 169–173, 1983.

Hewes, C.D., Holm-Hansen, O., Sakshaug, E., Alternate carbon pathways at the lower trophic levels in the Antarctic food web, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 277–283.

Hewes, C.D., Sakshaug, E., Reid, F.M.H., Holm-Hansen, O., Microbial autotrophic and heterotrophic eucaryotes in Antarctic waters: Relationships between biomass and chlorophyll, adenosine triphosphate and particulate organic carbon, *Mar. Ecol. Prog. Ser.*, 63, 27–35, 1990.

Hewitt, R.P., Demer, D.A., Dispersion and abundance of Antarctic krill in the vicinity of Elephant Island in the 1992 austral summer, *Mar. Ecol. Prog. Ser.*, 99, 29–39, 1993.

Heyerdahl, E.F., Hvalindustrien Kommander Chr. Christensens Hvalfangstrumuseum, Sandjeford. Publication No. 7, 1932.

Heywood, R.B., Light, J.J., First direct evidence of life under the Antarctic Ice Shelf, *Nature (Lond.)*, 254, 591–593, 1978.

Heywood, R.B., Priddle, J., Retention of phytoplankton in an eddy, *Cont. Shelf Res.*, 7, 937–955, 1987.

Heywood, R.B., Whitaker, T.M., The Antarctic marine flora, in *Antarctic Ecology,* Vol. 2, Laws, R.M., Ed., Academic Press, London, 1984, 373–419.

Heywood, R.B., Everson, I., Priddle, J., The absence of krill from the South Georgia zone, winter 1983, *Deep-Sea Res.*, 32, 369–378, 1985.

Hicks, G.R.F., Variation in zooplankton biomass with hydrological regime beneath the seasonal ice, McMurdo Sound, Antarctica, *N.Z. J. Mar. Freshwat. Res.*, 8, 67–77, 1974.

Higgenbottom, R., Hosie, G.W., Biomass and population structure of a large aggregation of krill near Prydz Bay, Antarctica, *Mar. Ecol. Prog. Ser.*, 58, 197–203, 1989.

Hill, K.T., Radthe, R.L., Gerontological studies on the damsel fish *Dascyllus albisella*, *Bull. Mar. Sci.*, 42, 424–434, 1988.

Hill, K.T., Womersley, C., Critical aspects of fluorescent age-pigment methodologies: Modification for accurate analysis and age assessments in aquatic organisms, *Mar. Biol.*, 109, 1–11, 1991.

Hinton, M.A.C., Report of papers left by the late Major Barrett-Hamilton, relating to the whales of South Georgia, Crown Agents for the Colonies, London, 1925, 57–209.

Hobbie, J.E., Holm-Hansen, O., Packard, T.T., Pomeroy, L.R., Sheldon, R.W., Thomas, J.P., Wiebe, W.J., A study of the distribution of activity of microorganisms in ocean water, *Limnol. Oceanogr.*, 17, 554–555, 1972.

Hobson, K.A., Stable isotope determinations of the trophic relationships of seabirds: Preliminary investigations of alcids from coastal British Columbia, in *Studies of High-Latitude Seabirds, 1: Behavioral, Energetic and Oceanographic Aspects of Seabird Feeding Ecology*, Occasional Paper No. 88, Canadian Wildlife Service, Ottawa, 16–20 pp, 1991.

Hobson, L.A., Menzel, D.W., Barber, R.T., Primary productivity and sizes of parts of organic carbon in the mixed layers of the ocean, *Mar. Biol.*, 19, 298–306, 1973.

Hodgson, R.E., Azam, F., Carlucci, A.F., Fuhrman, J.A., Karl, D.M., Holm-Hansen, O., Microbial uptake of dissolved organic matter in McMurdo Sound, Antarctica, *Mar. Biol.*, 71, 89–94, 1981.

Hoepffner, N., Strategies d'adaption photosynthetiques chez les diatomees de l'Ocean Antarctique: Variations du nombre et de la tailles des unites photosynthetiques, *J. Plankton Res.*, 6, 881–895, 1984.

Hofmann, E.E., Huntly, M.E., GLOBEC: Southern Ocean Program: GLOBEC Workshop on Southern Ocean on Marine Mammal Animal Populations and Global Change, *U.S. GLOBEC Reports No. 5*, 1991.

Hofmann, E.E., Murphy, E.J., Advection, krill and the Antarctic marine ecosystem, *Antarc. Sci.*, 16, 487–499, 2004.

Hofman, R., Erickson, A., Siniff, D., The Ross Seal (*Ommatophoca rossii*), *International Union for the Conservation of Nature and Natural Resources Publication New Series Supplementary Paper No. 39*, 1973, 129–139.

Hofman, R., Reichle, R., Siniff, D.B., Muller-Schwarze, D., The leopard seal (*Hydrurga leptonyx*) at Palmer Station, Antarctica, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 769–782.

Hofmann, E.E., Klinck, J.M., Lascara, C.M., Smith, D.A., Water mass distribution and circulation west of the Antarctic Peninsula, *Antarc. Res. Ser.*, 70, 61–80, 1996.

Holden, M.J., Long-term changes in landings of fish from the North Sea, *Rapp. P.-V. de la Reun. Conseil Permanent International de la Mer*, 172, 11–26, 1978.

Holdgate, M.W., The Antarctic ecosystem, *Philos. Trans. R. Soc. Lond., Ser. B*, 152, 363–383, 1967.

Holeton, G.F., Oxygen uptake and circulation by a haemoglobinless Antarctic fish (*Chaenocephalus aceratus* Lönnberg) compared with three red-blooded Antarctic fish, *Comp. Biochem. Physiol.*, 34, 447–471, 1970.

Holeton, G.F., Metabolic cold adaptation of polar fish: Fact or artefact?, *Physiol. Zool.*, 47, 137–152, 1974.

Holm-Hansen, O., Microbial uptake of dissolved organic matter in McMurdo Sound, Antarctica, *Mar. Biol.*, 61, 89–94, 1981.

Holm-Hansen, O., Nutrient cycles in Antarctic marine ecosystems, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 6–10.

Holm-Hansen, O., Forster, T.D., A multidisciplinary study of the eastern Scotia Sea, *Antarc. J. U.S.*, 16, 159–160, 1981.

Holm-Hansen, O., Huntley, M., Feeding requirements of krill in relation to food sources, *J. Crust. Biol.*, 4(Special Issue No.1), 156–173, 1984.

Holm-Hansen, O., Mitchell, B.G., Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait, *Deep-Sea Res.*, 38, 961–980, 1991.

Holm-Hansen, O., El-Sayed, S.Z., Franceschini, G.A., Cuhel, G.A., Cuhel, R.L., Primary production and the factors controlling phytoplankton growth in the Southern Ocean, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 11–73.

Holm-Hansen, O., Azam, F., Cambell, L., Carlucci, A.F., Karl, D.M., Microbial life beneath the Ross Ice Shelf, *Antarc. J. U.S.*, 13, 129–130, 1978.

Holm-Hansen, O., Neori, A., Koike, I., Phytoplankton distribution, biomass, and activity in the southwest Ross Sea, *Antarc. J. U.S.*, 17, 150–152, 1982.

Holm-Hansen, O., Mitchell, B.G., Hewes, C.P., Karl, D.M., Phytoplankton blooms in the vicinity of Palmer Station, *Polar Biol.*, 10, 49–57, 1989.

Holm-Hansen, O., Helbling, E.W., Lubin, D., Ultraviolet radiation in Antarctica: Inhibition of primary production, *Photochem. Photobiol.*, 58, 567–570, 1993.

Holm-Hansen, O., Villefane, V.E., De Vries, E.W., Effects of solar ultraviolet radiation on primary production in Antarctic waters, in *Antarctic Communities: Species, Structure and Survival*, Baggatalia, B., Valencia, J., Walton, D.W.H., Eds., Cambridge University Press, Cambridge,UK, 1997, 375–380.

Holt, S., Marine fisheries, in *Oceans Yearbook*, Vol. 1, Beregse, E.M., Ginsberg, N., Eds., Chicago University Press, Chicago, IL, 1978, 38–83.

Honjo, S., Roman, M.R., Marine copepod fecal pellets: Production, preservation and sedimentation, *J. Mar. Res.*, 36, 45–57, 1978.

Hooker, J.D., Diatomaceae, in *The Botany of the Antarctic Voyage of H.M. Discovery Ships Erebus and Terror, Years 1839–1843*, Vol. LVI, London, 1847, 503–521.

Hopkins, T.L., Zooplankton standing crop in the Pacific sector of the Antarctic, in *Biology of the Antarctic Sea VI,* Antarctic Research Series, Vol. 17, Llano, G.A., Wallen, I.E., Eds., American Geophysical Union, Washington, DC, 1971, 347–362.

Hopkins, T.L., The zooplankton community of Croker Passage, Antarctic Peninsula, *Polar Biol.*, 4, 161–170, 1985a.

Hopkins, T.L., Food webs of an Antarctic midwater ecosystem, *Mar. Biol.*, 89, 197–212, 1985b.

Hopkins, T.L., Midwater food web in McMurdo Sound, Ross Sea, Antarctica, *Mar. Biol.*, 96, 93–106, 1987.

Hopkins, T.L., Lancraft, T.M., The composition and standing stock of mesopelagic micronekton at 27° N 86° W in the eastern Gulf of Mexico, *Contrib. Mar. Sci., Univ. Tex.*, 27, 143–158, 1984.

Hopkins, T.L., Torres, J.J., Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea, *Deep-Sea Res.*, 36, 543–561, 1989.

Hopkins, T.L., Ainley, D.G., Torres, J.J., Lancraft, L.M., Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell Confluence region during spring (1983), *Polar Biol.*, 13, 389–397, 1983.

Hopkins, T.L., Lancraft, T.M., Torres, J.J., Donnelly, J., Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1978), *Deep-Sea Res.*, 40, 81–105, 1993.

Hoppe, H.G., Blue-green algae agglomeration in surface waters: A microbiotope of high bacterial activity, *Kiel. Meeresforsch.*, 5, 291–303, 1981.

Hoppe, H.G., Attachment of bacteria -advantage or disadvantage for survival in the aquatic environment, in *Microbial Adhesion and Aggregation*, Marshall, K.C., Ed., Springer, Berlin, 1984, 383–401.

Horne, A.J., Fogg, E.G., Eagle, D.J., Studies *in situ* of primary production of an area of inshore Antarctic sea, *J. Mar. Biol. Assoc. U.K.*, 49, 393–405, 1969.

Horner, R.A., Taxonomy of sea ice microalgae, in *Sea Ice Biota*, Horner, R.A., Ed., CRC Press, Boca Raton, FL, 1985, 147–157.

Horner, R.A., Ecology of sea ice microalgae, in *Sea Ice Biota*, Horner, R.A., Ed., CRC Press, Boca Raton, FL, 1986, 83–103.

Horner, R.A., Ice-associated diatoms, in *Polar Marine Diatoms*, Medlin, L.K., Priddle, J., Eds., British Antarctic Survey, Natural Environment Research, Cambridge, UK, 1990, 9–14.

Horner, R.A., Schrader, G.C., Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea, *Arctic*, 35, 485–503, 1982.

Horner, R.A., Syversten, E.E., Thomas, D.P., Lange, C., Proposed terminology and reporting units for sea ice algal assemblages, *Polar Biol.*, 8, 249–253, 1988.

Horner, R.A., Ackley, S.F., Dieckmann, G.S., Gulliksen, B., Hoshiai, T., Legendre, L., Melnikov, I.A., Reeburch, W.S., Spindler, M., Sullivan, C.W., Ecology of sea ice biota: Habitat, terminology and methodology, *Polar Biol.*, 12, 417–427, 1992.

Horwood, J.W., On the joint exploitation of krill and whales, in *Mammals in the Seas, Volume III*, FAO Fisheries Series, Rome, 1981, 355–383.

Hosaka, N., Nemoto, T., Size structure of phytoplankton carbon and primary production in the Southern Ocean south of Australia during the summer of 1983–1984, *Mem. Nat. Inst. Polar Res. Special Issue*, 40, 15–24, 1986.

Hoshiai, T., Seasonal variation of chlorophyll *a* and hydrological conditions under sea ice at Syowa Station, Antarctica, *Antarc. Rec.*, 35, 52–67, 1969. In Japanese with English abstract.

Hoshiai, T., Diatom distribution in sea ice near McMurdo Station and Syowa Station, *Antarc. J. U.S.*, 7, 85–87, 1972.

Hoshiai, T., Seasonal change of ice communities in the sea ice near Syowa Station, Antarctica, in *Polar Oceans*, Dunbar, M.J., Ed., Arctic Institute of North America, Calgary, 1977, 307–317.

Hoshiai, T., Feeding behaviour of *Notothenia rossii marmorata* Fischer at South Georgia, *Antarc. Rec.*, 66, 25–36, 1979.

Hoshiai, T., Proliferation of ice algae in the Syowa Station area, Antarctica, *Mem. Nat. Inst. Polar Res.*, 34, 1–12, 1981a.

Hoshiai, T., Solar radiations and stability of the undersurface of sea ice governing ice algal proliferation, *Antarc. Rec.*, 73, 23–29, 1981b.

Hoshiai, T., Autumn proliferation of ice algae in Antarctic sea ice, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 89–92.

Hoshiai, T., Kato, M., Ecological notes on the diatom community of the sea ice in Antarctica, *Bull. Mar. Biol. Station of Asamushi, Tohoku University*, 10, 221–230, 1961.

Hoshiai, T., Tanimura, A., Copepods in the stomach of a Nototheniid fish, *Trematomous borchgrevinki*, at Syowa Station, Antarctica, *Mem. Nat. Inst. Polar Res.*, 34, 44–88, 1981.

Hoshiai, T., Tanimura, A., Sea ice meiofauna at Syowa Station, *Mem. Nat. Inst. Polar Res. Special Issue*, 44, 118–124, 1986.

Hoshiai, T., Tanimura, A., Fukuchi, M., Watanabe, K., Feeding by the nototheniid fish *Pagothenia borchgrevinki* on the ice-associated copepod *Paralabidocera antarctica*, *Proc. NIPR Symp. Polar Biol.*, 2, 61–64, 1987a.

Hoshiai, T., Tanimura, A., Watanabe, K., Ice algae as food of an ice-associated copepod, *Paralabidocera antarctica* (I. C. Thompson), *Proc. NIPR Symp. Polar Biol.*, 1, 105–111, 1987b.

Hoshiai, T., Tanimura, A., Fukuchi, M., Watanabe, K., Feeding by the nototheniid fish *Pagothenia borchgrevinki* on the ice-associated copepod *Paralabidocera antarctica*, in *Proceedings of the NIPR Symposium on Polar Biology*, Vol. 2, 1989, 61–64.

Hosie, G.W., Distribution and abundance of euphausiid larvae in the the Prydz Bay region, Antarctica, *Antarc. Sci.*, 3, 167–180, 1991.

Hosie, G.W., The macrozooplankton communities in the Prydz Bay region, Antarctica, in *Southern Ocean Ecology: A BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, UK, 1994, 93–123.

Hosie, G.W., Cochran, T.G., Mesoscale distribution patterns of macrozooplankton communities in Prydz Bay, Antarctica—January to February 1991, *Mar. Ecol. Prog. Ser.*, 196, 21–39, 1994.

Hosie, G.W., Stolp, M., Krill and zooplankton in the western Prydz Bay region, September–November 1985, *Proc. NIPR Symp. Polar Biol.*, 2, 33–45, 1989.

Hosie, G.W., Cochran, T.G., Pauly, T., Beaumont, K.L., Wright, S.W., Kitchener, J.A., Zooplankton community structure of Prydz Bay, Antarctica, January–February 1993, *Proc. NIPR Symp. Polar Biol.*, 10, 90–133, 1997.

Houghton, J.T., Jenkins, G.J., Ephrauyms, J.J., *Climate Change: The IPPC Scientific Assessment*, Cambridge University Press, Cambridge, 1990a, 1–364.

Houghton, J.T., Jenkins, G.-J., Ephraum, J.J., *Climate Change. The IPPC Scientific Assessment*, World Meterological Organization/-United Nations Environment Programme, Cambridge University Press, Cambridge, 1990b, 1–365.

Houghton, J.T., Callander, B.A., Varney, S.K. Climate Change 1992: The Supplementary Report to the IPCC Scientific Assessment, Cambridge University Press, Cambridge, NY, 1992.

Houghton, J.T., Callander, B.A., Varney, S.K., *Climate Change. Supplementary Report to the IPPC Scientific Assessment*, World Meterological Organization/United Nations Environment Programme, Cambridge University Press, Cambridge, 2002, 1–200, *Ser.*, 107, 23–40, 1994.

Houghton, J.T., Filho, L.G.M., Callander, B.A., Harris, N., Kattenburg, A., Maskell, K., Climate Change 1995: The Science of Climate Change, Cambridge University Press, Cambridge, NY, 1996.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A., *Climate change 2001: The Scientific Basis*, Contribution of Working Group 1 to the third assessment report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, NY, 2001.

Houghton, J.T., Filho, L.G.M., Bruce, J.P., Lee, H., Callander, B.A., Haites, E.F., Climatic Change 1994: Radioactive Forcing of Climate Change and an Evaluation of the IPCC 1992 Emission Scenario, Cambridge University Press, Cambridge, NY.

Howington, J.P., McFeters, G.A., Barry, J.D., Smith, J.J., Distribution of the McMurdo Station sewage plume, *Mar. Pollut. Bull.*, 25, 324–327, 1992.

Howington, J.P., McPeters, G.A., Smith, J.J., The effect of low temperature on BOD in Antarctic seawater, *Water Res.*, 28, 2585–2587, 1994.

Hoyer, V., Occurrence, induction and physiological importance of UV-absorbing substances in polar microalgae, *Ber. Polarforsch.*, 440, 112–155, 2003.

Hoyer, V., Karsten, U., Sewell, T., Wiencke, C., Photoprotective substances in Antarctic macroalgae and their variation with respect to depth distribution, different tissues and development stages, *Mar. Ecol. Prog. Ser.*, 211, 117–120, 2001.

Hoyer, K., Karsten, U., Wiencke, C., Induction of sunscreen compounds in Antarctic microalgae by different radiation conditions, *Mar. Biol.*, 141, 619–627, 2002.

Hoyer, K., Karsten, U., Wiencke, C., Inventory of UV-absorbing microsporine-like amino acids in polar macroalgae and factors controlling their content, in *Antarctic Biology in a Global Context*, Huiskes, H.H., Gieskes, W., Eds., Backhuys Publishers, Leiden, The Netherlands, 2003, 56.

Hoyer, K., Schafer, S., Karsten, U., Wiencke, C., Interactive effects of temperature and radiation on polar macroalgae, *Ber. Polarforsch.*, 440, 69–89, 2003.

Hubold, G., The early life-history of the high-Antarctic silverfish, *Pleurogramma antarcticum*, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 445–451.

Hubold, G., Stomach contents of the Antarctic silverfish *Pleurogramma antarcticum* from the southern and eastern Weddell Sea, *Polar Biol.*, 5(1), 43–48, 1985.

Hubold, K.G., Seasonal pattern of ichthyoplankton in the southern Weddell Sea, in *Ecological Change and Conservation*, Springer, Berlin, 149 pp, 1990.

Hubold, G., Ecology of notothenioid fish in the Weddell Sea, in *Biology of Antarctic Fish*, Di Prisco, G., Maresco, B., Tota, B., Eds., Springer, Berlin, 1991, 3–22.

Hubold, G., Ekau, W., Midwater fish fauna of the Weddell Sea, Antarctica, in *Proceedings of the 5th European Ichthyological Congress*, Kullander, S.O., Fernholm, B., Eds., Swedish Museum of Natural History, Stockholm, 1987, 391–396.

Hubold, K.G., Tomo, A.P., Age and growth of Antarctic silverfish *Pleurogramma antarcticum* Boulenger, 1902, from the southern Weddell Sea and Antarctic Peninsula, *Polar Biol.*, 9, 205–212, 1989.

Hubold, G., Hempel, I., Meyer, M., Zooplankton communities in the southern Weddell Sea, *Meeresforschung*, 31, 185–192, 1985.

Hudson, R., Adult survival estimates for two Antarctic petrels, *Br. Antarc. Surv. Bull.*, 8, 63–73, 1966.

Huey, L.M., Capture of an elephant seal off San Diego, California, with notes on stomach contents, *J. Mammal.*, 11, 229–231, 1990.

Hughes, L., Biological consequences of global warming: Is the signal already apparent?, *Trends Ecol. Evol.*, 15(2), 41–81, 2000.

Hulley, P.A., Myctophidae (lanternfish), in *Fishes in the Southern Ocean*, Gon, O., Heenstra, P.C., Eds., Grahamstown Institute of Ichthyology, Grahamstown, South Africa, 1990, 146.

Hulley, P.A., Camus, P., Duhamel, G., Ichthyological results of cruise MD-42/SIBEX II. Part 1. Fishes from RMT-8stations with additional records from lanternfishes (Myctophidae: Osteichthyes) from Indian and Atlantic Seas of the Southern Ocean, *Cybium*, 13, 83–99, 1991.

Hunt, F., Observations on the seals of Elephant Island, South Shetland Islands, 1970–71, *Br. Antarc. Surv. Bull.*, 36, 99–104, 1973.

Hunt, G.L., Heinemann, D., Veit, R.R., Heywood, R.B., Everson, I., The distribution, abundance and community structure of marine birds in Southern Drake Passage and Bransfield Strait, Antarctica, *Cont. Shelf Res.*, 16, 243–257, 1990.

Hunt, B.P., Pakhomov, E.A., McQuaid, C.P., Short-term variation and long-term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago, *Mar. Biol.*, 138, 369–381, 2001.

Hunter, S., The food and feeding ecology of the giant petrels *Macronectes halli* and *M. giganteus* at South Georgia, *Aust. J. Zool.*, 200, 521–538, 1983.

Hunter, S., Breeding biology and population dynamics of giant petrels *Macronectes halli* and *M. giganteus* at South Georgia, *Aust. J. Zool.*, 203, 441–460, 1985.

Huntley, M.E., Brinton, E., Mesoscale variation in growth and early development of *Euphausia superba* Dana in the western Bransfield Strait region, *Deep-Sea Res.*, 38, 1213–1240, 1991.

Huntley, M.E., Escritor, F., Dynamics of *Calanoides acutus* (Copepoda: Calanoida) in Antarctic coastal waters, *Deep-Sea Res.*, 38, 1145–1167, 1991.

Huntley, M., Tandy, K.S., Eilertsen, H.C., On the trophic fate of *Phaeocystis pouchetii*, II: Grazing rates of *Calanus hyperboreus* feeding on diatoms and different size categories of *P. pouchetii*, *J. Exp. Mar. Biol. Ecol.*, 110, 197–212, 1987.

Huntley, M.E., Sykes, P.F., Marin, V., Biometry and trophodynamics of *Salpa thompsoni* (Tunicata: Thaliacea) near the Antarctic Peninsula in austral summer 1983–1984, *Polar Biol.*, 10, 59–70, 1989.

Huntley, M.E., Karl, D.M., Miller, P.P., Holm-Hansen, O., Research in Antarctic Coastal Ecosystem Roles (RACER) on interdisciplinary field experiments, *Deep-Sea Res.*, 58, 911–941, 1991.

Huntley, M.E., Nordhausen, W., Lopez, M.D.G., Elemental composition, metabolic activity and growth of Antarctic krill (*Euphausia superba*) during winter, *Mar. Ecol. Prog. Ser.*, 107, 23–40, 1994.

Hureau, J.-C., Biologie comparée de quelques poissons antarctiques (Nototheniidae), *Bull. Inst. Oceanogr. Fish.*, 68, 1–44, 1966.

Hureau, J.-C., La faune ichthyologique du secteur indien de l'ocean antarctique et estimation du stock de poissons autour de îles Kerguelen, *Mem. Mus. Nat. Hist. Natur.*, 43, 235–247, 1979.

Hureau, J.-C., The significance of fish in the marine Antarctic ecosystem, *Polar Biol.*, 14, 307–315, 1994.

Hureau, J.-C., Petit, D., Fine, I.M., Marneux, M., New cytological, biochemical and physiological data on the colourless blood of the Channichthyidae (Pisces, Teleostei, Perciformes), in *Adaptations within Antarctic Ecosystems*, Llano, G., Ed., Gulf Publishing Company, Houston, TX, 1977, 459–477.

Hustedt, F., Diatomeen aus der Antarktis und dem Südatlanktik Deutsche Antarktische Expedition 1938–39, *Wissenschaft Ergebnisse*, 2, 103–191, 1958.

Hutchins, P.A., Bruland, K.W., Iron-limited diatom growth and Si–N uptake ratios in a coastal upwelling regime, *Nature (Lond.)*, 393, 561–564, 1998.

Hyland, J., Laur, D., Jones, J., Shrake, J., Cadian, D., Harris, L., Effects of an oil spill on the soft-bottom macrofauna of Arthur Harbour, Antarctica, compared with long-term natural change, *Antarct. Sci.*, 6, 37–44, 1994.

Ichihara, T., The pigmy blue whale, *Balaenoptera musculus brevicauda*, a new subspecies from the Antarctic, in *Whales, Dolphins and Porpoises*, Norris, K.S., Ed., University of California Press, Berkeley, 1966, 79–111.

Ichihara, T., Criteria for determining age of the fin whale with reference to ear plug and baleen plate, *Sci. Rep. Whales Res. Inst. Tokyo*, 20, 17–82, 1966.

Ichii, T., Kato, H., Food and daily food consumption of southern minke whales in the Antarctic, *Polar Biol.*, 11, 479–487, 1991.

Idyll, P., The anchovy crisis, *Sci. Am.*, 288, 22–29, 1973.

Iganake, D., Matsura, E., Kunta, Y., Stock and quantitative distribution of the Antarctic krill (*Euphausia superba* Dana) in the Antarctic Ocean south of Australia, January and February 1984, *Trans. J. Tokyo Univ. Fish.*, 6, 139–147, 1984.

Iizuka, H., Tanabe, I., Meguro, H., Microorganisms in plankton-ice of the Antarctic Ocean, *J. Gen. Appl. Microbiol.*, 12, 101–102, 1966.

Ikeda, T., Relationship between respiration rate and body size in marine plankton animals as a function of the temperature of the habitat, *Bull. Hokkaido Univ. Fac. Fish.*, 21, 91–112, 1970.

Ikeda, T., Development of the Antarctic krill (*Euphausia superba*) observed in the laboratory, *J. Exp. Mar. Biol. Ecol.*, 75, 107–117, 1984.

Ikeda, T., Sequences in metabolic rates and elemental composition (C, N, P) during the development of *Euphausia superba* Dana and estimated food requirements during its life span, *J. Crust. Biol. Spec. Issues*, 4, 273–284, 1984.

Ikeda, T., Life history of Antarctic krill *Euphausia superba*: a new look from an experimental approach, *Bull. Mar. Sci.*, 37, 599–608, 1985.

Ikeda, T., Bruce, B., Metabolic activity and elemental composition of krill and other zooplankton from Prydz Bay, Antarctica during early summer (November–December), *Mar. Biol.*, 92, 545–555, 1986.

Ikeda, T., Dixon, P., Observations on the moulting in Antarctic krill (*Euphausia superba* Dana), *Aust. J. Mar. Freshwat. Res.*, 33, 71–76, 1982.

Ikeda, T., Dixon, P., Body shrinkage as a possible overwintering mechanism of the Antarctic krill *Euphausia superba* Dana, *J. Exp. Mar. Biol. Ecol.*, 62, 143–151, 1982.

Ikeda, T., Kirkwood, R., Metabolism and body composition of two Euphausiids (*Euphausia superba* and *E. crystallorophias*) collected from under the pack ice off Enderby Island, *Mar. Biol.*, 101, 339–343, 1989.

Ikeda, T., Dixon, P., Kirkwood, J., Laboratory observations of moulting, growth and maturation in Antarctic krill (*Euphausia superba* Dana), *Polar Biol.*, 4, 1–8, 1985.

Iken, K., Feeding ecology of the Antarctic gastropod *Laevilacunaria antarctica* Martens, *J. Exp. Mar. Biol. Ecol.*, 236(1), 133–148, 1999.

Iken, K., Quartino, M.L., Barrera-Oro, E., Palermo, J., Wiencke, C., Brey, T., Trophic relations between macroalgae and herbivores, in *The Potter Cove Coastal Ecosystem Synopsis 1998*, 1998, 258–262.

Imber, M.J., Breeding biology of the grey-faced petrel, *Pterodroma macroptera gouldi*, *Ibis*, 118, 51–64, 1976.

Ingham, S.E., Branding elephant seals for life history studies, *Polar Rec.*, 13, 447–449, 1967.

Inglis, G., The colonization and degradation of stranded *Macrocystis pyrifera* (L.) C. Ag. by the macrofauna of a New Zealand sandy beach, *J. Exp. Mar. Biol. Ecol.*, 125, 203–217, 1989.

Innamotati, M., Mori, G., Mazzi, L., Lazzari, L., Naccio, L., Phytoplankton biomass related to environmental factors, in *Ross Sea Ecology*, Faranda, F.M., Guglielmo, L., Ianora, A., Eds., Springer, New York, 2000, 217–245.

International Whaling Commission (IWC), *International Whaling Committee Reports*, 28 pp, 1978.

International Whaling Commission (IWC), Report of a special meeting on Southern Hemisphere minke whales, Seattle,WA, May 1978, *International Whaling Committee Reports*, 29 pp, 1979.

International Whaling Commission (IWC), Report of the Scientific Committee, *International Whaling Committee Reports*, 40 pp, 1990.

IPPC, *Climate Change: The IPPC Scientific Assessment*, Intergovernment Panel on Climate Change, World Meterelogical Organization/United Nations Environment Programme, Cambridge University Press, Cambridge, 1990.

IPPC, *IPPC First Assessment Overview and Policy Maker Summaries*, Intergovernmental Panel on Climate Change, Geneva, 168 pp. 1992.

IPPC, *Second IPPC Assessment—Climate Change 1996*, Intergovernmental Panel on Climate Change, Geneva, 64 pp, 1995a.

IPPC, *Climate Change 1995: The Science of Climate Change, Contribution of the Working Group I to the Second Assessment of the Intergovernmental Panel on Climate Change*, Haughton, J.T., Ed., Cambridge University Press, Cambridge, UK, 1995b.

Irwin, B.D., Primary production of ice algae on a seasonally-ice-covered continental shelf, *Polar Biol.*, 10, 247–254, 1990.

Iturriaga, R., Mitchell, B.G., Chromococcoid cyanobacteria: a significant component in the food web dynamics of the open ocean, *Mar. Ecol. Prog. Ser.*, 28, 291–297, 1986.

Ivanov, A.I., Characteristics of the phytoplankton in Antarctic waters at the whaling grounds of the flotilla Slava in 1957–58, *Soviet Antarct. Expedition Info. Bull.*, 1, 314–321, 1964.

Ivanov, B.G., On the biology of the Antarctic krill *Euphausia superba*, *Mar. Biol.*, 7, 340–351, 1970.

Iwanami, K., Futatsumachi, S., Taniguchi, A., Short-term variation of chemical property of water and microplankton community in the coastal area near Syowa Station, Antarctica, in midsummer of 1984, 1. Chemical property including chlorophyll *a*, *Mem. Nat. Inst. Polar Res. Special Issue*, 40, 1–14, 1986.

Jacka, J.T., Budd, W.P., Detection of temperature and sea ice extent changes in the Antarctic and Southern Ocean, *Ann. Glaciol.*, 27, 553–559, 1998.

Jackson, L.T., Linick, T.W., Michel, R.L., Williams, P.M., Tritium and carbon-14 distributions in McMurdo Sound, 1977, *Antarct. J. U.S.*, 13, 71–73, 1978.

Jacob, A., Kirst, G., Wiencke, C., Lehmann, H., Physiological responses of the Antarctic green alga, *Prasiola crispa* spp. *antarctica*, to salinity stress, *J. Plant Physiol.*, 139, 57–62, 1991.

Jacobs, S.S., Ross ice shelf project: physical oceanography, *Antarct. J. U.S.*, 12(4), 43–46, 1977.

Jacobs, S.S., On the nature and significance of the Antarctic slope front, *Mar. Chem.*, 35(1–4), 9–24, 1991.

Jacobs, S.S., Comiso, K., Sea and oceanic processes on the Ross Sea continental shelf, *J. Geophys. Res.*, 94, 18195–18211, 1989.

Jacobs, S.S., Giulivi, C.F., Thermohaline data and ocean circulation on the Ross Sea continental shelf, in *Oceanography of the Ross Sea, Antarctica*, Spezie, G., Manzella, G.M.R., Eds., Springer, Milan, 1999, 3–16.

Jacobs, S.S., Amos, A.F., Buckhausen, P.M., Ross Sea oceanography and Antarctic bottom water formation, *Deep-Sea Res.*, 17, 935–962, 1970.

Jacobs, S.S., Bruckhausen, P.M., Ardai, J.L., Physical oceanography of the Ross Sea, *Antarct. J. U.S.*, 13, 83–85, 1978.

Jacobs, S.S., Gordon, A.L., Ardai, J.L., Circulation and melting beneath the Ross Ice Shelf, *Science*, 203, 439–443, 1979.

Jacobs, S.S., Fairbanks, R., Horibe, Y., Origin and evolution of water masses near the Antarctic continental margin: Evidence from $H^{18}O/H_2^{16}O$ ratios in seawater, in Oceanology of the Antarctic Shelf, *Antarct. Res. Ser.*, Vol. 43, 1985, 59–85.

Jacobsen, D.J., Anderson, D.M., Thecate heterotrophic dinoflagellates: Feeding behaviour and mechanisms, *J. Phycol.*, 22, 249–258, 1986.

Jacobsen, T.R., Azam, F., Role of bacteria in copepod faecal pellet decomposition and colonization, growth rates and mineralization, *Bull. Mar. Sci.*, 35, 495–502, 1984.

Jacques, G., Some ecophysiological aspects of the Antarctic phytoplankton, *Polar Biol.*, 2, 27–33, 1983.

Jacques, G., Primary production in the open Antarctic ocean during the austral summer: A review, *Vie et Milieu*, 39, 1–17, 1989.

Jacques, G., Hoepffner, N., Sinking rates of subantarctic phytoplankton, *Comptes rendus de l'Académie des Sciences Paris 299 (Serie III)*, 14, 581–585, 1984.

Jacques, G., Minas, M., Production primaire dans le secteur indien de l'Océan Antarctique en fin d'été, *Oceanol. Acta*, 4, 33–41, 1981.

Jacques, G., Panouse, M., Biomass and composition of size-fractionated phytoplankton in the Weddell Sea Confluence area, *Polar Biol.*, 11, 315–325, 1991.

Jacques, G., Treguer, P., *Les Ecosystems Pelagiques Marins*, Collections Ecologiques 19, Masson, Paris, 1986.

Jakubowski, M., Byczkowski-Smyk, W., Respiratory surfaces of white-blooded fish *Chaenichthys rugosus* Regan (Perciformes), *Pol. Arch. Hydrobiol.*, 17, 273–281, 1970.

Jaragov, A., On the physico-geographical conditions of the krill habitat, *Trudy Vsesoiuznogo Naucho-issledovatel'skii Instituta Morskogo Rybnogo Khoziaistva i Okeanographii*, 61, 85–102, 1969. In Russian.

Jarman, S., Elliot, N., Nicol, S., McMinn, A., Newman, S., The base composition of the krill genome: Its potential susceptibility to damage by UV-B, *Antarct. Sci.*, 11, 23–26, 1999.

Jazdzewski, K., Porebski, J., Rakusa-Suszczewski, S., Witek, Z., Wolnomeijski, N., Biological studies on krill near South Shetland Islands, Scotia Sea and South Georgia in the summer 1978, *Pol. Arch. Hydrobiol.*, 25, 607–631, 1978.

Jazdzewski, K., Kittel, W., Lotaki, K., Krill monitoring in Admiralty bay (King George Island, South Shetland Islands) in summer 1979/80, *Polar Biol.*, 1, 117–125, 1982.

Jazdzewski, K., Jurasz, W., Kittel, W., Presler, E., Presler, P., Sicinski, J., Abundance and biomass estimates of the benthic fauna in Admiralty Bay, King George Island, South Shetland Islands, *Polar Biol.*, 6, 5–16, 1986.

Jenkins, D.G., Initiation of the protocircum-Antarctic current, *Nature (Lond.)*, 252, 371–373, 1974.

Jennings, J.C., Jr, Gordon, L.I., Nelson, D.M., Nutrient depletion indicates high primary productivity in the Weddell Sea, *Nature (Lond.)*, 309, 51–54, 1984.

Jerome, T.H., Bukata, R.P., Tracking the propogation of solar ultraviolet radiation: dispersal of ultraviolet photons in inland waters, *J. Great Lakes Res.*, 24, 666–690, 1998.

Jewell, P.A., Holt, S., Eds., *Problems of Management of Locally-Abundant Wild Animals*, Academic Press, London, 1982.

Jitts, H.R., Morel, A., Saijo, Y., The relationship of oceanic primary production to available photosynthetic radiation, *Aust. J. Mar. Freshwat. Res.*, 27, 441–454, 1976.

Jobling, M., Towards an explanation of specific dynamic action, *J. Fish Biol.*, 23, 549–555, 1983.

Johannes, R.E., Influence of marine protozoa on nutrient regeneration, *Limnol. Oceanogr.*, 10, 433–442, 1965.

Johanssen, O.O., Johanssen, J.A., Morison, J., Farrelly, B.A., Svendsen, E.A.S., Oceanographic conditions in the marginal ice zone north of Svalbard in early fall 1979, with an emphasis on mesoscale processes, *J. Geophys. Res.*, 88, 2755–2769, 1983.

John, D.D., The southern species of the genus *Euphausia*, *Discovery Rep.*, 14, 195–323, 1936.

John, D.D., Crinoidea, *Discovery Rep.*, 18, 121–122, 1938.

John, D.D., Crinoidea, *Br., Aust. N.Z. Antarct. Res. Expedition 1901–1904, Rep. B*, 4, 189–212, 1939.

John, D.M., Tinley, I., Lawson, G.W., Pugh, P.J.A., Distribution of seaweed flora in the Southern Ocean, *Bot. Mar.*, 37, 235–239, 1994.

Johnson, T.O., Smith, W.O., Jr.,, Sinking rates of phytoplankton assemblages in the Weddell Sea marginal ice zone, *Mar. Ecol. Prog. Ser.*, 33, 131–137, 1986.

Johnston, I.A., Walesby, N.J., Molecular mechanisms of temperature adaptation in fish myofibrillar adenosine triphosphate, *J. Comp. Physiol.*, 119, 195–206, 1977.

Johnston, I.A., Johnson, T.P., Battram, J.C., Low temperature limit burst swimming performance in Antarctic fish, in *Biology of Antarctic Fishes*, di Prisco, G., Maresca, B., Tolton, B., Eds., Springer, Heidelberg, 1991, 179–190.

Johnstone, G.W., Comparative feeding ecology of the giant petrels *Macronectes giganteus* (Gmelin) and *M. halli* (Mathews), in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 647–668.

Johnstone, G.W., Agonistic behaviour of the giant petrels *Macronectes giganteus* and *M. halli* feeding at seal carcasses, *Emu*, 79, 129–132, 1979.

Joint, I.R., Morris, R.J., The role of bacteria in the turnover of organic matter in the sea, *Oceanogr. Mar. Biol. Annu. Rev.*, 20, 65–118, 1982.

Jones, P.D., Antarctic temperatures over the present century—a study of the early expedition record, *J. Clim.*, 3, 1193–1203, 1990.

Jones, E.P.J., Nelson, D.M., Treguer, P., Chemical oceanography, in *Polar Oceanography*, Smith, W.O., Jr., Ed., Academic Press, San Diego, CA, 1990, 407–476.

Jonker, F.C., Bester, M.V., Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island, *Antarct. Sci.*, 10, 21–30, 1998.

Joris, C.R., Spring distributions and ecological role of seabirds and marine mammals in the Weddell Sea, Antarctica, *Polar Biol.*, 11, 415–424, 1991.

Jorgensen, B.B., Processes at the sediment-water interface, in *SCOPE 21, The Major Biogeochemical Cycles and Their Interactions*, Bolin, B., Cook, R., Eds., Wiley, Chichester, 1983, 477–515.

Jouventain, P., Mortality parameters in emperor penguins, in *The Biology of Penguins*, Stonehouse, B., Ed., MacMillan, London, 1975, 435–440.

Jouventein, P., Mougin, J.-L., Les strategies adaptatives des oiseau de mer, *Terre et la Vie, Revue d'Ecologie*, 35, 217–273, 1981.

Jouventin, P., Weimerskirch, H., Long-term change in seabird and seal populations in the Southern Ocean, in *Antarctic Ecosystems. Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin, 1990, 208–213.

Jouventin, P., Weimerskirch, H., Changes in the population size and demography of southern seabirds: the management implications, in *Bird Population Studies: Their Reference to Conservation and Management*, Perrina, C.M., Lebreton, J.D., Hirons, C.J.M., Eds., Oxford University Press, Oxford, 1991, 297–316.

Jouventin, P., Stahl, J.C., Weimerskirch, H., Mougin, J.L., The seabirds of the French Subantarctic islands and Adélie land: their status and conservation, in *The Status and Conservation of the World's Seabirds*, International Council for Bird Preservation Technical Publication, Vol. 2, 609–625 pp, 1984.

Joyce, T.M., Patterson, S.L., Cyclonic ring formation at the Antarctic Polar Front in the Drake Passage, *Nature (Lond.)*, 256, 131–133, 1977.

Joyce, T.M., Zenk, W., Toole, J.M., The anatomy of the Antarctic Front in the Drake Passage, *J. Geophys. Res.*, 83, 6093–6113, 1978.

Joyner, T., Mahnken, C.V.W., Clark, A.R., Salmon future harvest from the Antarctic Ocean, *Mar. Fish. Rev.*, 35, 20–28, 1974.

Kalinowski, J., Vertical migration of krill in the region of South Georgia, February–March 1976, *Pol. Arch. Hydrobiol.*, 25, 573–583, 1978.

Kalinowski, J., Witek, Z., Forms of Antarctic krill aggregations, *ICES Biological and Oceanographic Committee C.M., 1982/L 60*, 1982.

Kalinowski, J., Witek, Z., Elementy biologii formy grupowego wgstepowania i Zasoby Antarktycznego kryla *Euphausia superba* Dana (some aspects of biology, forms of aggregation and stocks of Antarctic krill, *Euphausia superba* Dana), Joint Ph.D. thesis, Sea Fisheries Institute, Godynia, Poland, 1983, In Polish.

Kalinowski, J., Witek, Z., Scheme for classifying aggregations of Antarctic krill. *BIOMASS Handbook No. 27*, 1985.

Kampa, E.M., Boden, B.P., Submarine illumination and twilight movements of a sonic scattering layer, *Nature (Lond.)*, 174, 869–873, 1954.

Kanda, K., Takagi, K., Seki, Y., Movement of the larger swarms of Antarctic krill, *Euphausia superba*, populations off Enderby Land during the 1976–77 season, *J. Tokyo Univ. Fish.*, 68, 24–42, 1982.

Kane, J.E., The distribution of *Parathemisto gaudichaudii* (Guer) with observations on its life history on the 0° to 20° E Sector of the Southern Ocean, *Discovery Rep.*, 34, 163–198, 1966.

Kang, S.-H., Fryxell, G.A., Phytoplankton in the Weddell Sea, Antarctica: Composition, abundance and distribution in water-column assemblages of the marginal ice edge zone during austral summer, *Mar. Biol.*, 116, 335–348, 1993.

Kang, S-H., Kang, J.S., Seasonal variation of environmental factors and nearshore microalgae in Marion Cove, King George Island, Antarctica, during 1996: Preliminary study for long-term monitoring, in *Environmental Monitoring on Human Impacts at King Sejong Station*, KORDI, 1997, 57–112.

Kang, S.-H., Lee, S.-H., Antarctic phytoplankton assemblage in the western Bransfield Strait region, February 1992: Composition, biomass and mesoscale distribution, *Mar. Ecol. Prog. Ser.*, 129, 253–267, 1995.

Kang, J.S., Kang, S.-H., Lee, J.H., Lee, S.H., Seasonal variation of microalgal assemblages at a fixed station on King George Island, Antarctica, 1996, *Mar. Ecol. Prog. Ser.*, 229, 19–32, 2002.

Kappen, L., Redon, J., Microclimate influencing the lichen vegetation on different aspects of a coastal rock in maritime Antarctica, *Serie Científica Instituto Antártico Chileno*, 31, 53–65, 1984.

Karantz, D., McEuen, F.S., Land, M.C., Dulop, A., Survey of mycosporine-like amino acid compounds in Antarctic marine organisms: potential protection from ultraviolet exposure, *Mar. Biol.*, 108, 157–166, 1991.

Karentz, D., Report on studies related to the ecological implications of ozone depletion on the Antarctic environment, *Antarct. J. U.S.*, 24, 175, 1989.

Karentz, D., Ecological considerations of Antarctic ozone depletion, *Antarct. Sci.*, 3, 3–11, 1991.

Karentz, D., Ultraviolet tolerance mechanisms in Antarctic marine organisms, in *Radiation in Antarctica: Measurements and Biological Effects*, Weller, C.S., Penhale, P.A., Eds., American Geophysical Union, Washington, DC, 1994, 93–110.

Karentz, D., Environmental change in Antarctica: Ecological impacts and responses, in *Antarctic Biology in a Global Context*, Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backhuys Publishers, Leiden, The Netherlands, 2003, 45–55.

Karentz, D., Lutz, L.H., Evaluation of biologically-harmful ultraviolet radiation in Antarctica with a biological dosimeter designed for aquatic environments, *Limnol. Oceanogr.*, 35, 549, 1990.

Karentz, D., McEuen, F.S., Lord, K.M., Dunlap, A., A survey of mycosporine-like amino acids in Antarctic marine organisms: Potential protection from ultraviolet radiation, *Mar. Biol.*, 188, 151–166, 1991.

Karentz, D., Bosch, I., Dunlop, W.C., Distribution of UV-absorbing compounds in the Antarctic limpet *Nacella concinna*, *Antarct. J. U.S.*, 27, 121–122, 1992.

Karentz, D., Bosch, I., Mitchell, D.M., Limited effect of Antarctic ozone depletion on sea urchin development, *Mar. Biol.*, 145, 277–292, 2004.

Karl, D.M., The grounding of the *Bahia Paraiso*: Microbial ecology of the 1989 Antarctic spill, *Microb. Ecol.*, 24, 77–89, 1992.

Karl, D.M., Microbial processes in the Southern Ocean, in *Antarctic Microbiology*, Friedman, E.I., Ed., Wiley-Liss, New York, 1993, 1–63.

Karl, D.M., Novitsky, J.A., Dynamics of microbial growth in surface layers of a coastal marine sediment ecosystem, *Mar. Ecol. Prog. Ser.*, 50, 169–176, 1988.

Karl, D.M., Tilbrook, D., Tein, G., Seasonal coupling of organic matter and particle flux in the western Bransfield Strait, Antarctica, *Deep-Sea Res.*, 38, 1097–1126, 1991.

Karpov, K.A., Cailliet, G.M., Feeding dynamics of *Loligo opalescens*, *Fish. Bull. (California Depart. Fish Game)*, 169, 45–65, 1978.

Karsten, U., Wiencke, C., Kirst, G.D., The effect of salinity changes upon the physiology of green microalgae from Antarctica and southern Chile, 1: Cell viability, growth, photosynthesis, and dark respiration, *J. Plant Physiol.*, 138, 667–673, 1991.

Karsten, U., Sewell, T., Hanelt, D., Bischof, K., Figuera, F., Moya, A., Wiencke, C., An inventory of UV-absorbing mycrosporine-like amino acids in macroalgae for polar and warm temperate regions, *Biol. Mar.*, 41, 443, 1998.

Kasamatsu, F., Joyce, G.G., Current status of odontocetes in Antarctica, in *Antarctic Biology in a Global Context*, Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backhuys Publishers, Leiden, The Netherlands, 2003, 26.

Kasamatsu, F., Ohsumi, S., Distribution pattern of minke whales in the Antarctic with special reference to the sex ratios of the catch, *Rep. Int. Whal. Commun. Rep.*, 34, 345–348, 1987.

Kasamatsu, F., Ensor, P., Joyce, G.G., Clustering and aggregation of minke whales in Antarctic feeding grounds, *Mar. Ecol. Prog. Ser.*, 168, 1–11, 1998.

Kato, H., Some considerations of the age at sexual maturity of Antarctic minke whales, *Int. Whaling Comm. Rep.*, 33, 393–399, 1983.

Kato, H., Diversity-dependent changes in growth parameters of the Southern minke whale, *Sci. Rep. Whales Res. Inst., Tokyo*, 38, 47–73, 1997.

Kato, M., Murano, M., Segawa, S., Estimates of the filtration rate of Antarctic krill under laboratory conditions, *Trans. J. Tokyo Univ. Fish.*, 3, 107–112, 1979.

Kato, M., Mujrano, M., Segawa, S., Estimates of the filtration rate of Antarctic krill, *Euyphausia superba* Dana, *Trans. Tokyo Univ. Fish.*, 5, 167–175, 1982.

Kato, M., Sehawa, S., Tanoue, E., Murano, M., Filtering and ingestion rates of Antarctic krill, *Euphausis superba* Dana, *Trans. Tokyo Univ. Fish.*, 5, 167–175, 1982.

Kaufman, G.W., Siniff, D.B., Reichle, R., Colony behaviour of Weddell seals (*Leptonychotes weddelli*) at Hutton Cliffs, Antarctica, *Rapports et Proces-Verbaux des Renunions Conseil International Pour l'Exploration de la Mer*, 169, 228–246, 1975.

Kawaguchi, K., Ishikawa, S., Matsuda, O., Overwintering strategy of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off Ongul Islands in Lützow-Holm Bay, Antarctica, *Mem. Nat. Inst. Polar Res. Special Issue*, 44, 67–85, 1986.

Kawakami, T., Doi, T., Natural mortality of krill and density of swarms, in *Comprehensive Report on the Population of Krill (Euphausia superba) in the Antarctic*, Doi, T., Ed., Tokai Regional Fisheries Research Laboratory, Japan, 1979, 19–21.

Kawamura, A., Food and feeding ecology in the southern sei whale, *Sci. Rep. Whales Res. Inst. Tokyo*, 22, 127–152, 1974.

Kawamura, A., A consideration of an available source of energy and its cost for locomotion in fin whales, with special reference to seasonal migrations, *Sci. Rep. Whales Res. Inst. Tokyo*, 27, 61–79, 1975.

Kawamura, A., An interim consideration on a possible interspecific relation in the southern baleen whales from the viewpoint of their food habits, *Int. Whaling Comm. Rep.*, 28, 411, 1978.

Kawamura, A., Food habitats of *Euphausia superba* Dana and the diatom community, in *Selected Contributions to the Woods Hole Conference on the Living Resources of the Southern Ocean*, El-Sayed, S.Z., Ed., BIOMASS Scientific Series 2, 1981, 65–68.

Kellerman, A., Zur Biologie der Jugendstadien der Notothenioidei (Pisces) an der Antarktischen Halbinsel, *Ber. Polarforsch.*, 31, 1–155, 1986.

Kellerman, A., Food and feeding ecology of postlarval and juvenile *Pleurogramma antarcticum* (Pisces: Notothenioidei) in the seasonal pack ice zone off the Antarctic Peninsula, *Polar Biol.*, 7, 307–315, 1987.

Kellerman, A., The larval food community in the zone of the seasonal pack ice cover and its seasonal and interannual variability, *Arch. Fischereiwiss.*, 39, 89–109, 1989.

Kellerman, A., Catalogue of early life stages of Antarctic notothenioid fishes, *Ber. Polarforsch.*, 67, 44–136, 1990a.

Kellerman, A., Food and feeding dynamics of the larval Antarctic fish *Nototheniops larseni*, *Mar. Biol.*, 106, 159–167, 1990.

Kellerman, A., Kock, K.-H., The distribution of postlarval and juvenile nothothenoids (Pisces: Perciformes) in the southern Scotia Sea (57–64° S/48–56° W) during FIBEX 1981, *Meeresforschung*, 30, 82–93, 1984.

Kellerman, A., North, A.W., The contribution of the BIOMASS Programme to Antarctic fish biology, in *Southern Ocean Ecology: The BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, UK, 1996, 191–210.

Kellogg, D.E., Kellogg, T.B., Dearborn, J.H., Edwards, E.C., Fratt, D.B., Diatoms from brittle star stomachs: Implications for sediment reworking, *Antarct. J. U.S.*, 17, 167–169, 1983.

Kennett, J.P., The fauna of the Ross Sea, Part 6: Ecology and distribution of the Foraminifera, *N.Z. Oceanogr. Inst. Mem.*, 46, 1–46, 1968.

Kennett, J.P., Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and their impact on global paleo-oceanography, *J. Geophys. Res.*, 82, 3843–3860, 1977.

Kennett, J.P., Paleooceanography: Global ocean evolution, *Rev. Geophys. Space Res.*, 21, 1258–1274, 1983.

Kennett, J.P., Houtz, R.E., Andrews, P.B., Edwards, A.R., Gostin, V.A., Hajas, M., Hampton, M. et al., Cenozoic paleo-oceanography in the southwest Pacific ocean, Antarctic glaciation, and the development of the circum-Antarctic current, *Initial Rep. Deep Sea Drilling Proj.*, 29, 1155, 1976.

Kennicutt, H.M.C., Oil spillage in Antarctica: Initial report of the National Science Foundation—sponsored quick-response team on the grounding of the *Bahia Paraiso*, *Environ. Sci. Technol.*, 24, 620–624, 1990.

Kennicutt, H.M.C., Sweet, S.T., Fraser, W.R., Stockton, W.I., Culver, M., Grounding of the *Bahia Paraiso* at Arthur Harbor, Antarctica: Distribution and fate of oil spill-related hydrocarbons, *Environ. Sci. Technol.*, 25(3), 509–518, 1991.

Kennicutt, H.M.C., McDonald, T.J., Denoux, G.J., McDonald, S.J., Hydrocarbon contamination in the Antarctic Peninsula, I: Arthur Harbor—subtidal sediments, *Mar. Pollut. Bull.*, 24(10), 499–506, 1992.

Kennicutt, H.M.C., McDonald, T.J., Denoux, G.J., McDonald, S.J., Hydrocarbon contamination on the Antarctic Peninsula, II: Arthur Harbor—inter- and subtidal limpets (*Nacella concinna*), *Mar. Pollut. Bull.*, 24(10), 506–511, 1992.

Kenny, R., Hayson, N., Ecology of the rocky shores organisms at Macquarie Island, *Pac. Sci.*, 16, 245–263, 1962.

Keyes, M.C., The nutrition of pinnipeds, in *The Behaviour and Physiology of Pinnipeds*, Harrison, R.J., Hubbard, R.C., Petersen, C.E., Schusterman, R.J., Eds., Appleton-Century-Crofts, New York, 1968, 359–395.

Keys, J.R., *Antarctic Marine Environments and Offshore Oil*, Commission for the Environment, New Zealand Government, Wellington, 1984.

Keysner, E.E., Tot, V.S., Shilov, V.N., Characteristics of the behaviour and biological cycles of the marbled notothenia (*Notothenia rossii*) in relation to bottom topography, bottom materials and currents, *J. Ichthyol.*, 14, 610–613, 1974.

Khailov, K.M., Burkalova, Z.D., Release of dissolved organic matter by marine seaweeds and distribution of their total organic production to inshore communities, *Limnol. Oceanogr.*, 14, 521–527, 1976.

Kikuno, T., Spawning behaviour and early development of the Antarctic krill, *Euphausia superba* Dana, observed on board R.V. *Kaiyo Maru* in 1979/80, *Antarct. Rec., Tokyo*, 73, 97–102, 1981.

Kils, U., Schwimmverhalten, Schwimmleistung, und Energiebilanz des Antarktischen Krills *Euphausia superba*, *Ber. Inst. Meereskd. Christian-Albrechts-Univ. Kiel*, 65, 1–79, 1979.

Kils, U., Swimming speed and escape response of Antarctic krill, *Euphausia superba*, *Meeresforschung*, 27, 264–266, 1979.

Kils, U., Swimming behaviour, swimming performance, and energy balance of Antarctic krill, *Euphausia superba, Biomass Scientific Series* 3, SCAR and SCOR, Scott Polar Research Institute, Cambridge, UK, 1981.

Kils, U., Swimming and feeding of Antarctic krill *Euphausia superba*—some outstanding energetics and dynamics—some unique morphological details, *Ber. Polarforsch.*, 4, 130–155, 1983.

Kim, D., Seasonality of marine algae and grazers of an Antarctic rocky intertidal, with emphasis on the role of the limpet *Nacella concinna* Strebel (Gastropoda: Patellidae), *Ber. Polarforsch.*, 397, 1, 2001.

Kinder, T.H., Hunt, G.L., Jr., Schneider, D., Schumacker, J.D., Correlations between seabirds and oceanic fronts around the Pribolof Islands, Alaska, *Estuar. Coast. Shelf Sci.*, 16, 309–319, 1983.

King, J.E., On a pup of the crabeater seal, *Lobodon carcinophagus*, *Ann. Mag. Nat. Hist. Ser.*, 12, 619–624, 1957.

King, J.E., The feeding mechanism and jaws of the crabeater seal (*Lobodon carcinophagus*), *Mammalia*, 25, 462–466, 1961.

King, J.E., Seals of the World, British Museum (Natural History), London, 1964.

King, J.E., Some aspects of the anatomy of the Ross seal, *Ommatophoca rossi* (Pinnipedia: Phocidae), *Br. Antarct. Surv. Sci. Rep.*, 63, 1–54, 1969.

Kirkwood, G.P., Estimating population sizes from relative abundance data: A simulation study, *Rep. Int. Whal. Commun.*, 36, 721–735, 1981.

Kirkwood, R., Robertson, G., The foraging ecology of female emperor penguins in winter, *Ecol. Monogr.*, 67, 155–176, 1997.

Kirst, G.O., Wiencke, C., Ecophysiology of polar algae, *J. Phycol.*, 31, 181–199, 1995.

Kittel, W., Stepnik, R., Distribution of *Euphausia crystallorophias, E. frigida*, and *Thysanoessa macrura* in the southern part of the Drake Passage and in the Bransfield Strait during 1983–1984 austral summer (BIOMASS-SIBEX), *Polar Res.*, 6, 133–149, 1983.

Klaas, C., Distribution and role of microprotozoa in the Southern Ocean, *Ber. Polarforsch.*, 253, 1–119, 1997.

Klages, M., Food and feeding ecology of emperor penguins in the eastern Weddell Sea, *Polar Biol.*, 9, 385–390, 1989.

Klages, M., Biology of the Antarctic gammaridean amphipod *Eusirus perdentatus* Gevreux (Crustacea: Amphipoda): Distribution, reproduction and population dynamics, *Antarct. Sci.*, 5, 349–359, 1993.

Klages, N.T.W., Bester, M.V., Fish as prey for fur seals, *Arctocephalus* spp., at subantarctic Marion Island, *Mar. Biol.*, 131(3), 559–566, 1998.

Klages, N.T.W., Gales, R., Pemberton, D., The stomach contents of Antarctic petrels *Thalassoica antarctica* feeding young chicks at Scuta Manotik, Marion Coast, Antarctica, *Polar Biol.*, 10, 545–547, 1990.

Klinck, J.M., Hofmann, E.E., Deep-flow variability in the Drake Passage, *J. Phys. Oceanogr.*, 16, 1281–1292, 1986.

Kloser, H., Description basica de cateta pottery y costas abertas adjacennes. Direccion Nacional del Antarcticos: Reporte de datos Estuctura y dinamica de unecosystema costera Antártico, Estacion cientifica “Terniente Jubany” en la Isla 25 de mayo (King George Island), Islas Shetland del Sur, Contribucion No. 419B, 1994.

Kloser, H., Habitats and distribution patterns of benthic diatoms in Potter Cove (King George Island) and its vicinity, *Ber. Polarforsch.*, 299, 95–105, 1998.

Kloser, H., Ferreyra, G., Schloss, I., Mercuri, G., Laturnus, F., Curtosi, A., Seasonal variation of algal growth and conditions in sheltered Antarctic bays: the example of Potter Cove (King George Island, South Shetlands), *Polar Biol.*, 14, 11–16, 1993.

Knox, G.A., Littoral ecology and biogeography of the Southern Ocean, *Proc. R. Soc. Lond. ,Ser. B Biol. Sci.*, 162, 577–624, 1960.

Knox, G.A., The biogeography and intertidal ecology of Australian coasts, *Oceanogr. Mar. Biol. Annu. Rev.*, 1, 341–404, 1963.

Knox, G.A., Antarctic marine ecosystems, in *Antarctic Ecology,* Vol. 1, Holdgate, M.W., Ed., Academic Press, London, 1970, 69–96.

Knox, G.A., The marine benthic ecology and biogeography, in *Biogeography and Ecology of New Zealand Shores*, Kuschel, G., Ed., Dr. W. Junk Publishers, The Hague, 1975, 353–405.

Knox, G.A., Distribution patterns of the Southern Hemisphere marine biota: some comments on their origin and evolution, in *Proceedings of the International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere, Auckland, July 1978*, 1979, 43–52.

Knox, G.A., Plate tectonics and the evolution of intertidal and shallow-water benthic biotic distribution patterns of the Southwest Pacific, *Palaeogeogr., Palaeoclimateol., Palaeoecol.*, 31, 267–297, 1980.

Knox, G.A., The living resources of the Southern Ocean: a scientific overview, in *Antarctic Resources Policy: Scientific, Legal and Political Issues*, Vicuna, F.O., Ed., Cambridge University Press, Cambridge, UK, 1983, 21–60.

Knox, G.A., The key role of krill in the ecosystem of the Southern Ocean, with special reference to the convention on the conservation of Antarctic Marine Living Resources, *Ocean Manage.*, 9, 113–156, 1984.

Knox, G.A., Recent New Zealand marine research in the Ross Sea Sector of Antarctica, *Mem. Nat. Inst. Polar Res. Special Issue*, 40, 245–363, 1986.

Knox, G.A., Primary production and consumption in McMurdo Sound, Antarctica, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin Heidelberg, 1990, 115–128.

Knox, G.A., *The Biology of the Southern Ocean*, Cambridge University Press, Cambridge, UK, 1994.

Knox, G.A., State of the Ross Sea region marine environment, in *Ross Sea Region: State of the Environment Report for the Ross Sea Region of Antarctica*, Antarctic Institute, Christchurch, 2001, 5.1–5.53.

Knox, G.A., Ensor, P.H., (in preparation), The shallow water benthic community beneath the McMurdo Ice Shelf at White Island, McMurdo Sound, Antarctica.

Knox, G.A., Lowry, J.K., A comparison between the benthos of the Southern Ocean and the North Polar Ocean, with special reference to the Amphipoda and Polychaeta, in *Polar Oceans*, Dunbar, M.J., Ed., Arctic Institute of North America, Calgary, 1977, 423–462.

Knox, G.A., Pierce, L., Bassett, J., (in preparation), The summer pelagic ecosystem beneath the sea ice at the edge of the McMurdo Ice Shelf, McMurdo Sound, Antarctica. *Polar Biol.*

Knox, G.A., Waghorn, E.H., Ensor, P.H., (in press), The summer plankton beneath the McMurdo Ice Shelf at White Island, McMurdo Sound, Antarctica.

Knust, R., Arntz, W.E., Boche, M., Brey, T., Gerdes, D., Mintenbeck, K., Schröder, A., Starmans, A., Teixidó, N., Iceberg scouring on the Eastern Weddell Sea shelf (Antarctica): a benthic system shaped by physical disturbances, in *Antarctic Biology in a Global Context*, Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., 2003, 96–107.

Kock, K.-H., Verbreitung und biologie der Wichtigsten nutzfischarten der Antarktis, *Mitt. Institut für Seefischerei, Hamburg*, 16, 1–75, 1975.

Kock, K.-H., On the fecundity of *Chamsocephalus gunnari* Lönnberg 1906 and *Chaenocephalus aceratus* Lönnberg 1906 (Pisces, Channichthyidae) off South Georgia Island, *Meeresforschung*, 27, 177–185, 1979.

Kock, K.-H., Fischereibiologische Untersuchungen an drei antarktischen Fischarten: *Chamsocephalus gunnari* Lönnberg 1905, *Chaenocephalus aceratus* Lönnberg 1906, and *Pseudochaenichthys georgianus* Norman 1937 (Notothenioidei: Channichthyidae), *Mitt. Institut für Seefischerei, Hamburg 32*, 1981, 1–127.

Kock, K.-H., Fischerbiologische Unterschungen bei Elephant Island im Marz, 1981, *Archiv für Fischereiwissenschaft*, 33, 127–142, 1982.

Kock, K.-H., Marine habitats—fish, in *Key Environments—Antarctica*, Bonner, W.N., Walton, D.W.H., Eds., Pergamon Press, Oxford, 1984, 17–192.

Kock, K.-H., Krill consumption by Antarctic notothenioid fish, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 437–444.

Kock, K.-H., Marine consumers: fish and squid, *Environ. Int.*, 13, 37–45, 1987.

Kock, K.-H., Reproduction in fish around Elephant Island, *Archiv für Fischerewissenschaft*, 39(1), 171–210, 1989.

Kock, K.-H., The status of exploited fish stocks in the Southern Ocean, *Archiv für Fischereiwissenschaft*, 41, 1–65, 1991.

Kock, K.-H., *Antarctic Fish and Fisheries*, Cambridge University Press, Cambridge, UK, 1992.

Kock, K.-H., Kellerman, A., Reproduction in Antarctic notothenioid fish, *Antarct. Sci.*, 3, 125–130, 1991.

Kock, K.-H., Koster, F.-W., The state of exploited fish stocks in the Atlantic sector of the Southern Ocean, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin, 1990, 308–322.

Kock, K.-H., Shimadzu, Y., Trophic relationships and trends in population size and reproductive parameters in Antarctic high-level predators, in *Southern Ocean Ecology: The BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, UK, 1996, 287–312.

Kock, K.-H., Stein, M., Krill and hydrographic conditions off the Antarctic Peninsula, *Meeresforschung*, 26, 79–95, 1978.

Kock, K.-H., Schneppenheim, R., Siegel, V., A contribution to the fish fauna of the Weddell Sea, *Archiv für Fischereiwissenschaft*, 34, 103–120, 1984.

Kock, K.-H., Duhamel, G., Hureau, J.-C., *Review of the biology and present status of exploited Antarctic fish stock*, Biomass Scientific Series No. 7, SCAR, Scott Polar Research Institute, Cambridge, UK, 1985.

Kock, K.-H., Belcher, M., Joines, C.D., Is the attempt to estimate the biomass of Antarctic fish from multi-species surveys appropriate for the targeted species? *Noththenia rossii* in the Atlantic Ocean sector revisited, *CCAMLR Sci.*, 13, 141–153, 2004.

Kogure, K., Fukami, K., Simidu, U., Taga, N., Abundance and production of bacterioplankton in the Antarctic, *Mem. Natl. Inst. Polar Res., Spec. Issue*, 40, 414–422, 1986.

Koike, I., Ronner, U., Holm-Hansen, O., Microbial nitrogen metabolism in the Scotia Sea, *Antarct. J. U.S.*, 16, 165–166, 1981.

Koike, I., Holm-Hansen, O., Biggs, D.C., Inorganic nitrogen metabolism by Antarctic phytoplankton, with special reference to ammonia cycling, *Mar. Ecol. Prog. Ser.*, 30, 105–116, 1986.

Koltun, V.M., Porifera, *Antarctic Map Folio Series*, Vol. 11, American Geographical Society, Washington, DC, 13–14 pp, 1969.

Komaki, Y., Technical notes on keeping euphausiids alive in the laboratory, with a review of experimental studies on euphausiids, *Bull. Plankton Soc. Japan*, 13, 95–106, 1966.

Kompowski, A., On feeding of *Champocephalus gunnari* Lönnberg, 1905 (Pisces: Chaenichthyidae) off South Georgia and Kerguelen Island, *Acta Ichtyol. Pisc.*, 10, 25–42, 1980.

Kompowski, A., Studies on juvenile *Chaenocephalus aceratus* Lönnberg, 1906 (Pisces: Chaenichthyidae) off South Georgia, *Acta Ichtyol. Pisc.*, 10(1), 45–53, 1980.

Kompowski, A., Biological characteristics of Scotia Sea icefish *Chaenocephalus aceratus* (Lönnberg, 1906) from the South Georgia area, *Rep. Sea Fish. Inst., Grodyna*, 22, 49–71, 1990.

Kooyman, G.L., Erythrocyte analysis of some Antarctic fishes, *Copeia*, 2, 457–458, 1963.

Kooyman, G.L., The physiology of diving in penguins, in *The Biology of Penguins*, Stonehouse, B., Ed., Macmillan, London, 1975, 115–137.

Kooyman, G.L., Crabeater seal—*Lobodon carcinophagus* (Hombron & Jacquinot, 1842), in *Handbook of Marine Mammals, Vol. 2: Seals*, Ridgeway, S.H., Harrison, R.J., Eds., Academic Press, London, 1981, 221–235.

Kooyman, G.L., Leopard seal—*Hydrurga leptonyx* (Blainville, 1820), in *Handbook of Marine Mammals, Vol. 2: Seals*, Ridgeway, S.H., Harrison, R.J., Eds., Academic Press, London/New York, 1981, 261–274.

Kooyman, G.L., Weddell seal—*Leptonychotes weddelli* Lesson, 1826, in *Handbook of Marine Mammals, Vol. 2: Seals*, Ridgeway, S.H., Harrison, R.J., Eds., Academic Press, London/New York, 1981, 275–296.

Kooyman, G.L., *Weddell Seal: Consummate Diver*, Cambridge University Press, New York, 1981.

Kooyman, G.L., Davis, R.W., Feeding behaviour of female Antarctic fur seals, *Arctocephalus gazella*, *Antarct. J. U.S.*, 15, 159–160, 1980.

Kooyman, G.L., Davis, R.W., Croxall, J.P., Costa, D.P., Diving depths and energy requirements of King Penguins, *Science*, 217, 726–727, 1971.

Kooyman, G.L., Keren, D.H., Campbell, W.B., Wright, J.J., Pulmonary gas exchange in freely diving Weddell seals, *Leptonychotes weddelli*, *Respir. Physiol.*, 17, 283–290, 1973.

Kooyman, G.L., Davis, R.W., Croxall, J.P., Diving behaviour of Antarctic fur seals, in *Fur Seals: Maternal Strategies on Land and at Sea*, Gentry, R.L., Kooyman, G.L., Eds., Princetown University Press, Princetown, 1986, 115–125.

Kooyman, G.L., Cherel, Y., Le Maho, Y., Croxall, J.P., Thorson, P.H., Ridoux, V., Kooyman, C.A., Diving behaviour and energetics during foraging cycles in king penguins, *Ecol. Monogr.*, 62, 143–163, 1992.

Kopczynska, E.E., Spatial structure of phytoplankton in the Scotia Front west of Elephant Island (BIOMASS II), October–November 1986, *Polar Biol.*, 9, 231–242, 1988.

Kopczynska, E.E., Fiala, M., Surface phytoplankton composition and carbon distribution in the Crozet Basin during austral summer of 1999: Variability across frontal zones, *Polar Biol.*, 27, 17–28, 2003.

Kopczynska, E.E., Weber, L.H., El-Sayed, S.Z., Phytoplankton species composition in the Indian sector of the Antarctic Ocean, *Polar Biol.*, 6, 161–169, 1986.

Kosahi, S., Takahashi, M., Yamaguchi, Y., Aruya, Y., Some characteristics of chlorophyll particles in the Southern Ocean, *Trans. Tokyo Univ. Fish.*, 6, 85–97, 1985.

Kosaka, S., Takahashi, M., Yamaguchi, Y., Aruya, Y., Size characteristics of chlorophyll particles in the southern Ocean, *Trans. Tokyo Univ. Fish.*, 6, 85–97, 1985.

Kott, P., Antarctic Ascidacea, *Antarct. Res. Ser.*, 13, 1–239, 1969.

Kott, P., Antarctic Ascidacea II, *Antarct. Res. Ser.*, 17, 18–82, 1971.

Kottmeier, S.T., Sullivan, C.W., Late winter primary production and bacterial production in sea ice and seawater west of the Antarctic Peninsula, *Mar. Ecol. Prog. Ser.*, 36, 287–298, 1987.

Kottmeier, S.T., Sullivan, C.W., Sea ice microbial communities (SIMCO) 9: Effects of temperature and salinity on rates of metabolism and growth of autotrophs and heterotrophs, *Polar Biol.*, 8, 293–304, 1988.

Kottmeier, S.T., Sullivan, C.W., Bacterial biomass and production in pack ice of Antarctic marginal ice zones, *Deep-Sea Res.*, 37, 1311–1330, 1990.

Kottmeier, S.T., Musat, A.M., Craft, L.L., Kastendiek, J.E., Sullivan, C.W., Ecology of sea ice microbial communities in McMurdo Sound, *Antarct. J. U.S.*, 19, 129–131, 1984.

Kottmeier, S.T., Miller, M.A., Lizotte, M.P., Craft, L.L., Sullivan, C.W., Ecology of sea ice microbial communities during the 1984 winter–summer transition in McMurdo Sound, Antarctica, *Antarct. J. U.S.*, 20, 128–130, 1986.

Kottmeier, S.T., Grossi, S.McG., Sullivan, C.W., Sea ice microbial communities, VIII: Bacterial production in annual sea ice of McMurdo Sound, Antarctica, *Mar. Ecol. Prog. Ser.*, 35, 175–186, 1987.

Kowalke, J., Abele, D., A first record of the sift bottom infauna community of Potter Cove, *Ber. Polarforsch.*, 299, 106–112, 1998.

Kozlov, A.N., Ecologophysiological peculiarities of *Notothenia rossii mamorata* Fischer and *Notothenia gibberifrons* Lönnberg at certain periods of the annual life cycle, in *An Ecological and Biological Description of Some Species of Antarctic Fishes*, All-Union Research Institute of Marine Fisheries and Oceanography, Moscow, 1980. In Russian.

Kozlov, A.N., Seasonal changes of morphophysiological characteristics of the marbled notothenia, *Notothenia rossii mamorata* Fischer (Nototheniidae). *Voprosy Ikhtiologii* 22, 782. In Russian published in English in *Journal of Ichthyology*, 22, 52–58, 1982.

Kozlov, A.N., A review of the trophic role of mesopelagic fish of the family Myctophidae in the Southern Ocean ecosystem, *CCAMLR Sci.*, 2, 71–77, 1995.

Kozlov, A.N., Tarverdiera, M.I., Feeding of different species of Myctophidae in different parts of the Southern Ocean, *J. Ichthyol.*, 29, 160–167, 1989. Translated from *Voprosy Ikhtiologii.*

Kramp, P.L., Hydromedusae from Discovery collections, *Discov. Rep.*, 29, 1–128, 1957.

Krause, G.H., Weis, E., Chlorophyll fluorescence and photosynthesis: the basics, *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 42, 313–349, 1991.

Krebs, W.M., Ecology of neretic diatoms, Arthur Harbor, Antarctica, *Micropalaeontology*, 29, 267–297, 1983.

Krebs, W.M., Lipps, J.H., Burckle, L.H., Ice diatom floras, Arthur Harbour, Antarctica, *Polar Biol.*, 7, 163–171, 1987.

Krembs, C., Eiken, H., Juinge, K., Deming, J.W., High concentrations of exopolymeric substances in Arctic winter sea ice: Implications for the polar ocean carbon cycle and cryoprotection of diatoms, *Deep-Sea Res.*, 49, 2163–2181, 2002.

Krempin, D.M., The role of bacterioplankton as producers in two high-productivity marine ecosystems, Ph.D. Dissertation, University of Southern California, Los Angeles, CA, 1985.

Kriss, A.Ye., Quantitative distribution of saprophytic bacteria between New Zealand and Antarctica, *Microbiology*, 42, 913–917, 1973.

Kristensen, T.K., Periodical growth rings in cephalopod statoliths, *Dana*, 1, 39–51, 1980.

Kristiansen, S., Syvertsen, E.E., Farbrot, T., Nitrogen uptake in the Weddell Sea during late winter and spring, *Polar Biol.*, 12, 245–251, 1992.

Kristiansen, S., Farbrot, T., Kosa, H., Myklestad, S., Quillfeldt, C.H., Nitrogen uptake in the infiltration community: An ice algal community in Antarctic pack ice, *Polar Biol.*, 19, 307–315, 1998.

Krzysztof, W., Opalinski-Maciejewska, M., Georgiera, L.V., Notes on food selection in Antarctic krill, *Euphausia superba*, *Polar Biol.*, 17, 350–357, 1997.

Kuhl, S., Schneppenheim, R., Electrophoretic investigation of genetic variation in two krill species, *Euphausia superba* and *E. crystallorophias* (Euphaudiidae), *Polar Biol.*, 6, 17–23, 1986.

Kundo, K., Fukuchi, M., Vertical distribution of chlorophyll *a* in the Indian sector of the Antarctic Ocean in 1972–1973, *Antarct. Rec.*, 74, 127–142, 1982.

Kunzmann, A., Blood physiology and ecological consequences in Weddell Sea fishes, *Ber. Polarforsch.*, 91, 1–79, 1996.

Kuosa, H., Norman, B., Kivi, K., Brandini, F., Effects of Antarctic sea ice biota on seeding as studied in aquarium experiments, *Polar Biol.*, 12, 333–339, 1992.

Kuparinen, J., Bjornsen, P.K., Spatial distribution of bacterioplankton across the Weddell-Scotia Confluence during early austral summer 1988–1989, *Polar Biol.*, 12, 197–204, 1992.

Kuramoto, S., Koyama, K., Preliminary report of the oceanographic observations on the 22nd Japanese Antarctic Research Expedition (1980–1981), *Mem. Natl. Inst. Polar Res., Spec. Issue*, 23, 5–12, 1982.

Kurtz, P.P., Bromwich, D.H., Satellite-observed behaviour of the Terra Nova Bay polyna, *J. Geophys. Res.*, 88, 9717–9722, 1983.

Kurtz, P.P., Bromwich, P.H., A recurring, atmospherically-formed polyna in Terra Nova Bay, in *Oceanology of the Antarctic Shelf, Antarctic Research Series 45*, Jacobs, S.S., Ed., American Geophysical Union, Washington, DC, 1985, 177–201.

Kussakin, O.G., Fauna of Isopoda and Tanaidacea in the coastal zones of Antarctic and sub-Antarctic waters: biological zones of the Antarctic and subantarctic waters, *Biological Reports of the Soviet Antarctic Expeditions (1955–1958)*, Akademiya nauk SSSR Zoologoscheskii Institut Issledovaniya a Fauny morei, 220–389 pp, 1967.

Laevastu, T., Favourite, F., Holistic simulation models of shelf-seas ecosystems, in *Analysis of Marine Ecosystems*, Longhurst, A.R., Ed., Academic Press, London, 1981, 701–727.

Laevastu, T., Larkin, H.H., *Marine Fisheries Ecosystem—Its Quantitative Evaluation and Management*, Fishing News Books, Farnham, Surrey, 1981.

Lake, S., Burton, H., van den Hoff, J., Regional, temporal, and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica, *Mar. Ecol. Prog. Ser.*, 254, 293–305, 2003.

La Mesa, M., Eastman, J.T., Vacchi, M., The role of notothenioid fishes in the food web of the Ross Sea shelf waters, *Polar Biol.*, 27, 321–338, 2004.

Lampitt, R.S., Noji, T., von Bodungen, B., What happens to zooplankton faecal pellets? Implication for material flux, *Mar. Biol.*, 104, 15–23, 1990.

Lancelot, C., Mathot, S., Biochemical fractionation of primary production by phytoplankton in Belgium coastal waters during short- and long-term incubations with ^{14}C-bicarbonate. II. *Phaeocysts pouchetii* colonial population, *Mar. Biol.*, 65, 13, 1985.

Lancelot, C., Keller, M.D., Rousseau, V., Smith, W.O., Jr., Mathot, S., Auto-ecology of the haptophyte *Phaeocystis* sp, in *The* *physiological ecology of harmful algal blooms*, NATO ASI Series Vol. G41, Anderson, D., Hallrgraeff, G., Cambella, A., Eds., Springer, Heidelberg, 1998, 211–224.

Lancraft, T.M., Torres, J.J., Hopkins, T.L., Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986), *Polar Biol.*, 9, 225–233, 1989.

Lancraft, T.M., Hopkins, T.L., Torres, J.J., Donnelly, J., Oceanic micronekton/macrozooplankton community structure and feeding in ice-covered Antarctic waters (AMERIEZ 1986), *Polar Biol.*, 11, 157–167, 1991.

Lange, M.A., Basic properties of Antarctic sea ice as revealed by textural analysis of ice cores, *Ann. Glaciol.*, 10, 95–101, 1988.

Lange, M.A., Ackley, S.F., Wadhams, P., Dieckman, G.S., Eicken, H., Development of sea ice in the Weddell Sea, *Ann. Glaciol.*, 12, 97–103, 1989.

Lange, M.A., Schlosser, P., Ackley, S.F., Wahdhams, P., Dieckmann, G.S., ^{18}O concentrations in sea ice of the Weddell Sea, Antarctica, *Ann. Glaciol.*, 36(124), 315–323, 1990.

Larrian, E., Consecuencia en la biota bentónica de las erupciones volcánicas en Isla Decepción (62° 57′S, 60° 29′S, 59° 04′ W) y su comparación con Bahía Chile (62° 29′S, 59° 04′W), *Antarc. Mem. Biol. Mar. Universidad de Concepción*, 1–150, 1986.

Larson, R.J., Pelagic Scyphomedusae (Scyphozoa: Coronatae and Semaeostomeae) of the Southern Ocean, *Antarct. Res. Ser.*, 41, 59–165, 1986.

Larsson, P., Jarnmnark, C., Sodergren, A., PCBs and chlorinated pesticides in the atmosphere and aquatic organisms of Ross Island, Antarctica, *Mar. Pollut. Bull.*, 25, 281–287, 1992.

Lasker, R., Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean, *J. Fish. Res. Board Can.*, 23, 1291–1317, 1966.

Lasker, R., Field criteria for survival of anchovy larvae: the relation between the inshore chlorophyll layers and successful first feeding, *U.S. Fish. Bull.*, 71, 453–462, 1975.

Lasker, R., Field criteria for survival of anchovy larvae: The relation between the inshore chlorophyll layers and successful first feeding, *U.S. Fish. Bull.*, 71, 847–855, 1980a.

Lasker, R., Factors contributing to variable recruitment of the northern anchovy (*Eugraulis mordax*) in the Californian current, contrasting years 1975 through 1978, in *Proceedings of the 2nd Symposium on the Early Life History of Fish*, ICES/EHL Symposium/PE, 1980b, 1–11.

Latogurskij, V.L., *Euphausia superba* Dana as a food item of Notothenia rossii marmorata, *Trudy Atl. NIRO*, 42, 167–169, 1972. In Russian.

Laubscher, R.K., Perrisinotto, R., McQuaid, C.D., Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean, *Polar Biol.*, 13, 471–481, 1993.

Lavigne, D.M., Barchard, W., Innes, S., Oritzland, N.A., Pinniped energetics, *FAO Fish. Ser.*, 4(5), 191–235, 1982.

Lavigne, D.M., Innes, S., Worthy, G.A.J., Kovacs, K.M., Schmitz, O.J., Hickie, J.P., Metabolic rates of seals and whales, *Can. J. Zool.*, 64, 279–284, 1986.

Laws, R.M., The elephant seal (*Mirounga leonina* Linn.), II: General, social and reproductive behaviour, *Falkl. Isl. Depend. Surv. Sci. Rep.*, 13, 1–88, 1956.

Laws, R.M., Problems of whale conservation, *Trans. N. Am. Wildl. Conf.*, 25, 304–309, 1960a.

Laws, R.M., The southern elephant seal (*Mirounga leonina* Linn.) at South Georgia, *Norsk Hvalfangst-Tidende*, 49, 466–476, 1960b.

Laws, R.M., Reproduction, growth, and age of Southern Hemisphere fin whales, *Discov. Rep.*, 31, 327–486, 1961.

Laws, R.M., Comparative biology of Antarctic seals, in *Biologie Antarctique*, Carrick, R., Holdgate, M.W., Prevost, J., Eds., Hermann, Paris, 1964, 445–457.

Laws, R.M., Population increase of fur seals at South Georgia, *Polar Biol.*, 16, 856–858, 1973.

Laws, R.M., Seals and whales of the Southern Ocean, *Philos. Trans. R. Soc. Lond., Ser. B*, 279, 81–96, 1977a.

Laws, R.M., The significance of vertebrates in the Antarctic marine ecosystem, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977b, 411–438.

Laws, R.M., Monitoring whale and seal populations, in *Monitoring the Marine Environment*, Symposium of the Institute of Biology No. 7, Nichols, D., Ed., 1979, 114–115.

Laws, R.M., Seal surveys, South Orkney Islands, 1971 and 1974, *Br. Antarct. Surv. Bull.*, 54, 136–139, 1981.

Laws, R.M., Seals, in *Antarctic Ecology*, Laws, R.M., Ed., Vol. 2, Academic Press, London, 1984, 621–715.

Laws, R.M., Decade of research on Antarctic and subantarctic seals, *S. Afr. J. Sci.*, 80, 25–35, 1984.

Laws, R.M., The ecology of the Southern Ocean, *Am. Sci.*, 73, 26–38, 1985.

Laws, R.M., Purves, P.E., The ear plug of Mysticeti as an indicator of age, with special reference to the North Atlantic fin whale, *Norsk Hvalgangsttid*, 45, 414–425, 1956.

Leakey, R.J., Archer, S.D., Grey, J., Microbial dynamics in coastal waters of East Antarctica: Bacterial production and nanoflagellate bactivory, *Mar. Ecol. Prog. Ser.*, 142, 3–17, 1996.

LeBlond, P.H., Satellite observations of the Labrador Current undulations, *Atmosphere-Ocean*, 20, 129–142, 1982.

LeBoeuf, R.J., Croker, D.E., Blackwell, S.B., Morris, P.A., Thorson, D.H., Sex differences in diving and foraging behaviour of northern elephant seals, *Symp. Zool. Soc. Lond.*, 66, 149–178, 1993.

Lee, H.J., Gerdes, D., Vanhove, S., Vinex, M., Meiofauna response to iceberg disturbance on the Antarctic continental shelf at Kapp Norvegia (Weddell Sea), *Polar Biol.*, 24(12), 926–933, 2001.

Lee, H.J., Vanhove, S., Peck, L.S., Vinex, M., Recolonization of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments, *Polar Biol.*, 24, 918–925, 2001.

Leford-Hoffman, P.A., DeMaster, D.J., Nittrouer, C.A., Biogenic-silica accumulation in the Ross Sea and the importance of the Antarctic continental shelf deposits in the marine silica budget, *Geochim. Cosmochim. Acta*, 50, 2099–2110, 1986.

Legechis, R., Oceanic polar front in the Drake Passage: Satellite observations during 1976, *Deep-Sea Res.*, 24, 701–704, 1977.

Legendre, L., Hydrodynamic control of marine phytoplankton production: the paradox of stability, in *Marine Interface Ecohydrodynamics*, Nihoul, J.C.J., Ed., Elsevier, Amsterdam, 1985, 191–207.

Legendre, L., The biological CO_2 pump in seasonally ice-covered waters, *Proc. NIPR Symp. Polar Biol.*, 9, 61–74, 1996.

Legendre, L., Le Fevre, J., Hydrodynamic singularities as controls of recycled versus export production in oceans, in *Productivity in the Oceans: Present and Past*, Berger, W.H. et al., Eds., Wiley, Chichester, 1989, 49–63.

Legendre, L., Le Fevre, J., Interactions between hydrodynamic and pelagic ecosystems: Relevance to resource exploitation and climate change, *S. Afr. J. Mar. Sci.*, 12, 477–486, 1992.

Legendre, L., Michaud, J., Flux of biogenic carbon in oceans: Size-dependent regulation by pelagic food webs, *Mar. Ecol. Prog. Ser.*, 164, 1–11, 1998.

Legendre, L., Rassoulzadegan, F., Food-web mediated export of biogenic carbon in oceans: Environmental control, *Mar. Ecol. Prog. Ser.*, 145, 179–193, 1996.

Legendre, M.L., Ingram, R.G., Poulin, M., Physical control of phytoplankton under sea ice (Monitounuk Sound, Hudson Bay), *Can. J. Fish. Aquat. Sci.*, 38, 1385–1392, 1981.

Legendre, L., Ackley, S.F., Dieckmann, G.S., Guillksen, B., Horner, R., Hoshiai, T., Melnikov, I.A., Reeburgh, W.S., Ecology of sea ice biota: Global significance, *Polar Biol.*, 12, 429–444, 1992.

Le Jehan, S., Treguer, P., The distribution of inorganic nitrogen, phosphorus, silicon, and dissolved organic matter in surface and deep waters of the Southern Ocean, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 22–29.

Le Maho, Y., Delclitte, P., Chatonnet, J., Thermoregulation in fasting emperor penguins, *Am. J. Physiol.*, 231, 913–922, 1976.

Le Maho, Y., Karmann, H., Briot, D., Handrich, Y., Robin, J.P., Mioskowski, E., Cherel, Y., Farni, J., Stress on birds due to routine handling and a technique to avoid it, *Am. J. Physiol.*, 263, 775–781, 1992.

Lenihan, H.S., Benthic marine pollution around McMurdo Station, Antarctica: A summary of findings, *Mar. Pollut. Bull.*, 25(9–12), 318–323, 1992.

Lenihan, H.S., Oliver, J.S., Oakden, J.M., Slattery, M.D., Intense and localized benthic marine pollution around McMurdo Sound, *Mar. Pollut. Bull.*, 21, 422–450, 1990.

Lenihan, H.S., Keist, K.A., Conlan, K.E., Slattery, P.N., Konar, B.H., Oliver, J.S., Patterns of survival and behaviour in Antarctic invertebrates exposed to contaminated sediments: Field and laboratory experiments, *J. Exp. Mar. Biol. Ecol.*, 192, 233–255, 1995.

Lessard, E.J., Swift, E., Species-specific grazing rates of heterotrophic dinoflagellates in oceanic waters measured with dual-labelled radioisotope technique, *Mar. Biol.*, 87, 289–296, 1985.

Lessard, E.J., Voytek, M., Rivkin, R., The heterotrophic-based nutrition of microzooplankton and macrozooplankton in McMurdo Sound, Antarctica, *EOS*, 68, 1773–1778, 1987.

Leventer, A., Sediment trap diatom assemblages from the northern Antarctic Peninsula, *Deep-Sea Res.*, 38(8/9), 1127–1143, 1991.

Leventer, A., Particulate flux from sea ice in polar waters, in *Sea Ice: An Introduction to its Physics, Chemistry, Biology and Geology*, Thomas, D.N., Dieckmann, G.S., Eds., Blackwell Science, Oxford, 2003, 303–332.

Leventer, A., Dunbar, R.B., Diatom flux in McMurdo Sound, Antarctica, *Mar. Micropaleontol.*, 12, 49–64, 1987.

Leventer, A., Domack, E.W., Ishman, S.E., Brachfeld, S., McClennen, C.E., Manley, P., Productivity cycles of 200–300 years in the Antarctic Peninsula region: Understanding linkages among the sun, atmosphere, oceans, sea-ice and biota, *Bull. Geol. Soc. Am.*, 108(12), 1626–1644, 1996.

Levin, S.A., Marin, A., Powell, T.M., Patterns and processes in the distribution and dynamics of Antarctic krill, in *Selected Scientific Papers, Part I. SC-CCAMLR-SS P/5*, Commission on the Conservation of Antarctic Marine Living Resources, Hobart, 281–299 pp, 1988.

Lewis, E.L., Perkins, R.G., Oceanographic investigations in McMurdo Sound, *Antarct. Res. Ser.*, 5, 1–37, 1985.

Lewis, E.L., Weeks, W.F., Sea ice: Some polar contrasts, in *Symposium on Antarctic Ice and Water Masses*, Deacon, G., Ed., Scientific Committee on Antarctic Research, Tokyo, 1971, 23–34.

Lewis, M.R., Horne, E.P.W., Cullen, J.J., Oakey, N.S., Platt, T., Turbulent motions may control phytoplankton photosynthesis in the upper ocean, *Nature (Lond.)*, 311, 49–50, 1984.

Leynaert, A., Nelson, D.M., Queguirer, R., Treguer, P., The silica cycle in the Antarctic Ocean: Is the Weddell Sea atypical?, *Mar. Ecol. Prog. Ser.*, 96, 1–15, 1993.

Li, W.K.W., Experimental approaches to field measurements: Methods and interpretations, *Can. J. Fish. Aquat. Sci.*, 214, 251–286, 1986.

Li, W.K.W., Subba Rao, D.V., Harrison, W.G., Smith, J.C., Cullen, J.J., Irwin, B., Platt, T., Autotrophic picoplankton in the tropical ocean, *Science*, 219, 292–295, 1983.

Liebezeit, G., Residual amino acid fluxes in the upper water column of the Bransfield Strait, *Oceanol. Acta*, 8, 59–65, 1985.

Liebezeit, G., Bolter, M., Distribution of particulate amino acids in the Bransfield Strait, *Polar Biol.*, 2, 225–228, 1986.

Liebezeit, G., von Bodungen, B., Biogenic fluxes in the Bransfield Strait: Planktonic versus microalgal sources, *Mar. Ecol. Prog. Ser.*, 36, 23–32, 1987.

Lien, R., Solheim, A., Elverhoi, A., Rokoengen, K., Iceberg scouring and sea bed morphology on the eastern Weddell Sea shelf, *Polar Res.*, 7, 43–57, 1989.

Ligowski, R., Phytogenic food of *Euphausia superba* Dana caught in the drake passageand bransfield strait, February–March 1981 (BIOMASS-FIBEX), *Polish Polar Biol.*, 3, 281–288, 1982.

Ligowski, R., Glony lodu morskiego Zatoka Admiralicji Pol redakeja prof. dr S. Rakusa-Susczwakego, Oficyna Wyd IE PAN Dziekanaw Lesny 85, 1992. In Polish.

Ligowski, R., Benthic feeding by krill, *Euphausia superba* Dana, in coastal waters off West Antarctica and in Admiralty Bay, South Shetland Islands, *Polar Biol.*, 23, 619–625, 2000.

Lillo, S., Guzman, O., Study of the abundance, distribution, and behaviour of krill at the Bransfield Strait and Drake Passage by means of hydroacoustic techniques, *Instituto Antártico Chileno (INACH) Scientific Series*, 28, 17–45, 1982.

Lin, Y., Raymond, J.A., DeVries, A.L., Compartmentalization of NaCl in frozen solutions of antifreeze glycoproteins, *Cryobiology*, 13(3), 334–340, 1976.

Lindeman, R.I., The trophic-dynamic aspect of ecology, *Ecology*, 23, 399–418, 1942.

Lindsay, A.A., Weddell seals in the Bay of Whales, Antarctica, *J. Mammal.*, 18, 127–144, 1937.

Linkowski, T.B., Population biology of the myctophid fish *Gymnoscopelus nicholsi* (Gilbert 1911) from the western South Atlantic, *J. Fish Biol.*, 27, 683–698, 1985.

Linkowski, T.B., Rembiszewski, J.M., Ichthyological observations off the South Georgia coasts, *Pol. Arch. Hydrobiol.*, 25, 697–704, 1978.

Linkowski, T.E., Presler, P., Zubowski, C., Food habits of Nototheniid fishes (Nototheniidae) in Admiralty Bay (King George Island, South Shetland Islands), *Pol. Polar Res.*, 4, 75–79, 1983.

Linley, E.A.S., Newell, R.C., Estimates of bacterial growth yields based on plant detritus, *Bull. Mar. Sci.*, 35, 409–425, 1984.

Lipps, J.H., Hickman, C.S., Origin, age, and evaluation of Antarctic deep-sea fauna, in *The Environment of the Deep Sea*, Errista, W.G., Morin, J.G., Eds., Prentice-Hall, Englewood Cliffs, NJ, 1982, 325–356.

Lipps, J.H., Krebs, W.N., Planktonic foraminifera associated with Antarctic sea ice, *J. Foram. Res.*, 4, 80–85, 1974.

Lipps, J.H., DeLaca, T.E., Krebs, W., Stockton, W., Shallow-water Foraminifera studies, Antarctic Peninsula, *Antarct. J. U.S.*, 7, 82–83, 1972.

Lipps, J.H., Krebs, W.N., Temnikow, N., Microbes under Antarctic ice shelves, *Nature (Lond.)*, 265, 232–233, 1977.

Lipps, J.H., DeLaca, J.F., Showeres, W. et al., Benthic marine biology: Ross Ice Shelf project, *Antarct. J. U.S.*, 13, 134–141, 1978.

Lipps, J.H., Roman, T.E., DeLaca, T.E., Life below the Ross Ice Shelf, Antarctica, *Science*, 203, 447–449, 1979.

Lipski, M., Chlorophyll *a* in the Bransfield Strait and the southern part of the Drake Passage during BIOMASS-SIBEX (December 1983–January 1984), *Pol. Polar Res.*, 6, 21–30, 1985.

Lishman, G.S., The food and feeding ecology of Adélie Penguins (*Pygoscelis adeliae*) and chinstrap penguins (*P. antarctica*) at Signy Island, South Orkney Islands, *J. Zool., Lond.*, 205, 245–263, 1985.

Lishman, G.S., Croxall, J.P., Diving depths of the chinstrap penguin, *Br. Antarct. Surv. Bull.*, 61, 21–25, 1983.

Lisitzin, A.P., *Sedimentation in the World Ocean*, Society for Economic Paleontology and Mineralogy, Special Publication 17, 1972.

Lisovenko, L.A., Svetlov, M.F., Some data on the biology of *Paraliparis* (Family Liparidae) for the South Shetlands, *J. Ichthyol.*, 20, 131–135, 1980.

Littlepage, J.R., Seasonal variation in lipid content of two Antarctic marine crustacea, in *Biologie Antarctique*, Carrrick, R., Holdgate, M.W., Prevost, J., Eds., Herman, Paris, 1964, 163–176.

Littlepage, J.R., Oceanographic investigations in McMurdo Sound, *Antarct. Res. Ser.*, 5, 1–37, 1965.

Littlepage, J.L., Pearse, J.C., Biological and oceanographic observations under an Antarctic ice shelf, *Science*, 137, 679–680, 1962.

Lizotte, M.P., Microbiology of sea ice, in *Sea Ice: An Introduction to its Physics, Chemistry, Biology and Geology*, Thomas, D.N., Dieckmann, G.S., Eds., Blackwell Science, Oxford, 2003, 184–210.

Lizotte, M.P., Sullivan, C.W., Photosynthesis-irradiance relationships in microalgae associated with Antarctic pack ice: Evidence for *in situ* activity, *Mar. Ecol. Prog. Ser.*, 71, 175–184, 1991.

Lizotte, M.P., Sullivan, C.W., Rates of photoadaptation in sea ice diatoms from McMurdo Sound, Antarctica, *J. Phycol.*, 27, 367–373, 1991.

Lizotte, M.P., Sullivan, C.W., Photosynthetic capacity in microalgae associated with Antarctic pack ice, *Polar Biol.*, 12, 497–502, 1992.

Lockyer, C., The age of sexual maturity of the southern fin whale (*Balaenoptera physalus*) using annual layer counts in the ear plug, *Journal du Conseil, Counseil Permanent International pour l'Exploration de la Mer*, 34, 276–294, 1972.

Lockyer, C., Wet weight, volume, and length correlation in Antarctic krill, *Euphausia superba*, *Discov. Rep.*, 36, 152–155, 1973.

Lockyer, C., Investigation of the ear plug of the southern sei whale, *Balaenoptera borealis*, as a valid means of determining age, *Journal du Conseil, Conseil Permanent International pour l'Exploration de la Mer*, 36, 71–81, 1974.

Lockyer, C., Estimates of growth and energy budget for the sperm whale, *Physeter catadon*, United Nations Scientific Consultation on Marine Mammals, Bergen, Norway, 31 August–9 September, 1976, FAO of the UN ACMRR/MM/SC/38, Rome, 1975.

Lockyer, C., Growth and energy budgets of large baleen whales from the Southern Hemisphere, United Nations Scientific Consultation on Marine Mammals, Bergen, Norway, 31 August–9 September, 1976, FAO of the UN ACMRR/MM/SC/41, Rome, 1976.

Lockyer, C., Observations on the diving behaviour of the sperm whale, *Physeter catadon*, in *A Voyage of Discovery*, Angel, M., Ed., Pergamon Press, Oxford, 1977, 591–609.

Lockyer, C., A theoretical approach to the balance between growth and food consumption in fin and sei whales, with special reference to the female reproductive cycle, *Int. Whaling Comm. Rep.*, 28, 243–249, 1978.

Lockyer, C., Growth and energy budgets of large baleen whales from the Southern Hemisphere, in *Mammals of the Sea*, FAO Fisheries Series No. 5, Vol. 3, Food and Agriculture Association of the United Nations, Rome, 379–487 pp, 1981a.

Lockyer, C., Estimates of the growth and energy budget for the sperm whale, *Physeter catadon*, in *Mammals of the Sea*, FAO Fisheries Series No. 5, Vol. 3, Food and Agriculture Organization of the United Nations, Rome, 489–504 pp, 1981b.

Lockyer, C., Brown, S.G., The migration of whales, in *Animal Migration*, Cambridge Society for Experimental Biology, Seminar Series 13, Ainley, D.G., Ed., Cambridge University Press, Cambridge, UK, 1981, 105–132.

Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., Trivelpiece, S., Effects of sea ice extent on krill salp dominance in the Antarctic food web, *Nature (Lond.)*, 307, 897–900, 1997.

Lomakina, N.B., The euphausiid fauna of the Antarctic and notal regions, in *Biological results of the Soviet Antarctic Expedition (1955–1958)*, Nauka, Moscow/Leningrad, 260–342 pp, 1964. In Russian.

Longhurst, A.R., Vertical migration, in *The Ecology of the Seas*, Cushing, D.H., Walsh, J. Eds., Blackwell Scientific Publications, Oxford, 1976, 116–137.

Longhurst, A.R., Significance of spatial variability, in *Analysis of Marine Systems*, Longhurst, A.R., Ed., Academic Press, New York, 1981, 415–441.

Lopez, M.D.G., Huntley, M.E., Lorette, J.T., *Calanoides acutus* in Gerlache Strait, Antarctica, I: Distribution of late copepodite stages and reproduction during spring, *Mar. Ecol. Prog. Ser.*, 100, 153–168, 1993.

Lorenzo, L.M., Arbones, B., Figueiras, F.G., Tiltstone, G.H., Figueroa, F.L., Photosynthesis, primary production, and phytoplankton growth rates in Gerlache and Bransfield Straits during Austral summer cruise FRUEIA 95, *Deep-Sea Res.*, 11, 707–721, 2002.

Lowry, J.K., The soft bottom macrobenthic community of Arthur Harbor, Antarctica, Master's Thesis, College of William and Mary, Williamsburg, Virginia, 1969.

Lowry, J.K., Soft bottom macrobenthic community of Arthur Harbor, Antarctica, *Antarct. Res. Ser.*, 23(1), 1–19, 1975.

Lowry, J.K., Studies on the macrobenthos of the Southern Ocean, Ph.D. Thesis in Zoology, University of Canterbury, Christchurch, 1976.

Lubimova, T.G., Zonation of the oceanographic structure and biological resources of the Southern Ocean, in *Tesisy Vesesoyaz konf po teorii formiarovaniya chiselnnosti i ratsionalonogo ispolzovaniya stad promyslovykh ryb*, VNIRO, Moscow, 1982, 205–207. In Russian.

Lubimova, T.G., Ecological basis of exploitation of the resources of Antarctic krill, *Mem. Natl. Inst. Polar Res., Spec. Issue*, 27, 211–219, 1983.

Lubimova, T.G., Shust, K.V., Quantitative study of Antarctic krill consumed by principal groups of species, in *Biological Resources of Antarctic Krill*, Lubimova, T.G., Ed., VNIRO, Moscow, 1980, 203–224.

Lubimova, T.G., Naumov, A.G., Lagunov, L.L., Prospects of the utilization of krill and other unconvential resources of the world ocean, *J. Fish. Res. Board Can.*, 30, 2196–2201, 1973.

Lubimova, T.G., Makarov, R.R., Maselenikov, V.V., Shevtsov, W., Shust, K.V., The ecological pecularities, stocks, and the role of *E. superba* in the trophic structure of the Antarctic ecosystem, in *Selected Papers Presented to the Scientific Committee of CCAMLR, 1981–1984, Part II*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1980, 391–505.

Lubimova, T.G., Makarov, R.R., Maselenikov, V.V. et al., The ecological pecularities, stocks and role of *E. superba* in the trophic structure of the Antarctic ecosystem, in *Selected Papers Presented to the Scientific Committee of CCAMLR 1981–1984, Part II*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 391–505, 1984.

Lubimova, T.G., Shust, K.V., Paphov, W., Ecology of mesopelagic fishes, family Myctophidae, Southern Ocean, in *Biological Resources of the Arctic and Antarctic*, Nauka, Moscow, 1987, 330–377.

Lubin, D., Mitchell, B.G., Frederick, J.E., Alberts, A.D., Booth, C.R., Lucas, T., Neuschuler, D., A contribution towards understanding the biospheric significance of Antarctic ozone depletion, *J. Geophys. Res.*, 97(D8), 7817–7827, 1992.

Lucchitta, R.K., Rosanova, C.E., Retreat of the northern margins of George VI and Wilkins Ice Shelves, Antarctic Peninsula, *Ann. Glaciol.*, 27, 41–46, 1998.

Lüning, K., Dieckman, I.T., Environmental triggers in algal seasonality, *Bot. Mar.*, 32, 389–397, 1989.

Lutjeharms, J.R.E., Walter, N.M., Allanson, B.R., Oceanic frontal systems and biological enhancement, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 11–21.

Luxmore, R.A., Moulting and growth in serolid isopods, *J. Exp. Mar. Biol. Ecol.*, 56, 63–85, 1982.

Lynnes, A.S., Reid, K., Croxall, J.P., Tratham, P.N., Foraging distribution and competition for prey between Adélie and chinstrap penguins, *Mar. Biol.*, 14, 1165–1175, 2002.

Lythgoe, J.M., Dartnall, H.J.A., A deep sea rhodopsin in a mammal, *Nature (Lond.)*, 227, 955–956, 1990.

Macaulay, M.C., Madriolas, A., Paly, K., Morrison, P., Hydroacoustic survey for prey organisms, in *AMLR 1989/90 Field Session Report: Objectives, Accomplishments and Tentative Conclusions. Administrative Report* LH-90-11, AERG staff, Ed., 1990, 34–36.

Macauley, M.C., English, T.S., Mathisen, O.A., Acoustic characterization of swarms of Antarctic krill (*Euphausia superba*) from Elephant Island and Bransfield Strait, *J. Crust. Biol.*, 4(Special Issue 3), 16–44, 1984.

MacDonald, J.A., Montgomery, J.C., Animal adaptations to the Antarctic environment, in *Antarctica: The Ross Sea Region*, Hatherton, T., Ed., DSIR Publishing, Wellington, 1990, 220–239.

MacDonald, C.M., Schneppenheim, R., Breeding structure and stock identity n the Antarctic krill, *Euphausia superba*, *Ber. Polarforsch.*, 4, 240–251, 1983.

MacDonald, C.M., Williams, R., Adams, M., Genetic variation and population structure of krill (*Euphausia superba* Dana) from the Prydz Bay region of Antarctic waters, *Polar Biol.*, 6, 233–236, 1986.

MacDonald, J.A., Montgomery, J.C., Wells, R.M.G., Comparative physiology of Antarctic fishes, *Adv. Mar. Biol.*, 24, 321–388, 1987.

Maciejewaka, K., Opalinski, K.W., Spatial and temporal differentiation of food in Antarctic krill, *Euphausia superba*, *Pol. Arch. Hydrobiol.*, 40, 291–311, 1993.

Mackintosh, N.A., Distribution of the macroplankton of the Atlantic sector of the Antarctic, *Discov. Rep.*, 9, 65–160, 1934.

Mackintosh, N.A., The seasonal circulation of the Antarctic macroplankton, *Discov. Rep.*, 16, 365–412, 1937.

Mackintosh, N.A., The southern stocks of whalebone whales, *Discov. Rep.*, 22, 197–300, 1942.

Mackintosh, N.A., *The Stocks of Whales*, Fishing News Books, London, 1965.

Mackintosh, N.A., Whales and krill in the twentieth century, in *Antarctic Ecology*, Vol. 1., Holdgate, M., Ed., Academic Press, London, 1970, 185–212.

Mackintosh, N.A., Life cycle of krill in relation to ice and water conditions, *Discov. Rep.*, 36, 1–94, 1972.

Mackintosh, N.A., Distribution of post-larval krill in the Antarctic, *Discov. Rep.*, 36, 95–156, 1973.

Mackintosh, N.A., Brown, S.G., Preliminary estimates of the southern populations of the larger baleen whale, *Norsk Hvalfangstti*, 45, 469–480, 1953.

Mackintosh, N.A., Wheeler, J.F., Southern blue and fin whales, *Discov. Rep.*, 1, 257–540, 1929.

Madin, L.P., Production, composition and sedimentation of salp faecal pellets in oceanic waters, *Mar. Biol.*, 67, 39–45, 1982.

Mague, T.H., Friberg, E., Hughes, D.H., Morris, I., Extracellular release of carbon by marine phytoplankton: A physiological approach, *Limnol. Oceanogr.*, 25, 262–279, 1979.

Maher, W.J., Breeding biology of the snow petrel near Cape Hallett, Antarctica, *Condor*, 64, 488–499, 1962.

Makarov, R.R., Life cycle and dispersion of *Euphausia superba* Dana, *Trudy VNIRO*, 77, 85–92, 1972. In Russian.

Makarov, R.R., Some peculiarities of the reproduction of *Euphausia superba* (Crustacea: Euphausiacea). Abstracts of papers from *All-Union Conference on Macroplankton*, All-Union Research Institute of Marine Fisheries and Oceanography, Moscow, 1973, 34–35. In Russian.

Makarov, R.R., A study of the repeated maturation of females in euphausiids (Eucarida: Euphausiacea), *J. Zool.*, 54, 670–681, 1975.

Makarov, R.R., Vertical distribution of euphausiid eggs and larvae of the northeastern coast of South Georgia Island, *Oceanology*, 15, 1101–1106, 1978.

Makarov, R.R., Spawning times of Antarctic euphausiids, *Biologii Morya, Vladivostok*, 3, 30, 1979a. In Russian.

Makarov, R.R., Larval distribution and reproductive ecology of *Thysanoessa macrura* (Crustacea: Euphausiacea), *Mar. Biol.*, 52, 377–386, 1979b.

Makarov, R.R., Size composition and conditions of existance of *Euphausia superba* Dana (Crustacea: Euphausiacea) in the eastern part of the Pacific sector of the Southern Ocean, *Oceanology*, 19, 582–585, 1979.

Makarov, R.R., Some problems in the investigation of larval Euphausiids in Antarctica, *Ber. Polarforsch.*, 4, 58–69, 1983.

Makarov, R.R., Solyankin, E.V., Living conditions and structure of the population of *Euphausia superba* in the Lasarev Sea area. Tez dolkl III Veses Korf "Prolemy natsional" nogo ispol 'zovaniya promyslovykh bespozvonochnykh, Atlant NIRO, Karlingrad, 61–66, 1982. In Russian.

Makarov, R.R., Spiridonov, V.V., Life cycle and distribution of the Antarctic krill: Some results of the studies and problems, in *Pelagic Ecosytems of the Southern Ocean*, Veronina, N., Ed., Nauka Press, Moscow, 1993, 158–168. In Russian.

Makarov, R.R., Sysoera, N.V., Biological conditions and distribution of *Euphausia superba* Dana in the Lazarev Sea and adjacent waters, in *Antarctic Krill: The Distribution Pattern and Environment*, Makarov, R.R., Ed., Legkajaiopishevaja Promyshlennost Press, Moscow, 1983, 110–117. In Russian.

Makarov, R.R., Naumov, A.G., Shevstov, V.V., The biology and distribution of Antarctic krill, in *Antarctic Ecology* Vol. 1, Holdgate, M.W., Ed., Academic Press, London, 1970, 173–176.

Makinrtosh, N.A., Maintenance of living *Euphausia superba* and frequency of moults, *Nortsk Hvalfangst-Tidinde*, 5, 97–102, 1967.

Maksimov, I.V., *Atlas of Antarctica*, Vol. 1, VNIRO, Moscow, 1966.

Malakoff, D., Antarctic ice sheet collapses, *Science*, 295, 2359–2365, 2002.

Malone, T.C., Algal size, in *The Physiological Ecology of Phytoplankton*, Morris, I., Ed., Blackwell Scientific Publications, London, 1980, 433–463.

Mandelli, E.F., Burkholder, P.R., Primary productivity in the Gerlache and Bransfield Straits of Antarctica, *J. Mar. Res.*, 24, 15–27, 1966.

Mangel, M., Switzer, P.V., A model of the level of foraging trip for the indirect effects of krill (*Euphausis superba*) on krill predators, *Ecol. Model.*, 105, 235–256, 1998.

Mann, K.H., *Ecology of Coastal Waters: A Systems Approach*, University of California Press, Berkeley, CA, 1982.

Mansfield, A.W., The breeding behaviour and reproductive cycle of the Weddell seal (*Leptonychotes weddelli* Lesson), *Falkland Islands Dependencies Survey, Scientific Reports*, 18, 1–41, 1958.

Marchant, H.J., Choanoflagellates in the Antarctic marine food chain, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 271–276.

Marchant, H.J., Possible impacts of climate change on the organisms of the Antarctic marine ecosystem, in *Impact of Climate Change on Antarctica–Australia*, Australian Government Publication Service, Canberra, 26–33 pp, 1992.

Marchant, H.J., Impacts of ozone depletion on Antarctic organisms, in *Antarctic Communities: Species, Structure and Survival*, Baggatalia, B., Valencia, J., Walton, D.W.H., Eds., Cambridge University Press, Cambridge, UK, 1997, 367–374.

Marchant, H.J., Davidson, A.T., Possible impacts of ozone depletion on trophic interactions and biogenic vertical carbon flow, in *Proceedings of the International Conference on the Role of Polar Regions in Global Climate Change*, Weller, G., Wilson, C.L., Severin, B.A.B., Eds., Geophysical Institute, Fairbanks, 1991, 397–400.

Marchant, H.J., McEldowney, A., Nanoplankton siliceous cysts from Antarctica are algae, *Mar. Biol.*, 92, 53–57, 1986.

Marchant, H.J., Murphy, E.J., Interactions at the base of the Antarctic food web, in *Antarctic Ecology: The BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, UK, 1996, 267–286.

Marchant, H.J., Davidson, A.T., Wright, S.W., The distribution and abundance of chroococcoid cyanobacteria in the Southern Ocean, *Proc. Natl Inst. Polar Res. Symp. Polar Biol.*, 1, 1–9, 1987.

Marchant, H.J., Davidson, A.T., Kelly, G.J., UV-B protecting compounds in the marine alga *Phaeocystis pouchetii* from Antarctica, *Mar. Biol.*, 109, 391–395, 1991.

Marchant, H.J., Watanabe, ?., Kawacke, M., Marine snow in Antarctic coastal waters, *Proc. NIPR Symp. Polar Biol.*, 9, 75–83, 1996.

Marchant, H.J., Davidson, A.T., Wright, S.W., Glasebrook, J., The distribution and abundance of viruses in the Southern Ocean during spring, *Antarct. Sci.*, 12, 414–417, 2000.

Margolis, S., Kennett, J.P., Antarctic glaciation during the Tertiary recorded in sub-Antarctic deep-sea cores, *Science*, 170, 1085–1087, 1970.

Marin, V., The oceanographic structure of the eastern Scotia Sea, IV: Distribution of copepod species in relation to hydrography in 1981, *Deep-Sea Res.*, 34, 105–121, 1987.

Marin, V., Independent life cycles: An alternative to the asynchronism hypothesis for Antarctic calanoid copepods, *Hydrobiol.*, 167/168, 161–168, 1988a.

Marin, V., Qualitative models of the life cycles of *Calanoides acutus, Calanus propinquus*, and *Rhincalanus gigas*, *Polar Biol.*, 8, 439–446, 1988b.

Marin, V.H., Schnack-Schiel, S.B., The occurrence of *Rhincalanus gigas, Calanoides acutus*, and *Calanus propinquus* (Copepoda: Calanoida) in late May in the area of the Antarctic Peninsula, *Polar Biol.*, 13, 35–40, 1993.

Marin, V., Brinton, E., Huntley, M., Depth relationships of *Euphausia superba* eggs and adults near the Antarctic Peninsula 1986–1987, *Deep-Sea Res.*, 38, 1241–1249, 1991.

Marlow, R.J., Mating behaviour of the leopard seal, *Hydrurga leptonyx*, in captivity, *Aust. J. Zool.*, 15, 1–5, 1967.

Marr, J.S., The natural history and geography of the Antarctic krill *Euphausia superba*, *Discov. Rep.*, 32, 33–464, 1962.

Marra, J., Vertical mixing and primary production, in *Primary Productivity in the Sea*, Falkowski, P.G., Ed., Plenum Press, New York, 1980, 121–137.

Marschall, H.-P., Sinking speed of krill eggs and timing of early life history stages, *Ber. Polarforsch.*, 4, 70–73, 1983.

Marschall, H.-P., Overwintering strategy of the Antarctic krill under the pack-ice of the Weddell Sea, *Polar Biol.*, 9, 129–135, 1988.

Marshall, N.B., Egg size in Arctic, Antarctic and deep-sea fishes, *Evolution*, 7, 328–341, 1953.

Marshall, N.B., Fish, in *Antarctic Research*, Priestly, R., Adie, R.J., Robin, G.de Q., Eds., Butterworth, London, 1964, 206–217.

Marshall, S.M., Orr, A.P., On the biology of *Calanus finmarchicus*, VIII: Food uptake, assimilation, and excretion in adult stage V, *J. Mar. Biol. Assoc. U.K.*, 34, 495–529, 1955.

Martin, D., Kauffman, P., Parkinson, C., The movement and decay of ice bands in the Bering Sea, *J. Geophys. Res.*, 88, 2803–2812, 1983.

Martin, J.H., Knauer, G.A., Karl, P.M., Broenkow, W.W., VERTEX: Carbon cycling in the northeast Pacific, *Deep-Sea Res.*, 34, 267–285, 1987.

Martin, J.H., Fitzwater, S.E., Gordon, R.M., Iron deficiency limits phytoplankton growth in Antarctic waters, *Global Biogeochem. Cycles*, 4, 5–12, 1990a.

Martin, J.H., Fitzwater, S.E., Gordon, R.M., Iron in Antarctic waters, *Nature (Lond.)*, 345, 156–158, 1990b.

Martinez, R., Pycnocline and psychotrophic respiratory metabolism in Antarctic microplankton, *Polar Biol.*, 16, 483–489, 1996.

Martinson, D.G., The role of Southern Ocean/sea ice interaction in global climate change, in *International Conference on the Role of Polar Regions in Global Change, University of Alaska, June 11–15, 1990*, 1990, 269–274.

Martinson, D.G., Killworth, P.D., Gordon, A.L., A convective model for the Weddell Polynya, *J. Geophys. Res.*, 11, 466–488, 1981.

Maruyama, T., Toyodo, H., Suzuki, S., Preliminary report on the biomass of macroplankton and micronekton collected with a bongo net during the Umituka Moni FIBEX Cruise, *Trans. Tokyo Univ. Fish.*, 5, 145–153, 1982.

Masaka, Y., Yearly changes of the biological parameters for the Antarctic sei whale, *Rep. Int. Whal. Commun.*, 29, 175–195, 1979.

Masaki, Y., Yearly changes in of the biological parameters for the Antarctic sei whale, *Int. Whaling Comm. Rep.*, 27, 421–429, 1977.

Masaki, Y., Yearly changes in the biological parameters of the minke whale, *Rep. Int. Whal. Commun.*, 29, 375–395, 1979.

Maslennikov, V.V., On the effect of water dynamics on the distribution of *Euphausia superba* Dana in the area of South Georgia, *Trudy Vesesoiuznogo Naucho-issledovatel'skii institita Morskogo Rybngo Khoziaiska i Okeanographii*, 75, 107–117, 1972.

Maslennikov, V.V., Long-term variability in hydrometeorological characteristics of the Southwest Antarctic Atlantic Ocean, *Trudy VNIRO*, 136, 50–56, 1979.

Maslennikov, V.V., Modern concepts of large-scale circulation of Atlantic water and results of mass drift of *Euphausia superba*, in *Biological Resources of Antarctic Krill*, Lubimova, T.G., Ed., VIRNO, Moscow, 1980, 8–27. In Russian.

Maslennikov, V.V., Solyankin, E.V., Patterns of fluctuations in the hydrological conditions of the Antarctic and their effect on the distribution of krill, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin, 1988, 209–213.

Massalaski, A., Leppard, G.G., Morphological examination of fibrillar colloids associated with algae and bacteria in lakes, *J. Fish. Res. Board Can.*, 36, 922–938, 1979.

Mathisen, O.A., Macaulay, M.C., The morphological features of a super swarm of krill, *Mem. Natl Inst. Polar Res., Spec. Issue*, 27, 153–164, 1983.

Mathot, S., Dundois, T.-M., Lancelot, C., Gross and net primary production in the Scotia-Weddell Sea sector of the Southern Ocean during spring 1988, *Polar Biol.*, 12, 321–332, 1992.

Mathot, S., Dundois, T.-M., Lancelot, C., Gross and net primary production in the Scotia-Weddell Sea sector of the Southern Ocean during spring 1988, in *Weddell Sea Ecology*, Hempel, G., Ed., Springer, Berlin, 1995, 321–332.

Mathewa, L.H., The humpback whale, *Megaptera nodosa*, *Discov. Rep.*, 17, 70–92, 1937.

Matsuda, O., Ishikawa, S., Kawaguchi, K., Seasonal variation of downward flux of particulate organic matter under the Antarctic fast ice, *Proc. NIPR Symp. Polar Biol.*, 1, 23–34, 1987.

Matsuda, O., Ishikawa, S., Kawaguchi, K., Fine-scale observation on salinity stratification in an ice hole during the melting season, *Antarct. Rec.*, 34, 357–362, 1990.

Matsuoka, K., Watanabe, T., Ichii, T., Kishimata, H., Nishiwaki, S., Large-scale distribution (south of 60° S, 35° E–130° E) in relation to the southern boundary of the Antarctic Circumpolar Current, in *Antarctic Biology in a Global Context*, Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backuys Publishers, Leiden, The Netherlands, 2003, 26–30.

Matthews, L.H., The natural history of the elephant seal, *Discov. Rep.*, 1, 233–250, 1929.

Matthews, L.H., *South Georgia: The British Empire's Subantarctic Outpost*, Simpkin Marshall, London, 1931.

Mauchline, J., Antarctic krill biology, *BIOMASS Rep. Ser.*, 10, 1–52, 1979.

Mauchline, J., The biology of mysids and euphausiids, *Adv. Mar. Biol.*, 18, 1–681, 1980a.

Mauchline, J., Studies of patches of krill, *Euphausia superba* Dana. *BIOMASS Handbook No. 6*, 1980b.

Mauchline, J., Fisher, L.R., The biology of euphausiids, *Adv. Mar. Biol.*, 7, 1–454, 1969.

Maxwell, J.G.H., The breeding biology of *Chorismus antarcticus* (Pieffer) and *Notocragnon antarcticus* (Pieffer) (Crustacea: Decapoda) and its bearing on the problem of the impoverished Antarctic decapod fauna, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Gulf Publications, Houston,TX, 1977, 335–342.

Maxwell, J.G.H., Ralph, R., Non-cold-adapted metabolism in the decapod *Chlorismus antarcticus* and other sub-Antarctic marine crustaceans, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 397–406.

May, R.M., Beddington, J.R., Clark, C.W., Holt, S.J., Laws, R.M., Management of multispecies fisheries, *Science*, 205, 267–277, 1979.

Maykut, G.A., The ice environment, in *Sea Ice Biota*, Horner, R.A., Ed., CRC Press, Boca Raton, FL, 1985, 21–82.

Maykut, G.A., Grenfell, T.C., The spectral distribution of light beneath first-year sea ice in the Arctic Ocean, *Limnol. Oceanogr.*, 20, 554–563, 1975.

Maynard, S.D., Riggs, F.V., Walters, J.F., Mesopelagic micronekton in Hawaiian waters: Faunal composition, standing stock and diel vertical migration, *Fish. Bull.*, 73, 726–736, 1973.

Mayzand, P., Faber-Lorda, J., Corre, M.C., Aspects of nutritional metabolism of two Antarctic euphausiids: *Euphausia superba* and *Thysanoessa macrura*, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 330.

McAlister, W.B., Sayer, G.A., Perez, M.S., Preliminary estimates of pinnipoed-finfish relationship in the Bering Sea. *Background Paper 19th Meeting Fur Seal Commission, Moscow, 1976*, U.S. Department of Commerce, NOAA, NMFS, Seattle, WA, 1976, 1–10.

McCann, T.S., Population structure and social organization of southern elephant seals, *Mirounga leonina* (L.), *Biol. J. Linn. Soc.*, 14, 133–150, 1980a.

McCann, T.S., Territoriality and breeding behaviour of adult male Antarctic fur seals, *Arctocephalus gazella*, *J. Zool. (Lond.)*, 192, 295–310, 1980b.

McCann, T.S., Aggression and sexual activity of male southern elephant seals, *Mirounga leonina*, *J. Zool. (Lond.)*, 195, 295–310, 1981a.

McCann, T.S., The social organization and behaviour of the southern elephant seal, *Mirounga leonina* (L.), Ph.D. thesis, University of London, 1981b.

McCann, T.S., Population size and demography of the southern elephant seal, in *Sea Mammals of Southern Latitudes*, Bryden, M.M., Ling, J., Eds., South Australia Museum, Adelaide, 1983, 1–19.

McCarthy, J.J., Canziani, O.F., Leung, N.A., Dokken, D.J., White, J.S., *Climate change 2001: Impacts, adaptations and vulnerability*, Contribution of the Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK, 2001.

McClatchie, S., Food-limited growth of *Euphausia superba* in Admiralty Bay, South Shetland Islands, Antarctica, *Cont. Shelf Res.*, 8, 329–345, 1988.

McClatchie, S., Boyd, C.M., A morphological study of sieve efficiencies and mandibular surfaces in the Antarctic krill *Euphausia superba*, *Can. J. Fish. Aquat. Sci.*, 40(7), 955–967, 1983.

McClintock, J.B., Karentz, K., Mycosporine-like amino acids in 38 species of subtidal marine organisms from McMurdo Sound, *Aquat. Sci.*, 9, 392–398, 1997.

McConville, M.J., Wetherbee, R., The bottom-ice microalgal community from the annual ice in the inshore waters of East Antarctica, *J. Phycol.*, 19, 431–439, 1983.

McConville, M.J., Mitchell, C., Wetherbee, R., Productivity and patterns of carbon assimilation in a microalgal community from annual sea ice, East Antarctica, *Polar Biol.*, 4, 135–141, 1985.

McDonald, S.J., Kennicutt, M.C. III, Sericano, J., Wade, T.L., Liu, H., Safe, S.H., Correlation between bioassay-derived P4501 A1 induction activity and chemical analysis of clam (*Laternula elliptica*) extracts from McMurdo Sound, Antarctica, *Chemosphere*, 28, 2237–2248, 1994.

McElroy, J.K., The economics of harvesting krill, in *The Management of the Southern Ocean*, Mitchell, B., Sandbrook, R., Eds., International Institute for Environment and Development, London, 1980a, 81–103.

McElroy, J.K., Economic evaluation of krill fishing systems, in *Advances in Fish Science and Technology*, Connell, J.J., Ed., Fishing News Books Ltd, Farnham, 1980b, 314–321.

McFeters, G.A., Barry, J.P., Howington, J.P., Distribution of enteric bacteria in Antarctic seawater surrounding a sewage outfall, *Water Res.*, 27(4), 645–650, 1993.

McHugh, J.L., The role and history of the International Whaling Commission, in *The Whale Problem: A Status Report*, Schevil, W.E., Ed., Harvard University Press, Harvard, NJ, 1974, 359–368.

McMinn, A., Preliminary investigation of the contribution of fast-ice algae to the spring phytoplankton bloom in Ellis Fjord, Antarctica, *Polar Biol.*, 16, 301–307, 1996.

McMinn, A., Heijnis, H., Hodgson, D., Preliminary sediment core evidence against short-term UV-B induced changes in Antarctica coastal diatom communities, in *Antarctic Communities: Species, Structure and Survival*, Baggatalia, B., Valencia, H., Walton, D.W., Eds., Cambridge University Press, Cambridge, UK, 1997, 381–387.

McMinn, A., Skerratt, J., Trull, T., Ashworth, C., Lizotte, M., Nutrient stress gradient in the bottom 5 cm of fast ice, McMurdo Sound, Antarctica, *Polar Biol.*, 21, 220–227, 1999.

McRoy, C.P., Goering, J.J., The influence of ice on the primary productivity of the Bering Sea, in *Oceanography of the Bering Sea*, Hand, D.W., Ed., Institute of Marine Science, University of Alaska, Fairbanks, AK, 1974, 403–421.

McSweeny, E.S., Systematics and morphology of the Antarctic cranchiid squid *Galiteuthis glacialis* (Chun.), *Antarct. Res. Ser.*, 27, 1–39, 1978.

McWhinnie, M.A., Denys, C., Biological studies of Antarctic krill, austral summer, *Antarct. J. U.S.*, 13, 133–137, 1978a.

McWhinnie, M.A., Denys, C., *Antarctic Marine Living Resources With Special References to Krill Euphausia superba: Assessment of Adequacy of Present Knowledge*, Antarctic Science Foundation, Washington, DC, Report No. NSF/RA 768/4889, 1978b.

McWhinnie, M.A., Denys, C., Parkin, R., Parkin, K., Biological investigations of *Euphausia superba* Dana, *Antarct. J. U.S.*, 14, 163–164, 1979.

Medlin, K., Priddle, J., Eds., *Polar Marine Diatoms*, British Antarctic Survey, Natural Research Council, Cambridge, UK, 1990.

Meguro, H., Plankton ice in the Antarctic Ocean, *Antarc. Rec.*, 14, 1192–1199, 1962.

Meguro, H., Ito, K., Fukushima, H., Ice flora (bottom type): A mechanism of primary production in polar seas and the growth of diatoms in sea ice, *Arctic*, 20, 114–133, 1967.

Meissner, E.E., Tom, V.S., Silon, V.N., Characteristics of the behaviour and biological cycles of the marbled Notothenia, *Notothenia rossii*, in relation to bottom topography, bottom materials, and currents, *J. Ichthyol.*, 14, 706–708, 1974.

Mengesha, S., Dehairs, F., Fiala, M., Elskens, M., Goryens, L., Seasonal variation of phytoplankton community structure and nitrogen uptake regime in the Indian Sector of the Southern Ocean, *Polar Biol.*, 20, 259–272, 1998.

Menshenina, L.L., Mrlnihov, I.A., Under-ice zooplankton of the western Weddell Sea, *Proc. NIPR Symp. Polar Biol.*, 8, 126–138, 1995.

Mercer, J.H., West Antarctic ice sheets and greenhouse effect: A threat of disaster, *Nature (Lond.)*, 271, 321–325, 1978.

Meredith, M.P., Renfrew, A., Claeke, A., King, J.C., Brandon, M.A., Impact of the 1997; 98 ENSO on upper waters in Marguerite Bay, western Antarctic Peninsula, *J. Geophys. Res.*, 109, 2240–2257, 2004.

Meridith, M.P., Vassie, J.M., Hayward, K.J., Spencer, R., On temporal variability in the transport through Drake passage, *J. Geophys. Res.*, 101, 22485–22494, 1996.

Metz, C., Feeding of *Oncaea curvata* (Poecilostomatoida: Copepoda), *Mar. Ecol. Prog. Ser.*, 229, 229–235, 1998.

Metz, C., Schnack-Schiel, S.B., Observations on carnivorous feeding in Antarctic calanoid copepods, *Mar. Ecol. Prog. Ser.*, 129, 71–75, 1995.

Metz, B., Davidson, O., Swaet, R., Pari, J., Eds., *Climate Change 2001: Mitigation Contribution of Working Group III to the Third Assessment of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, UK, 2001.

Meyer, M.A., El-Sayed, S.Z., Grazing of *Euphausia superba* on natural populations, *Polar Biol.*, 1, 193–197, 1983.

Meyer, B., Atkinson, A., Blume, B., Bathmann, U.V., Feeding and energy budgets of larval Antarctic krill (*Euphausia superba*) in summer, *Mar. Ecol. Prog. Ser.*, 257, 167–178, 2003.

Mezykowski, T., Rakusa-Suszczewski, S., The circadian rhythms in *Euphausia superba* Dana and its carbohydrate metabolism, *Meeresforschung*, 27, 124–129, 1979.

Michel, R.L., Linck, T.W., Williams, P.M., Tritium and carbon-14 distributions in sea water from under the Ross Ice Shelf Project Hole, *Science*, 203, 445–446, 1989.

Mileikovsky, S.A., Types of larval development in marine bottom invertebrates, their distribution, and ecological significance: A re-evaluation, *Mar. Biol.*, 10, 193–213, 1971.

Miller, D.G.M., Cannibalism in *Euphausia superba* Dana, *S. Afr. J. Antarc. Res.*, 12, 50–57, 1982.

Miller, D.G.M., The South African SIBEX I Cruise to the Prydz Bay region, 1984. IX: Krill (*Euphausia superba* Dana), *S. Afr. J. Antarc. Res.*, 15, 33–41, 1985.

Miller, D.G.M., Results from biological investigations of krill (*Euphausia superba* Dana) in the Southern Ocean during SIBEX I, *Mem. Natl Inst. Polar Res., Spec. Issue*, 40, 117–139, 1986a.

Miller, D.G.M., Modelling and decision-making as part of the CCAMLR management regime. SC-CAMLR-V/BG/17 in *Selected scientific papers 1986*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1986b, 295–322.

Miller, D.G.M., Antarctic krill and ecosystem management, *WG-Emm-01 Presentation Paper, CCAMLR Science*, 9, 174–212, 2003.

Miller, D.G.M., Hampton, I., *Biology and Ecology of the Antarctic Krill (Euphausia superba Dana): A Review*, BIOMASS Scientific Series No. 9, 1–166 pp, 1985.

Miller, D.G.M., Hampton, I., *Biology and Ecology of Antarctic Krill* (*Euphausia superba* Dana), 9, 1–166, 1989.

Miller, K.A., Pearse, J.S., Ecological studies of seaweeds in McMurdo Sound, Antarctica, *Am. Zool.*, 31, 35–48, 1991.

Miller, M.A., Krempin, D.W., Manahan, D.T., Sullivan, C.W., Growth rates, distribution, and abundance of bacteria in the ice-edge zone of the Weddell and Scotia Seas, Antarctica, *Antarct. J. U.S.*, 19, 103–105, 1984.

Miller, D.G.M., Hampton, I., Henry, J., Abrams, R.W., Cooper, J., The relationship between krill food requirements and phytoplankton production in a sector of the Southern Indian Ocean, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 362–371.

Minagawa, M., Wada, E., Stepwise enrichment of ^{15}N along food chains: Further evidence and the relationship between ^{15}N and annual age, *Geochim. Cosmochim. Acta.*, 48, 1135–1140, 1984.

Minelli, A., *Ecology and Systematics. The State of the Art*, Chapman and Hall, London, 1993.

Minks, S., Smith, C.M., DeMaster, D., Persistance of labile organic matter and microbial biomass in Antarctic shelf sediments: Evidence of a sediment "food bank", *Mar. Ecol. Prog. Ser.*, 300, 3–19, 2005.

Mitchell, B.G., Predictive bio-optical relationship for polar oceans and marginal ice zones, *J. Mar. Syst.*, 3, 91–105, 1992.

Mitchell, E., Trophic relationships and competition for food in northwest Antarctic waters, in *Proceedings of the Canadian Zoologists Annual Meeting*, Burt, O., Ed., 1975, 123–133.

Mitchell, E., Trophic relationships and competition for food in northwest Antarctic whales, in *Proceedings of the Canadian Zoologists Annual Meeting*, Burt, M.D.B., Ed., 1994, 123–125.

Mitchell, B.G., Holm-Hansen, O., Observations and modelling of the Antarctic phytoplankton standing crop in relation to mixing depth, *Deep-Sea Res.*, 38, 981–1007, 1991.

Mitchell, B.G., Karentz, D., The induction and repair of DNA photodamage in the environment, in *Environmental UV Photobiology*, Young, A.R., Ed., Plenum Press, New York, 1993, 345–377.

Mitchell, B., Sandbrook, R. *The Management of the Southern Ocean*, Institute for Environment and Development, London, 1980.

Mitchell, J.G., Silver, M.W., Modern archaeomonads indicate sea-ice environments, *Nature (Lond.)*, 196, 437–439, 1982.

Mitchell, B.G., Brody, E.A., Holm-Hansen, O., McCain, C., Bishop, J., Light limitation of phytoplankton biomass and macronutrient utilization in the Southern Ocean, *Limnol. Oceanogr.*, 36, 1662–1677, 1991.

Mitskevich, I.N., Kriss, A.Ye., Total numbers and production of microorganisms in the waters of the Southern Ocean, *Microbiologia*, 44, 135–140, 1973.

Mitskevitch, L.G., Mosolov, V.V., A study of proteolytic enzymes of krill, in *Krill Processing Technology*, Bykov, V.P., Ed., VNIRO, Moscow, 1981, 21–24. In Russian with English summary.

Mizroch, S.A., Some notes on southern hemisphere baleen whale pregnancy trend rates, *Int. Whaling Comm. Rep.*, 30, 361–374, 1980.

Mizroch, S.A., Further notes on southern hemisphere baleen whale pregnancy rates, *Int. Whaling Comm. Rep.*, 31, 629–633, 1981a.

Mizroch, S.A., Analysis of some biological parameters of the Antarctic fin whale (*Balaenoptera physalus*), *Int. Whaling Comm. Rep.*, 31, 425–434, 1981b.

Mizroch, S.A., Reproductive rates in southern hemisphere baleen whales, M.A. Thesis, University of Washington, 1983.

Mizroch, S.A., York, A.E., Have pregnancy rates of southern hemisphere fin whales, *Balaenoptera physalis*, increased, in *Whales, Dolphins and Porpoises*, International Whaling Commission Special Issue, 6, 401–410, 1984.

Mizroch, S.A., Rice, D.W., Bengtson, J.L., *Prodomus of an Atlas of Balaenopterid Whale Distribution in the Southern Ocean Based on Pelagic Catch Data*, U.S. National Marine Fisheries Service, National Marine Laboratory, Seattle, WA, 1986.

Mizutani, H., Wada, E., Nitrogen and carbon isotope ratios in seabird rookeries and their ecological implications, *Ecology*, 69, 340–349, 1988.

Moe, R.L., DeLaca, T.E., Occurrence of macroscopic algae along the Antarctic Peninsula, *Antarc. J. U.S.*, 11, 20–24, 1976.

Moebus, K., Johnson, K.M., Exudation of dissolved organic carbon by brown algae, *Mar. Biol.*, 26, 117–125, 1974.

Moiseev, P.A., Some aspects of commercial use of krill resources of the Antarctic seas, in *Antarctic Ecology*, Vol. 1, Holdgate, M.W., Ed., Academic Press, London, 1970, 213–216.

Moline, M.A., Prezelin, B.B., Longterm monitoring and analysis of physical factors regulating variability in coastal Antarctic phytoplankton biomass, *in situ* productivity and taxonomic composition over subseasonal, seasonal and interannual time scales, *Mar. Ecol. Prog. Ser.*, 145, 143–160, 1996.

Moline, M.A., Preslen, B.B., High resolution time series data for 1991/1992 primary production and related parameters at a Palmer LTER coastal site: Implications for modelling carbon fixation in the Southern Ocean, *Polar Biol.*, 97, 39–53, 1997.

Moline, M.A., Prézelin, B.B., Schofield, O., Smith, R.C., Temporal dynamics of coastal Antarctic phytoplankton: Environmental driving forces and impact of a 1991/92 summer diatom bloom on the nutrient regimes, in *Antarctic Communities: Species, Structure and Survival*, Battaglia, B., Valencia, H., Walton, D.W.H., Eds., Cambridge University Press, Cambridge, UK, 1997, 67.

Molloy, K.D., Holman, M.A., Mitchell, D., Dietrich, H.W., Solar UVB-induced DNA damage and photosynthetic DNA repair in Antarctic zooplankton, *Proc. Natl Acad. Sci. USA*, 94, 1258–1263, 1997.

Monmin, E., Indermühle, A., Dällenbach, A., Flückiger, J., Stauffer, B., Stocker, T.F., Raynaud, D., Barnola, J.-M., Atmospheric CO_2 concentrations over the last glacial termination, *Science*, 291, 112–114, 2001.

Montague, T.L., Food of Antarctic petrels (*Thalassoica antarctica*), *Emu*, 84, 144–245, 1984.

Montu, M., de Olivera, I.R., Zooplankton associations, trophic relationships, standing stock of krill, and other groups of the community near Elephant Island (February–March 84/85), *Neritica*, 1, 111–130, 1986.

Moors, P.J., Spier, T.W., Lyon, G.L., Soil analyses and ^{13}C/^{12}C ratios identify sites of deserted Rockhopper Penguin colonies, *The Auk*, 106, 796–799, 1985.

Mopper, K., Zhou, V., Hydroxyl radical photoreproduction in the sea and its potential impact on marine processes, *Science*, 250, 661–664, 1990.

Morales, C.E., Harris, R.D., Head, R.V., Tranter, P.R.G., Copepod grazing in the oceanic northeast Atlantic during a 6-week drifting station: The contribution of size classes and vertical migration, *J. Plankton Res.*, 15, 185–211, 1993.

Moran, X.A.G., Gasol, J.M., Pedros-Alio, C., Estrada, M., Dissolved and particulate primary production and bacterial production on offshore Antarctic waters during austral summer: Coupled or uncoupled?, *Mar. Ecol. Prog. Ser.*, 222, 25–39, 2001.

Mordy, C.W., Penny, D.M., Sullivan, C.W., Spatial distribution of bacterioplankton biomass and production in the marginal ice-edge zone of the Weddell-Scotia Sea during austral winter, *Mar. Ecol. Prog. Ser.*, 122, 9–19, 1995.

Moreno, C.A., Somatometria y alimentación natural de *Hapagifer georgians antarctica* Nyblin, en Bahia Fildes, Isla Rey Jorge, Antártica, *Bol. Inst. Antárt. Chil.*, 6, 9–14, 1971.

Moreno, C.A., Observations on food and reproduction in *Trematomus bernacchii* (Pisces: Nototheniidae) from Palmer Archipelago, Antarctica, *Copeia*, 1, 171–173, 1980.

Moreno, C.A., Bahamonde, N., Nichos alimentarios y competercia por alimento entre *Notothenia coreiiceps neglecta* Nybelin y *Notothenia rossii marmmorata* Fischeren Shetland del Sur Antarctica, *Instituto Antárctico Chileno, Serie Científico*, 3, 45–62, 1975.

Moreno, C.A., Osorio, H.H., Bathymetric food habits in the Antarctic fish *Notothenia gibberifrons* Lönnberg (Pisces: Nototheniidae), *Hydrobiologica*, 55, 139–144, 1977.

Morita, R.Y., Psychrophilic bacteria, *Bacteriol. Rev.*, 39, 144–167, 1975.

Morita, R.Y., Griffith, R.P., Hayasaka, S.S., Heterotrophic activity of microorganisms in Antarctic waters, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 99–113.

Morris, D.J., Filtration rates of *Euphausia superba* Dana: Under- or overestimates?, *J. Crust. Biol.*, 4(Special Issue No. 1), 185–197, 1984.

Morris, D.J., Integrated model of moulting and feeding of Antarctic krill *Euphausia superba* off South Georgia, *Mar. Ecol. Prog. Ser.*, 22, 207–217, 1985.

Morris, D.J., Keck, A., The time course of the moult cycle and growth of *Euphausia superba* in the laboratory, *A Preliminary Study. Meeresforschung*, 30, 94–100, 1984.

Morris, D.J., Priddle, J., Observations on feeding and moulting of the Antarctic krill, *Euphausia superba* Dana, *Br. Antarc. Surv. Bull.*, 65, 57–63, 1984.

Morris, D.J., Ricketts, C., Feeding of krill around South Georgia, I: A model of feeding activity in relation to depth and time of day, *Mar. Ecol. Prog. Ser.*, 16(1), 1–7, 1984.

Morris, D.J., Ward, P., Clarke, A., Aspects of the feeding in Antarctic krill, *Euphausia superba*, *Polar Biol.*, 2, 21–26, 1983.

Morris, D.J., Watkins, J., Ricketts, C., Buchholz, F., Priddle, J., An assessment of the merits of length and weight measurements of Antarctic krill, *Euphausia superba*, *Br. Antarc. Surv. Bull.*, 79, 27–50, 1988.

Mortensen, T., Echinoidea and Ophiuroidea, *Discov. Rep.*, 12, 199–348, 1936.

Motoi, T., Ono, N.O., Wakatsuchi, M., A mechanism for the formation of the Weddell Polyna in 1974, *J. Phys. Oceanogr.*, 17, 2241–2247, 1987.

Mougin, J.-L., Ecologie comparée des Procelariidae antarctique et subantarctique, *Comité National Français des Recherches Antartiques*, 36, 1–195, 1975.

Mougin, J.-L., Prévost, J., Evolution annuelle des effectifs de des biomasses des oiseaux antarctiques, *Rev. Ecol. (Terre Vie)*, 34, 101–133, 1980.

Muench, R.D., Mesoscale oceanographic features associated with the central Bering Sea ice edge: February–March 1981, *J. Geophys. Res.*, 88, 2715–2722, 1983.

Muench, R.D., Charnell, R.L., Observations on medium-scale features along the seasonal ice edge in the Bering Sea, *J. Phys. Oceanogr.*, 7, 602–606, 1977.

Muench, R.D., LeBond, P.H., Hachmeister, L.E., On some possible interactions between internal waves and sea ice in the marginal ice zone, *J. Geophys. Res.*, 88, 2819–2826, 1983.

Mujica, A.R., Asencio, V., Distribution and abundance of krill larvae (*Euphausia superba* Dana), *Ber. Polarforsch.*, 4, 21–29, 1983.

Mujica, A.R., Torres, A.G., Quantitative and qualitative analysis of Antarctic zooplankton, *Ser. Cient. INACH*, 28, 165–174, 1982.

Müller-Karger, F., Alexander, V., Nitrogen dynamics in a marginal sea-ice zone, *Cont. Shelf Res.*, 7, 805–823, 1987.

Müller-Schwarze, D., Müller-Schwarze, C., Relations between leopard seals and Adélie Penguins, *Rapp. P.-V. Reun. CIESM Mediterr. Monaco*, 169, 394–404, 1975.

Müller-Schwarze, D., Müller-Schwarze, C., Interactions between South Polar skuas and Adélie Penguins, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 619–646.

Mullin, M.M., *In situ* measurement of filtering rates of the salp, *Thalia democratica*, on phytoplankton and bacteria, *J. Plankton Res.*, 5, 279–288, 1983.

Mullin, M.M., Brooks, R.E., Extractable lipofuscin in larval *Euphausia superba*, *Fisheries Bulletin of the United States*, 86, 407–415, 1989.

Mullins, B.W., Priddle, J., Relationships between bacteria and phytoplankton in the Bransfield Strait and Southern Drake Passage, *Br. Antarc. Surv. Bull.*, 76, 51–64, 1987.

Mumm, N., Zur Ernahrungsphyiologies des Krill (*Euphausia superba*) im Winter Untersuchungen anhand der Verdauungstenzyme Amylase und Trypsin. Diplomarbeit, Universität Keil, 1987.

Murano, M., Segawa, S., Kato, M., Moulting and growth of the Antarctic krill in the laboratory, *Transactions of the Tokyo University of Fishery*, 3, 99–106, 1979.

Murphy, R.C., Notes on the sea elephant, *Mirounga leonina* Linne, *Bull. Am. Mus. Nat. Hist.*, 33, 63–79, 1914.

Murphy, G.I., Clupeoids, in *Fish Population Dynamics*, Gulland, J.A., Ed., Wiley, London, 1977, 283–308.

Murphy, E.J., Reid, K., Modelling Southern Ocean krill population dynamics: Biological processes generating fluctuations in the South Georgia ecosystem, *Mar. Ecol. Prog. Ser.*, 217, 175–189, 2001.

Murphy, E.J., Morris, D.J., Watkins, J.L., Priddle, J., Scales of interaction between Antarctic krill and the environment, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin, 1988, 120–130.

Murphy, E.J., Everson, I., Murray, A., Analysis of acoustic line-transect data from the waters around South Georgia: Estimation of krill (*Euphausia superba* Dana) biomass, in *Selected scientific papers, 1991*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1991, 225–243.

Murphy, E.J., Watkins, J.L., Reid, K., Trathan, P.N., Everson, I., Croxall, J.P.., Priddle, J., Brandon, M.A., Brierley, A.S., Hofmann, E., Interannual variability of the South Georgia marine ecosystem: Biological and physical sources of variation in the abundance of krill, *Fish. Oceanogr.*, 7, 381–390, 1998.

Murray, A.G., Jackson, G.A., Viral dynamics, 2: a model of the interaction of ultraviolet light and mixing processes on viral survival in seawater, *Mar. Ecol. Prog. Ser.*, 102, 105–114, 1993.

Muzzarelli, R.A.A., *Chitin*, Pergamon Press, Oxford, 1977.

Nagata, Y., Michada, Y., Umimura, Y., Variation in the positions and structures of oceanic fronts in the Indian ocean for the period from 1965 to 1987, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin/Heidelberg, 1988, 92–98.

Naito, Y., Iwami, T., Fish fauna in the northeastern parts of Lützow-Holm Bay, with some notes on stomach contents, *Memoirs Natl Inst. Polar Res., Spec. Issue*, 32, 64–72, 1982.

Naito, Y., Taniguchi, A., Hamada, E., Some observations on swarms and mating behaviour of Antarctic krill (*Euphausia superba* Dana), *Memoirs Natl Inst. Polar Res., Spec. Issue*, 40, 153–161, 1986.

Nakamura, S., Development of *Euphausia* as a valuable protein for humans. Unpublished note, FAO Internal Consultation on Krill, Rome, 1974.

Nast, F., The vertical distribution of larval and adult krill (*Euphausia superba* Dana) on a time station south of Elephant Island, South Shetlands, *Meeresforschung*, 27, 103–118, 1978.

Nast, F., The assessment of krill (*Euphausia superba* Dana) biomass from a net sampling programme, *Meeresforsch*, 24, 154–159, 1982.

Nast, F., Gieskes, W.W.C., Phytoplankton observations relative to krill abundance around Elephant Island in November 1983, *Arch. Fischereiwiss.*, 37, 95–106, 1986.

Nasu, K., Hydrography in relation to the distribution of euphausiids in the Antarctic Ocean, *Bull. Jap. Soc. Fish. Oceanogr.*, 24, 35–38, 1974.

Nasu, K., On the geographic boundary of Antarctic krill distribution, *Ber. Polarforsch.*, 4, 216–222, 1983.

National Academy of Sciences, An Evaluation of Antarctic Marine Ecosystem Research. (1981), National Academy of Sciences Press, Washington, DC, 1981.

Naumov, A.G., Some features of the distribution and biology of *Euphausia superba* Dana, *Informational Bulletin of the Soviet Antarctic Expedition*, 39, 191–193, 1962.

Naumov, A.G., Chekunova, V.I., Energy requirements of pinnipeds (Pinnipedia), *Oceanology (Mosc.)*, 20, 348–350, 1980.

Naumov, A.G., Permitin, Y.Y., Trophic relationships of *Euphausia superba* Dana and fish of the Southern Ocean (Scotia Sea), *Trudy VNIRO*, 93, 216–229, 1973. In Russian.

Neale, P.J., Lesser, M.P., Cullen, J.J., Effects of ultraviolet radiation on the photosynthesis of phytoplankton in the vicinity of McMurdo Station, Antarctica, in *Ultraviolet Radiation in Antarctica: Measurements and Biological Effects*, Sweiler, C., Penhale, P.A., Eds., American Geophysical Union, Washington, DC, 1994, 125–142.

Neale, P.J., Davis, R.F., Cullen, J.J., Interactive effects of ozone depletion and vertical mixing on photosynthesis of Antarctic phytoplankton, *Nature (Lond.)*, 392, 585–589, 1998.

Nedwell, D.B., Walker, T.R., Sediment-water fluxes of nutrients in an Antarctic coastal environment: Influence of bioturbation, *Polar Biol.*, 15, 57–64, 1995.

Nelson, D.M., Particulate matter and nutrient distributions in the ice-edge zone of the Weddell Sea: Relationship to hydrography during the late summer, *Deep-Sea Res.*, 36, 191–209, 1989.

Nelson, D.M., Gordon, L.I., Production and dissolution of biogenic silica in the Southern Ocean, *Geochim. Cosmochim. Acta.*, 46, 491–501, 1982.

Nelson, D.M., Smith, W.O., Jr., Phytoplankton bloom dynamics of the western Ross Sea ice edge, II: Mesoscale cycling of nitrogen and silica, *Deep-Sea Res.*, 33, 1389–1412, 1986.

Nelson, D.M., Smith, W.O., Jr., Sverdrup revisited: Critical depths, maximum chlorophyll levels, and the control of Southern Ocean productivity by the irradiance-mixing regime, *Limnol. Oceanogr.*, 36, 1650–1661, 1991.

Nelson, D.M., Goering, J.J., Boisseau, D., Consumption and regeneration of silicic acid in three coastal upwelling systems, in *Coastal Upwelling*, Richards, F.A., Ed., American Geophysical Union, Washington, DC, 1981, 242–256.

Nelson, D.M., Smith, W.O., Jr., Gordon, L.I., Huber, B.A., Spring distributions of density, nutrients and phytoplankton biomass in the ice edge zone of the Weddell Sea, *J. Geophys. Res.*, 92, 7181–7190, 1987.

Nelson, D.M., Smith, W.O., Jr., Muench, R.D., Gordon, L.I., Sullivan, C.W., Husby, D.M., Particulate matter and nutrient distributions in the ice-edge zone of the Weddell Sea: Relationship to hydrography during the late summer, *Deep-Sea Res.*, 36, 191–209, 1989.

Nemoto, T., Food of baleen whales with reference to whale movements, *Sci. Rep. Whales Res. Inst. Tokyo*, 14, 149–290, 1959.

Nemoto, T., Feeding of bakeen whales and the value of krill as a marine resource, in *Symposium on Antarctic Oceanography, Santiago, Chile, 1966*, Currie, R.I., Ed., Scott Polar Research Institute, Cambridge, 1966, 340–353.

Nemoto, T., Feeding patterns of baleen whales in the ocean, in *Marine Food Chains*, Steele, J.H., Ed., University of California Press, Berkeley, CA, 1970, 241–252.

Nemoto, T., History of research into food and feeding of euphausiids, *Proc. Rl. Soc. Edinb., Ser. B (Biol.)*, 73, 259–265, 1972.

Nemoto, T., Harrison, G., High-latitude ecosystems, in *Analysis of Marine Ecosystems*, Longhurst, A.R., Ed., Academic Press, London/New York, 1981, 95–126.

Nemoto, T., Nasu, K., Present status of exploitation of krill in the Antarctic, in *Oceanology International 75*, BPS Exhibitions Ltd, London, 1975, 353–360.

Nemoto, T., Doi, T., Nasu, K., Biological characteristics of krill caught in the Southern Ocean, in *Biological Investigations of Marine Antarctic Systems and Stocks, Volume II*, El-Sayed, S.Z., Ed., SCAR and SCOR, Scott Polar Research Institute, Cambridge, UK, 1981, 46–63.

Nemoto, T., Okiyama, M., Takahashi, M., Aspects of the roles of squid in food chains of marine Antarctic ecosystems, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 415–420.

Neori, A., Holm-Hansen, O., Effect of temperature on rate of photosynthesis in Antarctic phytoplankton, *Polar Biol.*, 1, 33–38, 1982.

Nettleship, D.N., Sanger, G.A., Springer, P.F., Marine birds: Their feeding ecology and commercial fisheries relationships, Canadian Fisheries and Wildlife Service, Ottawa, Special Publication, 1984.

Neushul, M., Benthic marine algae, *Antarctic Map Folio Series*, Vol. 10, American Geographical Society, Washington, DC, 9–10 pp, 1968.

Newell, R.C., *The Biology of Intertidal Animals*, 3rd Ed., Marine Ecological Surveys, Faversham, Kent, 1979, 781.

Newell, R.C., Linley, E.A.S., Significance of microheterotrophs in the decomposition of phytoplankton: Estimates of carbon and nitrogen flow based on the biomass of plankton communities, *Mar. Ecol. Prog. Ser.*, 16, 105–119, 1984.

Newell, R.C., Lucas, M.I., Linley, E.A.S., Rate of degradation and efficiency of conversion of phytoplankton debris by marine microorganisms, *Mar. Ecol. Prog. Ser.*, 6, 123–136, 1981.

Newman, S.J., Nicol, S., Ritz, D., Marchant, H., Susceptibility of Antarctic krill (*Euphausia superba*) to ultraviolet radiation, *Polar Biol.*, 22(1), 50–55, 1999.

Newman, S.I., Dunlap, W.C., Nicol, S., Ritz, D., Antarctic krill (*Euphausia superba*) acquire a UV-absorbing mycosporine-like amino acid from dietary algae, *J. Exp. Mar. Biol. Ecol.*, 255, 93–110, 2000.

New Zealand Antarctic Institute, *Ross Sea Region: A State of the Environment Report for the Ross Sea Region of Antarctica* (2001), New Zealand Antarctic Institute, Wellington, 2001.

Nicol, D., Some characteristics of cold-water marine pelecypods, *J. Paleontol.*, 41, 1330–1340, 1967.

Nicol, S., Some limitations on the use of lipofuscin aging technique, *Mar. Biol.*, 93, 609–614, 1987.

Nicol, D., Lack of shell-attached pelecypods in Arctic and Antarctic waters, *Nautilus*, 77, 92–93, 1964; B53, 1–119, 1988.

Nicol, S., Age-old problem of krill longevity, *BioScience*, 40(11), 833–836, 1990.

Nicol, S., CCAMLR and its approach to management of the krill fishery, *Polar Biol.*, 27, 220–236, 1991.

Nicol, S., Stolf, M., Sinking rates of cast exoskeletons of Antarctic krill (*Euphausia superba*) and their role in the vertical flux of particulate matter and fluoride in the Southern Ocean, *Deep-Sea Res.*, 36, 1753–1762, 1989.

Nicol, S., de la Mare, W.K., Stolf, M., The energetic cost of egg production in Antarctic krill (*Euphausia superba* Dana), *Antarct. Sci.*, 7, 25–30, 1995.

Nicol, S., Constable, A.J., Pauly, T., Estimates of circumpolar abundance of Antarctic krill based on recent acoustic measurements, *CCAMLR Sci.*, 7, 87–99, 2000.

Niebauer, H.J., Sea ice and temperature variability in the eastern Bering Sea and relation to atmospheric fluctuations, *J. Geophys. Res.*, 85, 7507–7575, 1980.

Nimon, A.J., Schroter, R.C., Stonehouse, B., Heart rate of disturbed penguins, *Nature (Lond.)*, 374, 415, 1995.

Nishida, S., Nanoplankton flora in the Southern Ocean, with special reference to siliceous varieties, *Memoirs of the National Institute for Polar Research, Special Issue*, 40, 56–68, 1986.

Nishikawa, J., Tsuda, A., Diel vertical migration of the tunicate *Salpa thompsoni* in the Southern Ocean during summer, *Polar Biol.*, 24, 299–302, 2001.

Nishino, Y., Kawamura, A., Food habits of the Antarctic krill (*Euphausia superba* Dana) collected in the South Shetland waters, *Bull. Plankton Soc. Japan*, 43, 9–19, 1996.

Nishiwaki, M., Age characteristics of ear plugs in whales, *Sci. Rep. Whales Res. Inst. Tokyo*, 12, 23–32, 1957.

Nishiwaki, M., Distribution of toothed whales in the Antarctic Ocean, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 783–789.

Nishiwaki, M., Ichihara, T., Ohsumi, S., Age studies of the fin whale based on the ear plug, *Sci. Rep. Whales Res. Inst. Tokyo*, 13, 155–169, 1958.

Noble, R.T., Fuhrman, J.A., Virus decay and its causes in coastal waters, *Appl. Environ. Microbiol.*, 33, 77–83, 1997.

Noji, T.T., Estep, K.W., MacIntyre, F., Norrbin, F., Image analysis of faecal material grazed upon by three species of copepods: Evidence for coprohexy, coprophagy and coprochaly, *J. Mar. Biol. Ass. U.K.*, 71, 465–486, 1991.

Norhko, A., Thrush, S.F., Cummings, V.J., Funnell, G.A., Schwarz, A.-M., Andrew, N.L., Hawes, I., Ecological role of *Phyllophora antarctica* drift accumulations in coastal soft-sediment communities of McMurdo Sound, Antarctica, *Polar Biol.*, 27(8), 482–494, 2004.

Norman, J.R., B.A.N.Z. Antarctic Research Expedition 1929–1931 under the command of Douglas Mawson, Kt OBE, BE, D.Sc., FRS. Fishes, *Reports of the B.A.N.Z. Antarc. Res. Exped., Ser. B*, 1, 49, 1937.

Norris, K.S., Mohl, B., Do odontocetes debilitate their prey acoustically, in *Fourth Biennial Conference on the Biology of Marine Animals, San Francisco, California 14–18 December 1981*, 1981, 12–18.

North, A.W., Distribution of fish larvae at South Georgia: Horizontal, vertical and temporal distribution and early life history relative to monitoring year-class strength and recruitment, *CCAMLR Selected Scientific Reports (WG-FSA-87-19)*, 105–142, 1987.

North, A.W., Kellerman, A., Key to the early stage of Antarctic fish, *Ber. Polarforsch.*, 67, 1–44, 1990.

North, A.W., Ward, D., Initial feeding of fish larvae during winter at South Georgia, *Cybium*, 15, 357–364, 1989.

North, A.W., White, M.G., Key to fish postlarvae from the Scotia Sea, *Cybium*, 6, 13–32, 1982.

North, A.W., White, M.G., Reproductive strategies of Antarctic fish, in *Proceedings of the Vth Congress of the European Ichthyological Society 1985, Stockholm 1987*, 381–390 pp, 1987.

North, A.W., Croxall, J.D., Doidge, D.W., Fish prey of the Antarctic fur seal *Arctocephalus gazella* at South Georgia, *Br. Antarct. Surv. Bull.*, 61, 27–37, 1983.

Norton, O.I., Slater, J.G., A model for the evolution of the Indian Ocean and the breakup of Gondwanaland, *J. Geophys. Res.*, 84, 6803–6830, 1979.

Nöthig, E.-M., Untersuchungen zur Okologie des Photoplanktons in südöstlichen Weddellmeer im Januar/Februar 1985 (Antarktis III/3), *Ber. Polarforsch.*, 53, 1–119, 1988.

Nöthig, E.-M., Occurrence and vertical flux of faecal pellets of probably protozoan origin in the Weddell Sea (Antarctica), *Mar. Ecol. Prog. Ser.*, 56, 281–289, 1989.

Nöthig, E.-M., Gowing, M.M., Late winter abundance and distribution of phaeodarian radiolarians, other large protozooplankton and copepod nauplii in the Weddell Sea, Antarctica, *Mar. Biol.*, 111, 473–484, 1991.

Nöthig, E.-M., von Bodungen, B., Occurrence and vertical flux of faecal pellets of probably protozoan origin in the southeastern Weddell Sea (Antarctica), *Mar. Ecol. Prog. Ser.*, 56, 281–289, 1989.

Nöthig, E.-M., von Bodungen, B., Sui, Q., Phyto- and protozooplankton biomass during austral summer in surface waters of the Weddell Sea and vicinity, *Polar Biol.*, 11, 293–304, 1991.

Novitsky, J.A., Microbial growth rates and biomass production in a marine sediment: Evidence for a very active but mostly nongrowing community, *Appl. Environ. Microbiol.*, 53, 2368–2372, 1987.

Nowlin, W.D., Jr., Clifford, M., The kinematic and thermohaline zonation of the Antarctic Circumpolar Current at Drake Passage from short-term measurements, *J. Mar. Res.*, 40, 481–507, 1977.

Nowlin, W.D., Jr., Whitworth, T. III, Pillsbury, R.D., Structure and transport of the Antarctic Circumpolar Current at Drake Passage from short-term measurements, *J. Phys. Oceanogr.*, 7, 788–802, 1977.

Nybelin, O., Antarctic fishes, *Sci. Res. Norweg. Ant. Exped., 1927–1928*, 26, 1–76, 1947.

Nyssen, F., Brey, T., Lepoint, G., Bouquegneau, J.-M., De Broyer, C., Dauby, P., A stable isotope approach to the eastern Weddell Sea trophic web: Focus on benthic amphipods, *Polar Biol.*, 25, 280–287, 2002.

Obermüller, B., Karsten, U., Portner, H.O., Abele, D., Effects of UV-radiation on oxidative stress parameters in polar marine amphipods, and the role of UV-absorbing mycosporine-like amino acids (AAAS) in their diet, in *Antarctic Biology in a Global Context*, Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backhuys Publishers, Leiden, The Netherlands, 2003, 63–68.

O'Brien, D.P., Description of escape responses of krill (Crustacea: Euphausiacea), with particular reference to swarming behaviour and the size and proximity of the predator, *J. Crust. Biol.*, 7, 449–457, 1987.

Obst, B.S., Densities of Antarctica seabirds at sea and the presence of krill *Euphausia superba*, *The Auk*, 102, 540–549, 1985.

Odate, T., Fukuchi, M., Distribution and community structure of picophytoplankton in the Southern Ocean during the late austral summer of 1992, *NIPR Symp. Polar Biol.*, 8, 86–100, 1995.

Oelenschlager, J., Manthy, M., Fluoride content of Antarctic marine animals caught off Elephant Island, *Polar Biol.*, 1, 125–137, 1982.

Oelke, H., Breeding behaviour and success in a colony of Adélie Penguins, *Pygoscelis adeliae*, at Cape Crosier, Antarctica, in *The Biology of Penguins*, Stonehouse, B., Ed., Macmillan, London, 1975, 363.

Offredo, C., Ridoux, V., The diet of emperor penguins, *Aptenodytes forsteri*, in Adélie Land, Antarctica, *Ibis*, 128, 409–413, 1986.

Offredo, C., Ridoux, V., Clarke, M.R., Cephalopods in the diets of emperor penguins and Adélie Penguins in Adélie Land, Antarctica, *Mar. Biol.*, 86, 199–202, 1985.

Ohno, M., Fukada, Y., Fukuchi, M., Vertical distribution and standing stocks of chlorophyll *a* in the coastal waters of the Antarctic Ocean, *Antarct. Rec.*, 31, 93–106, 1987.

Ohsumi, S., Examination on age determination of the fin whale, *Sci. Rep. Whales Res. Inst. Tokyo*, 18, 49–88, 1964.

Ohsumi, S., Some investigations of the school structure of the sperm whale, *Sci. Rep. Whales Res. Inst. Tokyo*, 23, 1–25, 1971.

Ohsumi, S., Examination of the recruitment rate of Antarctic fin whale stock by use of mathematical models, *Int. Whaling Committee Rep.*, 22, 69–90, 1972.

Ohsumi, S., An attempt to standardize fishing efforts as applied to stock assessment of the minke whale in Antarctic Area IV, *Int. Whaling Committee Rep.*, 26, 404–408, 1976.

Ohsumi, S., Feeding habits of the minke whale in the Antarctic, *Int. Whaling Committee Rep.*, 29, 473–476, 1979.

Ohsumi, S., Masaki, Y., Biological parameters of the Antarctic minke whale at the virginal population level, *J. Fish. Res. Bd. Canada*, 32, 995–1004, 1975.

Ohsumi, S., Nasu, K., Range and habitat of the female sperm whale, with reference to the oceanographic structure. International Whaling Commission Paper Sp/7 to Special Meeting on Sperm Whale Biology and Stock Assessments, 1970 (Honolulu), 1970.

Ohsumi, S., Masaki, Y., Kawamura, A., Stock of Antarctic minke whale, *Sci. Rep. Whales Res. Inst. Tokyo*, 20, 1–16, 1970.

Okutani, T., Clarke, M.R., Identification key and species description for Antarctic squids, BIOMASS Handbook No. 21, 1985.

Oliver, J.S., Slattery, P.N., Effects of crustacean predators on species composition and population structure of soft-bodied infauna from McMurdo Sound, Antarctica, *Ophelia*, 24(3), 155–175, 1985.

Oliver, J.S., Oakden, J.M., Slattery, P.S., Phoxocephalid amphipod crustaceans as predators on larvae and juveniles in marine soft bottom communities, *Mar. Ecol. Prog. Ser.*, 7, 179–184, 1982.

Oliver, J.S., Slattery, P.N., O'Connor, E.F., Lowry, L.F., Walrus *Odobenus rosmarus* feeding in the Bering Sea: A benthic perspective, *Fish. Bull.*, 81(3), 501–512, 1983.

Olsen, S., South Georgia cod, *Notothenia rossii marmorata* Fischer, *Norsk Hvalfangstid*, 43, 373–382, 1954.

Olsen, S., A contribution to the systematics and biology of Chaenichthyid fishes from South Georgia, *Nytt Magasin fur Zoologi, Oslo*, 3, 79–93, 1955.

Olson, R.J., Nitrate and ammonium uptake on Antarctic waters, *Limnol. Oceanogr.*, 25, 1064–1074, 1980.

Ommaney, F.D., *Rhincalanus gigas* (Brady), a copepod of the southern macrozooplankton, *Discov. Rep.*, 13, 279–362, 1936.

Omori, M., Zooplankton fisheries of the world: A review, *Mar. Biol.*, 48(3), 199–205, 1978.

Omori, M., Ikeda, T., *Methods in Zooplankton Ecology*, Wiley, New York, 1984.

Omura, H., A review of pelagic whaling operations in the Antarctic based on the effort and catch data in 10 squares of latitude and longitude, *Sci. Rep. Whales Res. Inst. Tokyo*, 25, 105–203, 1973.

Omura, H., Ohsumi, S., Nemoto, T., Nasu, K., Kasuya, T., Black right whales in the North Pacific, *Sci. Rep. Whales Res. Inst. Tokyo*, 21, 1–78, 1969.

Øresland, V., Feeding and predation impact of the chaetognath *Eukrohnia hamata* in Gerlache Strait, Antarctica, *Mar. Ecol. Prog. Ser.*, 63, 201–209, 1990a.

Øresland, V., Feeding of the carnivorous copepod *Euchaeta antarctica* in Antarctic coastal and oceanic waters, *Mar. Ecol. Prog. Ser.*, 78, 41–47, 1990b.

Øresland, V., Winter population structure and feeding of the chaetognath *Eukrohnia antarctica* in the Gerlache Strait, Antarctic Peninsula, *Mar. Ecol. Prog. Ser.*, 119, 77–84, 1995.

Øresland, V., Ward, P., Summer and winter diet of four carnivorous copepod species around South Georgia, *Mar. Ecol. Prog. Ser.*, 98, 73–78, 1993.

Ørheim, O., Iceberg discharge and mass balance of Antarctica, in *Glaciers, Ice Sheets, and Sea Level Effect of CO_2-induced Climate Change*, U.S. Department of Energy, Washington, DC, 13 pp, 1985.

Øritzland, T., Biology and population dynamics of Antarctic seals, in *Antarctic Ecology, Volume 1*, Holdgate, M.W., Ed., Academic Press, London/New York, 1970a, 361–372.

Øritzland, T., Sealing and seal research in the Southwest Atlantic pack ice, September–October, 1964, in *Antarctic Ecology, Volume 1*, Holdgate, M.W., Ed., Academic Press, London/New York, 1970b, 367–376.

Øritzland, T., Food consumption of seals in the Antarctic pack ice, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 749–768.

Orsi, A.H., Whitworth, T. III, Nowlin, W.D., Jr., On the meridional extent and fronts of the Antarctic Circumpolar Current, *Deep-Sea Res.*, 42, 641–673, 1995.

Ostapoff, F., Antarctic oceanography, in *Biogeography and Ecology in Antarctica*, Van Meigham, J., van Oye, P., Eds., Dr. W. Junk, The Hague, 1965, 97–126.

Ottestad, P., On the biology of some southern Copepoda, *Hvalradets Skr.*, 5, 1–61, 1932.

Overland, J.E., Reynolds, R.M., Pearse, C.H., A model of the atmospheric boundary layer over the marginal ice zone, *J. Geophys. Res.*, 88, 2836–2840, 1983.

Owens, N.J.P., Priddle, J., Whitehouse, M.J., Variations in phytoplankton nitrogen assimilation around South Georgia and in the Bransfield Strait (Southern Ocean), *Mar. Chem.*, 35, 287–304, 1991.

Pace, M.L., Glasser, J.E., Pomeroy, L.R., A simulation analysis of continental shelf food webs, *Mar. Biol.*, 82, 47–63, 1984.

Paerl, H.W., Bacterial uptake of dissolved organic matter in relation to detrital aggregation in marine and freshwater systems, *Limnol. Oceanogr.*, 19, 966–972, 1974.

Pages, F., Lurbjewtt, F., Vertical distribution and abundance of mesoplanktonic medusae and siphonophores from the Weddell Sea, Antarctica, *Polar Biol.*, 14, 243–251, 1994.

Paine, R.T., Food web complexity and species diversity, *Am. Nat.*, 100, 65–75, 1966.

Painting, S.J., Lucas, M.I., Stenton-Dosey, J.M.E., South African SIBEX I criuse to the Prydz Bay region, 1984, 10: Biomass and production of bacterioplankton, detritus and bacterial relationships, *S. Afr. J. Antarct. Res.*, 15, 42–52, 1985.

Pakhomov, E.A., Demographic studies of Antarctic krill *Euphausia superba* in the Cooperation and Cosmonaut Seas (Indian Sector of the Southern Ocean), *Mar. Ecol. Prog. Ser.*, 119, 45–61, 1995.

Pakhomov, E.A., Froneman, P.W., Macroplankton/microplankton dynamics in the vicinity of Prince Edward Islands (Southern Ocean), *Mar. Biol.*, 134, 501–516, 1999.

Pakhomov, E.A., Froneman, P.W., Zooplankton dynamics in the eastern Atlantic sector of the Southern Ocean during austral summer 1997/1998, Part I: Community structure, *Deep-Sea Res. II*, 51, 2599–2616, 2004.

Pakhomov, E.A., McQuaid, C.D., Distribution of surface zooplankton and seabirds across the Southern Ocean, *Polar Biol.*, 15, 271–286, 1996.

Pakhomov, E.A., Perissinotto, R., Trophodynamics of the hyperiid amphipod *Themisto gaudichaudii* in the South Georgia region during the late summer, *Mar. Ecol. Prog. Ser.*, 134, 91–100, 1996.

Pakhomov, E.A., Perissinotto, R., McQuaid, C.P., Comparative structure of the macrozooplankton communities of the Subtropical and Antarctic Polar Fronts, *Mar. Ecol. Prog. Ser.*, 111, 655–669, 1994.

Pakhomov, E.A., Verheye, H.M., Atkinson, A., Laubscher, R.K., Tainton-Clark, J., Structure and grazing impact of the mesozooplankton community during late summer 1994 near South Georgia, Antarctica, *Polar Biol.*, 18, 180–192, 1997.

Palmisano, A.C., Changes in photosynthetic metabolism of sea-ice microalgae during a spring bloom in McMurdo Sound, *Antarct. J. U.S.*, 21, 176–177, 1986.

Palmisano, A.C., Garrison, D.L., Microorganisms in Antarctic sea ice, in *Antarctic Microbiology*, Friedman, E.I., Ed., Wiley Liss, New York, 1993, 167–218.

Palmisano, A.C., Sullivan, C.W., Physiology of sea ice diatoms, I: Response of three diatoms to a simulated summer–winter transition, *J. Phycol.*, 18, 489–498, 1982.

Palmisano, A.C., Sullivan, C.W., Sea ice microbial communities (SIMCO) I: Distribution, abundance and primary production of ice microalgae in McMurdo Sound, Antarctica, in 1980, *Polar Biol.*, 2, 171–177, 1983a.

Palmisano, A.C., Sullivan, C.W., Physiology of sea ice diatoms, II: Dark survival of three ice diatoms, *Can. J. Microbiol.*, 29, 157–160, 1983b.

Palmisano, A.C., Sullivan, C.W., Pathways of photosynthetic carbon assimilation in sea-ice microalgae from McMurdo Sound, Antarctica, *Limnol. Oceanogr.*, 30, 674–678, 1985.

Palmisano, A.C., Sullivan, C.W., Growth, metabolism, and dark survival in sea ice algae, in *Sea Ice Algae*, Horner, R.A., Ed., CRC Press, Boca Raton, FL, 1985b, 131–146.

Palmisano, A.C., Sullivan, C.W., Physiological response of micro-algae in the ice-platelet layer to low-light conditions, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985c, 84–88.

Palmisano, A.C., SooHoo, J.B., Sullivan, C.W., Photoadaptation in sea-ice microalgae in McMurdo Sound, *Antarct. J. U.S.*, 19, 131–132, 1984.

Palmisano, A.C., SooHoo, J.B., Sullivan, C.W., Photosynthesis-irradiance relationship in sea ice microalgae from McMurdo Sound, Antarctica, *J. Phycol.*, 21, 341–346, 1985a.

Palmisano, A.C., Kottmeier, S.T., Moe, R.L., Sullivan, C.W., Sea ice microbial communities, VI: The effect of light perturbation on microalgae at the ice-seawater interface in McMurdo Sound, Antarctica, *Mar. Ecol. Prog. Ser.*, 21, 37–45, 1985b.

Palmisano, A.C., SooHoo, J.B., White, D.C., Smith, G.A., Stanton, G.R., Shade-adapted benthic diatoms beneath Antarctic sea ice, *J. Phycol.*, 21, 664–667, 1985c.

Palmisano, A.C., SooHoo, J.B., SooHoo, S.L., Craft, L.L., Sullivan, C.W., Photoadaptation in *Phaeocystis pouchetii* advected beneath the annual sea ice in McMurdo Sound, Antarctica, *J. Plankton Res.*, 8, 891–906, 1986.

Palmisano, A.C., SooHoo, J.B., Sullivan, C.W., Effects of four environmental variables on photosynthesis-irradiance relationships in Antarctic sea-ice microalgae, *Mar. Biol.*, 94, 299–306, 1987a.

Palmisano, A.C., SooHoo, J.B., Moe, R.L., Sullivan, C.W., Sea ice microbial communities, VII: Changes in under-ice spectral irradiance during the development of Antarctic sea ice microalgal communities, *Mar. Ecol. Prog. Ser.*, 35, 165–173, 1987b.

Palmisano, A.C., Lizotte, M.P., Smith, G.A. et al. Changes in photosynthetic carbon assimilation in Antarctic sea-ice diatoms during a spring bloom: Variation in the synthesis of lipid classes, *J. Exp. Mar. Biol. Ecol.*, 116, 1–13, 1988.

Papenfuss, G.F., Problems in taxonomy and geographical distribution of Antarctic marine algae, in *Biiologie Antarctique*, Prevost, J., Ed., Herman, Paris, 1964, 155–160.

Paranjape, M.A., Moulting and respiration of euphausids, *J. Fish. Res. Board Can.*, 24, 1229–1240, 1967.

Park, Y.H., Gamberoni, L., Charriaud, E., Frontal structure and transport of the Antarctic Circumpolar Current in the South Indian Ocean sector, 40–80° E, *Mar. Chem.*, 35, 45–62, 1991.

Park, M.-G., Yang, S.-H., Chung, K.H., Shim, J.H., Phytoplankton biomass and primary production in the marginal ice zone of the northwestern Weddell Sea during the austral summer, *Polar Biol.*, 21, 251–261, 1999.

Parke, M., Green, J.C., Martin, I., Observations on the fine structure of zooids of the genus *Phaeocystis* (Haptophyceae), *J. Mar. Biol. Ass. U.K.*, 51, 927–932, 1992.

Parkinson, C.L., Southern Ocean sea-ice distributions and extent, *Philos. Trans. R. Soc. Lond., Ser. B*, 338, 241–256, 1992.

Parkinson, C.L., Southern Ocean sea-ice and its wider linkages: Insights revealed from models and observations, *Antarct. Sci.*, 16(4), 387–400, 2004.

Parmelee, D.F., Banded South Polar skua found in Greenland, *Antarct. J. U.S.*, 11, 111–117, 1976.

Parmelee, D.F., Parmelee, J.M., Revised penguin numbers and distribution for Anvers Island, Antarctica, *Br. Antarct. Surv. Bull.*, 76, 65–73, 1987.

Parry, G.D., The influence of the cost of growth in ectotherm metabolism, *J. Theor. Biol.*, 101, 453–477, 1983.

Parsons, T.R., LeBrasseur, R.J., Fulton, J.P., Some observations on the dependence of zooplankton grazing on cell size and concentration of phytoplankton blooms, *J. Oceanogr. Soc. Jap.*, 23, 10–17, 1967.

Paterson, R., Paterson, P., The status of the recovering stock of humpback whales in east Australian waters, *Biol. Conserv.*, 47, 33–48, 1989.

Pauly, D., On the inter-relationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks, *Journal du Conseil*, 39, 175–192, 1980.

Pavlov, V. Ya., On the quantitative composition of food for *Euphausia Superba* Dana, *Trudy VNIRO*, 86, 142, Translation Series of the Fisheries Research Board of Canade, 1977, 1953, 42–54.

Pavlov, V.Ya., The feeding of krill and some features of its behaviour, *Trudy VNIRO*, 66, 207–222, MAAF translation No. NS 94, 1969.

Pawson, D.L., Holothuroidea, *Antarctic Map Folio Series* II, American Geographical Society, Washington, DC, 36–38 pp, 1969a.

Pawson, D.L., Echinoidea, *Antarctic Map Folio Series* II, American Geographical Society, Washington, DC, 38–41 pp, 1969b.

Payne, M.R., Growth of a fur seal population, *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 279, 67–79, 1977.

Payne, M.R., Population size and age determination in the Antarctic fur seal, *Arctocephalus gazella*, *Mamm. Rev.*, 8, 67–73, 1978.

Payne, M.R., Growth of the Antarctic fur seal, *Arctocephalus gazella*, *J. Zool. (Lond.)*, 187, 1–20, 1979.

Pearce, P.A., Wilson, W.H., Review of viruses in Antarctic ecosystems, *Antarct. Sci.*, 15, 319–331, 2003.

Pearcy, W.G., Seasonal and inshore/offshore variation in the standing stock of micronekton and macrozooplankton off Oregon, *Fish. Bull. U. S.*, 74, 70–80, 1976.

Pearse, J.S., Reproductive periodicities of *Odontaster validus* Koehler, a common Antarctic asteroid, *Antarc. Res. Ser. II*, 5, 39–85, 1965.

Pearse, J.S., Giese, C., Food, reproduction, and organic constitution of the common Antarctic echinoid *Sterechinus neumayeri* (Meissner), *Biol. Bull.*, 130, 387–401, 1966.

Pearse, D.A., Wilson, W.H., Review. Viruses in Antarctic ecosystems, *Antarct. Sci.*, 15, 3198–3331, 2003.

Pearse, J.S., Bosch, I., McClintock, J.B., Marinovic, B., Brittan, R., Contrasting tempos of reproduction by shallow-water animals in McMurdo Sound, Antarctica, *Antarct. J. U.S.*, 31, 182–184, 1986.

Peck, L.S., Temperature and basal metabolism in two Antarctic marine herbivores, *J. Exp. Mar. Biol. Ecol.*, 127, 1–12, 1989.

Peck, L.S., Brockington, S., Vanhove, S., Beghyn, M., Community recovery following catastrophic iceberg impacts in a soft-sediment shallow water site at Signy Island, Antarctica, *Mar. Ecol. Prog. Ser.*, 186, 1–8, 1999.

Penhale, P.A., Research team focuses on environmental impact of an oil spill, *Antarct. J. U.S.*, 24, 9–12, 1989.

Penhale, P.A., Coosen, J., Marschoff, E.R., The *Bahia Paraiso*: A case study in environmental impact, remediation and monitoring, in *Antarctic Communities: Species, Structure and Survival*, Battaglia, B., Valencia, J., Walton, D.W.H., Eds., Cambridge University Press, Cambridge, UK, 1997, 437–444.

Penny, R.L., Lowry, G., Leopard seal predation on Adélie Penguins, *Ecology*, 48, 878–882, 1967.

Perissinotto, R., McQuaid, C.D., Land-based predator impact on vertically-migrating zooplankton and micronekton advected to a Southern Ocean archipelago, *Mar. Ecol. Prog. Ser.*, 80, 15–27, 1992.

Perissinotto, R., Pakhomov, E.A., The trophic role of the tunicate *Salpa thompsoni* in the Antarctic marine ecosystem, 17, 361–374 pp, 1998.

Perissinotto, R., Duncombe, R.C.M., Boden, B.P., Allanson, B.R., Vertical stability as a controlling factor of marine phytoplankton production at the Prince Edward Archipelago (Southern Ocean), *Mar. Ecol. Prog. Ser.*, 60, 205–209, 1990.

Perissinotto, R., Pakhomov, E.A., McQuaid, C.P., Froneman, P.W., *In situ* grazing rates and daily ration of Antarctic krill *Euphausia superba* feeding on phytoplankton at the Antarctic Polar Front and the Marginal Ice Zone, *Mar. Ecol. Prog. Ser.*, 160, 77–91, 1997.

Perissinotto, R., Guruey, L., Pakhomov, E.A., Contribution of heterotrophic material to the diet and energy budget of Antarctic krill, *Euphausia superba*, *Mar. Biol.*, 136, 129–135, 2000.

Permitin, Yu.E., Fecundity and reproductive biology of icefish (Channichthyidae), fish of the family Muraenolepidae, and dragonfish (Bathydraconidae) of the Scotia Sea (Antarctica), *J. Ichthyol.*, 13, 204–215, 1973.

Permitin, Yu.E., Species composition and zoogeographical analysis of bottom fish of the Scotia Sea, *Vopr. Ikhtiol.*, 17, 843–863, 1977.

Permitin, Yu.E., Sil'yanova, Z.S., New data on the reproductive biology and fecundity of fishes of the genus *Notothenia* (Richardson) in the Scotia Sea (Antarctica), *J. Ichthyol.*, 11, 693–705, 1971.

Permitin, Yu.E., Traverdiyeva, M.I., The food of some Antarctic fish in the South Georgia area, *J. Ichthyol.*, 12, 104–114, 1978a.

Permitin, Yu.E., Traverdiyeva, M.I., Feeding of fishes of the families Nototheniidae and Chaenichthyidae in the South Orkney Islands, *Biol. Morya*, 2, 75–81, 1978b. In Russian.

Perrin, R.A., Lu, P., Marchant, H.J., Seasonal variation in marine phytoplankton and ice algae at a shallow coastal site, *Hydrobiologia*, 146, 33–46, 1987.

Peterson, B.J., Aquatic primary productivity and the $^{14}CO_2$ method: A history of the productivity problem, *Annu. Rev. Ecol. Syst.*, 11, 359–385, 1980.

Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davisk, M., Delaygue, G., Delmotte, M., Kotlyakov, V.M., Legrand, M., Lipenkov, V.Y., Lorius, C., Pépin, L., Ritz, C., Saltzmank, E., Stievenard, M., Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica, *Nature (Lond.)*, 399, 429–436, 1999.

Phillips, K.L., Jackson, G.D., Nichols, D.D., Predation on myctophids by the squid *Monoteuthis ingens* around Macquarie and Heard Islands: stomach contents and fatty acid analysis, *Mar. Ecol. Prog. Ser.*, 215, 179–189, 2001.

Piakowski, U., Map of the geographical distribution of macrozooplankton in the Atlantic sector of the Southern Ocean, *Ber. Polarforsch.*, 30, 264–279, 1985a.

Piakowski, U., Distribution, abundance and diurnal migration of macrozooplankton in Antarctic surface waters, *Meeresforschung*, 20, 264–279, 1985b.

Piakowski, U., Rodhouse, P.G., White, M.G., Bone, D.G., Symon, C., Nekton community of the Scotia Sea as sampled by RMT 25 during austral summer, *Mar. Ecol. Prog. Ser.*, 112, 13–28, 1994.

Piatkowski, U., Zoogeographische Untersuchungen und Germein schaftsanalysen an antariktischen Makroplankton, *Ber. Polarforsch.*, 34, 1–150, 1987.

Picken, G.B., Non-pelagic reproduction of some Antarctic prosobranch gastropods from Signy Island, South Orkney Islands, *Malacologia*, 19, 109–128, 1978a.

Picken, G.B., Growth, production and biomass of the Antarctic gastropod bivalve *Laevikitorina antarctica* Martin 1885, *J. Exp. Mar. Biol. Ecol.*, 40, 71–74, 1978b.

Picken, G.B., Reproductive adaptations of Antarctic benthic invertebrates, *Biol. J. Linn. Soc.*, 14, 67–75, 1980.

Picken, G.B., Marine habitats—benthos, in *Key Environments—Antarctica*, Bonner, W.N., Walton, D.W.H., Eds., Pergamon Press, Oxford, 1985a, 154–172.

Picken, G.B., Benthic research in Antarctica, in *Marine Biology of Polar Regions and the Effect of Stress on Marine Organisms*, Grey, J.S., Christiansen, M.E., Eds., Wiley, London, 1985b, 167–184.

Pimm, S.L., The complexity and stability of ecosystems, *Nature (Lond.)*, 307, 321–326, 1984.

Pingnee, R.D., Cyclonic eddies and cross frontal mixing, *J. Mar. Biol. Ass. U.K.*, 58, 955–963, 1978.

Platt, H.M., Ecology of King Edward Cove, South Georgia, I: Macrobenthos and the benthic environment, *Bull. Br. Antarc. Surv.*, 49, 231–238, 1980.

Platt, T., Harrison, W.G., Biogenic fluxes of carbon and oxygen in the ocean, *Nature (Lond.)*, 318, 55–58, 1985.

Platt, T., Harrison, W.G., Lewis, M.R., Li, W.K.W., Sathyendranath, S., Smith, R.E., Vezina, A.F., Biological production of the oceans: the case for consensus, *Mar. Ecol. Prog. Ser.*, 52, 77–88, 1989.

Platt, T., Sabba Rao, D.V., Irwin, B., Photosynthesis of picoplankton in the oligotrophic ocean, *Nature (Lond.)*, 300, 702–704, 1993.

Plotz, J., Summer diet of Weddell Seals (*Leptonychotes weddelli*) in the eastern and southern Weddell Sea, Antarctica, *Polar Biol.*, 6, 97–102, 1986.

Plotz, J., Weidel, H., Bersch, M., Winter aggregation of marine mammals and birds in the north-eastern Weddell Sea pack ice, *Polar Biol.*, 11, 305–309, 1991.

Plotz, J., Bornmann, H., Knust, R., Schroder, A., Bester, M., Foraging behaviour of Weddell Seals and its ecological implications, *Polar Biol.*, 24, 901–909, 2001.

Pocklington, R., An oceanographic interpretation of seabird distributions in the Indian Ocean, *Mar. Biol.*, 51, 9–21, 1979.

Poisson, A., Metzl, N., Brunet, C., Schauer, B., Bres, B., Ruiz-Pino, D., Louanchi, F., Variability of sources and sinks of CO_2 in the western Indian and Southern Oceans during the year 1991, *J. Geophys. Res.*, 8, 22759–22778, 1993.

Poleck, T.P., Denys, C.J., Effects of temperature on the moulting, growth, and maturation of the Antarctic krill, *Euphausia superba* (Crustacea: Euphausiacea), under laboratory conditions, *Mar. Biol.*, 70, 255–265, 1982.

Pollard, P.C., Moriarty, D.J.W., Validity of titriated thymidine method for estimating bacterial growth rates: Measurement of isotope dilution during DNA synthesis, *Appl. Environ. Microbiol.*, 48, 1076–1083, 1984.

Pomeroy, L.R., The ocean's food web: A changing paradigm, *BioScience*, 24, 499–504, 1974.

Pomeroy, L.R., Secondary production mechanisms of continental shelf communities, in *Ecological Processes in Coastal and Marine Systems*, Livingston, P.J., Ed., Plenum Press, New York, 1979, 163–182.

Pomeroy, L.R., Diebel, D., Aggregation of organic matter by pelagic tunicates, *Limnol. Oceanogr.*, 25, 643–652, 1980.

Pomeroy, L.R., Diebel, D., Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters, *Science*, 233, 359–361, 1986.

Pomeroy, L.R., Wiebe, W.J., Temperature and substrates: An interactive limiting factor for marine heterotrophic bacteria, *Aquat. Microb. Ecol.*, 23, 187–204, 2004.

Pomeroy, I.R., Wiegert, W.J., Temperature and substrates an interactive limiting factor for marine heterotrophic bacteria, *Aquat. Microb. Ecol.*, 23, 197–204, 2001.

Pomeroy, L.R., Darley, W.M., Dunn, E.L., Gallagher, J.L.K., Haines, E.B., Whitney, D.M., Primary production, in *The Ecology of a Salt Marsh*, Pomeroy, L.R., Wiegert, R.G.W., Springer, Berlin, 1981, 39–67.

Pomeroy, L.R., Hanson, R.B., McGillivary, P.A., Sherr, B.F., Kirchman, D.L., Deibel, D. et al., Microbiology and chemistry of fecal products of pelagic tunicates: Rates and fates, *Bull. Mar. Sci.*, 35, 426–439, 1984.

Poncet, S., Poncet, J., Censuses of penguin population on the Antarctic Peninsula, *Br. Antarct. Surv. Bull.*, 77, 109–129, 1987.

Pond, D., Watkins, J., Priddle, J., Sergent, J., Variation in lipid content and composition of Antarctic krill, *Euphausia superba*, at South Georgia, *Mar. Ecol. Prog. Ser.*, 117, 49–57, 1995.

Pople, A., Simpson, R.D., Cairns, S.C., An incident of Southern Ocean oil pollution: Effects of a spillage of diesel fuel on the rocky shore of Macquarie Island (sub-Antarctic), *Aust. J. Mar. Freshwater Res.*, 41, 603–620, 1990.

Porter, K.G., Sherr, E.B., Sherr, B.F., Pace, M., Sanders, R.W., Protozoa in planktonic food webs, *J. Protozool.*, 32, 409–415, 1985.

Post, A., Paralepididae (Barracudinas), in *Fishes of the Southern Ocean*, Gon, O., Heenstra, P.C.H., Eds., J.B.L. Smith Institute of Ichthyology, Grahamstown, South Africa, 1990, 138–141.

Poulet, S.A., Comparison between five coexisting species of copepods feeding on naturally-occurring particulate matter, *Limnol. Oceanogr.*, 23, 1126–1143, 1978.

Poulet, S.A., Chanut, J.P., Nonselective feeding of *Pseudocalanus*, *J. Fish. Res. Bd. Canada*, 32, 706–713, 1975.

Powell, A.W.B., Mollusca of Antarctic and subantarctic seas, in *Biogeography and Ecology in Antarctica*, von Mieghan, J., van Oye, P., Eds., Dr. W. Junk, The Hague, 1965, 333–380.

Powell, W.M., Clarke, G.L., The reflection and absorption of daylight at the surface of the ocean, *Jour. Opt. Soc. Amer.*, 26, 111, 1936.

Presler, P., Necrophagous invertebrates of Admiralty Bay of King George Island (South Shetland Islands), *Pol. Polar Res.*, 7, 25–61, 1986.

Prévost, J., *Ecology du Manchot Empereur*, Hermann, Paris, 1961.

Prévost, J., Population, biomass, and energy requirements of Antarctic birds, in *Biological Investigation of Antarctic Systems and Stocks (BIOMASS Volume II)*, El-Sayed, S.Z., Ed., SCAR, Cambrige, UK, 1981, 125–181.

Prévost, J., Mougin, J.-L., *Guide des oiseaux et mammiferes des terres australes et Antarctiques Francaises*. Neuchâtel, Delachaux et Niestle, 1979.

Prézelin, B.B., Aldridge, A.L., Primary production of marine snow during and after an upwelling event, *Limnol. Oceanogr.*, 28, 1156–1167, 1983.

Prézelin, B.B., Ley, A.C., Photosynthesis and chlorophyll *a* fluorescence rhythms in marine phytoplankton, *Mar. Biol.*, 55, 295–307, 1980.

Price, H.J., Swimming behaviour of krill in relation to algal patches: A mesocosm study, *Limnol. Oceanogr.*, 34, 649–659, 1989.

Price, H.J., Boyd, K.R., Boyd, C.M., Omnivorous feeding behaviour of the Antarctic krill, *Euphausia superba*, *Mar. Biol.*, 97, 67–77, 1988.

Priddle, J., Antarctic planktonic ecosystem, in *Polar Marine Diatoms*, Mullins, B.W., Priddle, J., Eds., British Antarctic Survey, Natural Environment Research Council, Cambridge, UK, 1990, 47–51.

Priddle, J., Hawes, I., Ellis-Evans, J.C., Antarctic aquatic ecosystems as habitats for phytoplankton, *Biol. Rev.*, 61, 199–238, 1986a.

Priddle, J., Heywood, R.B., Theriot, E., Some environmental factors influencing phytoplankton production in the Southern Ocean around South Georgia, *Polar Biol.*, 5, 65–79, 1986b.

Priddle, J., Croxall, J.P., Everson, I., Heywood, R.B., Murphy, E.J., Prince, P.A., Sear, C.B. et al., Large-scale fluctuations in distribution and abundance of krill—A discussion of possible causes, in *Antarctic Ocean and Resources Variability*, Sahrhage, D. et al. Eds., Springer, Berlin, 1988, 169–182.

Priddle, J., Watkins, J., Morris, D., Ricketts, C., Buchholz, F., Variation of feeding in krill swarms, *J. Plankton Res.*, 12, 1189–1205, 1990.

Priddle, J., Smetacek, V., Bathmann, U., Antarctic marine primary production, biochemical carbon cycles, and climate change, *Philos. Trans. R. Soc. Lond. ,Ser. B*, 338, 279–289, 1992.

Prince, P.A., The food and feeding ecology of blue petrel (*Halobaena caerula*) and dove prion (*Pachyptila desolata*), *J. Zool. (Lond.)*, 190, 59–76, 1980a.

Prince, P.A., The food and feeding ecology of grey-headed albatross, *Diomedea chrysostoma*, and black-browed albatross, *D. melanophris. Ibis*, 122, 476–488, 1980b.

Prince, P.A., Population and energetic aspects of relationship between black-browed and grey-headed albatrosses and the Southern Ocean marine environment, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 473–477.

Prince, P.A., Payne, M.R., Current status of birds at South Georgia, *Br. Antarct. Surv. Bull.*, 48, 103–118, 1979.

Priscu, J.C., Priscu, L.R., Palmisano, A.C., Sullivan, C.W., The effect of temperature on inorganic nitrogen and carbon metabolism in sea-ice microalgae, *Antarct. J. U.S.*, 20, 196–198, 1987.

Priscu, J.C., Downes, M.J., Priscu, R., Palmisano, A.C., Sullivan, C.W., Dynamics of ammonium oxidizer activity and nitrous oxide (N_2O) within and beneath Antarctic sea ice, *Mar. Ecol. Prog. Ser.*, 62, 37–46, 1990.

Priscu, J.C., Lizotte, M.P., Cota, G.F., Palmisano, A.C., Sullivan, C.W., Comparison of irradiance response of photosynthesis and nitrogen uptake in sea-ice microalgae, *Mar. Ecol. Prog. Ser.*, 70, 201–210, 1991.

Probyn, T.A., Painting, S.J., Nitrogen uptake by size-fractionated phytoplankton populations in Antarctic surface waters, *Limnol. Oceanogr.*, 30, 1327–1332, 1985.

Propp, M.V., The study of the bottom fauna at Halswell Islands by scuba diving, in *Antarctic Ecology, Volume I*, Holdgate, M.W., Ed., Academic Press, London, 1970, 239–241.

Prut'ko, V.G., On the occurrence of the opah, *Lampris guttatus* (Osteichthyes: Lampridae), in the southern part of the Indian Ocean, *J. Ichthyol.*, 19, 140–141, 1979.

Pugh, P.R., Gelatinous zooplankton—the forgotten fauna, *Progress in Underwater Science*, 14, 67–78, 1989.

Pugh, P.R., MacAlister, H.E., Acri of the subtropical zone on sub-Antarctic South Georgia, *Pedobiologia*, 38, 552–565, 1994.

Purves, P.E., The wax plug in the external auditory meatus of the Mysticeti, *Discov. Rep.*, 27, 293–302, 1955.

Putz, K., The post-moult diet of emperor penguins (*Aptenodytes forsteri*) in the eastern Weddell Sea, *Polar Biol.*, 15, 457–463, 1995.

Pyke, G.H., Pulliam, H.R., Charnov, E.L., Optimal foraging: A selective review of theory and tests, *Quart. Rev. Biol.*, 52, 137–154, 1977.

Pyle, J.A., Carriner, G., Grenfell, J.L., Kettleborough, J.A., Lary, D.J., Ozone loss in Antarctica: Implications for global change, *Philos. Trans. R. Soc. Lond., Ser. B*, 338, 219–226, 1992.

Quartino, M.L., Kloser, H., Schloss, I.R., Wiencke, C., Biomass and associations of benthic marine macroalgae from inner Potter Cove (King George Island, Antarctica) related to depth and substrate, *Polar Biol.*, 24, 349–355, 2001.

Quetin, L.B., Ross, R.M., School composition of the Antarctic krill, *Euphausia superba*, in the waters west of the Antarctic Peninsula in the austral summer of 1982, *J. Crust. Biol.*, 4(Special Issue No. 1), 96–106, 1984.

Quetin, L.B., Ross, R.M., Feeding by Antarctic krill, *Euphausia superba*: Does size matter?, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 372–377.

Quetin, L.B., Ross, R.M., Effects of oxygen, temperature and age on the metabolic rate of the embryos and early larval stages of Antarctic krill, *Euphausia superba* Dana, *J. Exp. Mar. Biol. Ecol.*, 125, 43–62, 1989.

Quetin, L.B., Ross, R.M., Behavioural and physiological characteristics of the Antarctic krill, *Euphausia superba*, *Am. Zool.*, 31, 49–63, 1991.

Quetin, L.B., Ross, R.M., Factors affecting distribution and abundance of zooplankton, with an emphasis on Antarctic krill, *Euphausia superba*, *Antarc. Res. Ser.*, 70, 357–371, 1996.

Quetin, L.B., Ross, R.M., Environmental variability and its impact on the reproductive cycle of Antarctic krill, *Am. Zool.*, 41, 74–89, 2001.

Quetin, L.B., Ross, R.M., Episodic recruitment in Antarctic krill, *Euphausia superba*, in the Palmer LTER study region, *Mar. Ecol. Prog. Ser.*, 259, 185–200, 2003.

Quetin, L.B., Ross, R.M., Clarke, A., Krill energetics: Seasonal and environmental aspects of the physiology of *Euphausia superba*, in *Southern Ocean Ecology: The BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, UK, 1994, 165–184.

Quetin, L.B., Ross, R.M., Fraser, T.K., Haberman, K.L., Factors affecting distribution and abundance of zooplankton, with emphasis on Antarctic krill, *Euphausia superba*, *Antarct. Res. Ser.*, 70, 113, 1996.

Quetin, L.B., Ross, R.M., Fraser, T.K., Amsler, M.O., Wyatt-Evens, C., Oakes, S.A. et al., Growth of larval krill, *Euphausia superba*, in fall and winter west of the Antarctic Peninsula, *Mar. Biol.*, 143, 833–843, 2003.

Quetin, L.B., Ross, R.M., Fraser, T.K., Haberman, K.L., Factors affecting distribution and abundance in macrozooplankton, with an emphasis on Antarctic krill, *Euphausia superba*, in *Foundations for Ecological Research West of the Antarctic Peninsula*, Antarctic Research Series Vol. 70, 357–371, 1996.

Quuilty, P.G., Evolution of the modern glaciation of Antarctica, in *Impact of Climate Change on Antarctica–Australia*, Australian Government Publishing Service, Canberra, 1992, 10–16.

Racovitza, E.G., La vie des animaux et des plantes dans l'Antartique, *Bull. Soc. Roy. Belgique de Geographie (Brussels)*, 24, 177–230, 1900.

Radok, U., Streten, N., Weller, G.E., Atmosphere and ice, *Oceanus*, 18(4), 15–27, 1975.

Radthe, R.L., Hourigan, T.F., Age and growth of the Antarctic fish *Nototheniopsis nudifrons, Fish. Bull.*, 1990, 537–571.

Radthe, R.L., Targett, T.E., Rhythmic structure and chemical pattern in otoliths of the Antarctic fish *Notothenia larseni*: Their application to age determination, *Polar Biol.*, 3, 203–210, 1984.

Radthe, R.L., Targett, T.E., Kellerman, A., Bell, J.L., Hill, K.T., Antarctic fish growth profile of *Trematomus newnesi*, *Mar. Ecol. Prog. Ser.*, 51, 103–117, 1989.

Ragulin, S.G., Underwater observations of krill, *Trudy Vsecoiuznogo Nauche-assledovatel'skii Instit. Morskogo Rybnogo Koziaiskia i Okeanographie (VNIROTrudy VNIRO) Moscow*, 66, 231–234, 1969.

Rakusa-Suszczewski, S., The biology of Paramoera walkeri Stebbing (Amphipoda) and the Antarctic sub-fast ice community, *Pol. Arch. Hydrobiol.*, 19, 11–36, 1972.

Rakusa-Suszczewski, S., Environmental conditions within krill swarms, *Pol. Arch. Hydrobiol.*, 25, 585–587, 1978.

Rakusa-Suszczewski, S., Feeding of *Euphausia superba* Dana under natural conditions, *Pol. Polar Res.*, 3, 289–297, 1982.

Ralph, R., Maxwell, J.G.H., Growth of two Antarctic lamellibranches: *Adamussium colbecki* and *Laternula elliptica*, *Mar. Biol.*, 42, 171–175, 1977.

Ralph, R., Maxwell, J.G.H., The oxygen consumption of the Antarctic limpet *Nacella (Patinigera) concinna*, *Br. Antarc. Surv. Bull.*, 45, 19–23, 1977b.

Ralph, R., Maxwell, J.G.H., The oxygen consumption of the Antarctic lamellibranch *Gaimardia trapesina* in relation to cold adaptation in polar invertebrates, *Br. Antarc. Surv. Bull.*, 45, 41–46, 1977c.

Rassolzadegan, F., Sheldon, R.W., Predator-prey interactions of nanozooplankton and bacterial in an oligotrophic marine environment, *Limnol. Oceanogr.*, 31, 1010–1029, 1986.

Rassoulzadegan, F., Laval-Pueto, M., Sheldon, R.W., Partition of the food ration of marine ciliates between picoplankton and nanoplankton, *Hydrobiologia*, 159, 75–88, 1988.

Rau, G.H., Low ^{15}N/^{14}N in hydrothermal vent animals: Ecological implications, *Nature (Lond.)*, 289, 484–485, 1981.

Rau, G.H., Hopkins, H., Torres, J.J., ^{15}N/^{14}N and ^{13}C/^{12}C in Weddell Sea invertebrates: Implications for feeding diversity, *Mar. Ecol. Prog. Ser.*, 77, 1–6, 1991a.

Rau, G.H., Sullivan, C.W., Gordon, J.J., ^{13}C and ^{15}C variations in Weddell Sea particulate organic matter, *Mar. Chem.*, 35, 335–369, 1991b.

Rau, G.H., Ainley, D.G., Bengston, H., Torres, J.J., Hopkins, T.L., ^{15}N/^{14}N and ^{13}C/^{12}C in Weddell Sea birds, seals, and fish: Implications for diet and trophic structure, *Mar. Ecol. Prog. Ser.*, 84(1), 1–8, 1992.

Rauchet, M., Ergebrisse der faunistichen Abeiten in Benthal von King George Island (Südschtlandirodetn, Antarktis), *Ber. Polarforsch.*, 76, 1–75, 1991.

Rauglin, A.G., Underwater observations of krill, *Trudy, Vsessoyuznogo Naucho-issledo-vatel'skogo Instituta Morskogo Rybnogo Khozyaistiva i Okeanografi (VNIROTrudy VNIRO)*, 66, 231–234, 1969 (MAAF Translation No. NS 92).

Rawlence, D.J., Ensor, P.H., Knox, G.A., Summer tide-crack phytoplankton at White Island, McMurdo Sound, Antarctica, *N.Z. J. Mar. Freshwat. Res.*, 21, 91–97, 1987.

Ray, G.C., in *Population Ecology of Antarctic Seals*, Holdgate, M.W., Ed., *Antarctic Ecology*, Vol. 1, Academic Press, London, 1970, 389–414.

Ray, G.C., Ross seal, in *Handbook of Marine Mammals*, Ridgway, S.H., Harrison, R.J., Eds., Academic Press, London, 1981, 237–260.

Raymond, J.A., DeVries, A.L., Adsorption inhibition as a mechanism of freezing resistance in polar fishes, *Proc. Natl Acad. Sci. USA*, 74, 2589–2593, 1977.

Raymont, J.E.C., *Plankton and Productivity in the Oceans*, 2nd edition, Pergamon Press, London, 1980.

Raytheon Service Company, *Report on the McMurdo Sound Water Quality Study*. Unpublished Report to the U.S, Office of Polar Programs, 1983.

Reay, D.S., Nedwell, D.B., Priddle, J., Ellis-Evans, J.C., Temperature dependence of inorganic nitrogen uptake reduced affinity for nitrate at subtropical temperatures in both algae and bacteria, *Appl. Environ. Microbiol.*, 65, 2577–2584, 1999.

Reay, D.S. et al. Regulation of low temperature of phytoplankton growth and nutrient uptake in the Southern Ocean, *Mar. Ecol. Prog. Ser.*, 219, 51–64, 2001.

Redvers, G., Dispersion and fate of sewage and wastewater components from Scott Base, Antarctica, M.Sc. thesis, University of Auckland, Auckland, 2000.

Reeburg, W.S., Fluxes associated with brine motion in growing sea ice, *Polar Biol.*, 3, 29–33, 1984.

Regan, C.T., Fishes, *British Antarctic ("Terra Nova") Expedition 1910, Natural History Reports, Zoology*, 1, 1–54, 1914.

Regel, J., Putz, K., Effect of human disturbance on body temperature and energy expenditure in penguins, *Polar Biol.*, 18, 246–253, 1997.

Reichardt, W., Differential temperature effects on the efficiency of carbon pathways in Antarctic marine benthos, *Mar. Ecol. Prog. Ser.*, 40, 127–135, 1987.

Reid, B., An interpretation of the age structure and breeding status of an Adélie Penguin population, *Notornis*, 15(3), 193–197, 1968.

Reid, F.M.H., Biomass estimation of components of marine nanoplankton and picoplankton by the Utermohl settling technique, *J. Plankton Res.*, 5, 235–252, 1983.

Reid, K., Growth of Antarctic krill, *Euphausia superba*, at South Georgia, *Mar. Biol.*, 138, 57–62, 2001.

Reid, K., Arnould, J.P.Y., The diet of Antarctic fur seals, *Arctocephalus gazella*, during the breeding season at South Georgia, *Polar Biol.*, 16, 105–114, 1996.

Reid, J.L., Nowlin, W.D., Jr., Patzert, W.C., On the characteristics and circulation of the southwestern Atlantic Ocean, *J. Phys. Oceanogr.*, 7, 62–91, 1977.

Reid, K., Croxall, J.P., Prince, P.A., The fish diet of black-browed albatross (*Diomedea melanophris*) and grey-headed albatross (*D. chryostoma*) at South Georgia, *Polar Biol.*, 16, 469–477, 1996.

Reid, K., Croxall, J.P., Edwards, T.M., Interannual variation in the diet of the Antarctic prion *Pachyptila desolata* at South Georgia, *Emu*, 97, 126–143, 1997.

Reid, K., Barlow, K.E., Croxall, J.P., Taylor, R.I., Predicting changes in the Antarctic krill, *Euphausia superba*, population at South Georgia, *Mar. Biol.*, 135, 647–652, 1999.

Rembiszewski, J.M., Krzeptowski, M., Linkowski, T., Fishes (Pisces) as a by-catch in fisheries of krill, *Euphausia superba* Dana (Euphausia: Crustacea), *Pol. Arch. Hydrobiol.*, 25, 677–695, 1971.

Repenning, C.A., Peterson, R.S., Hubbs, C.L., Contribution to the systematics of southern fur seals, with particular reference to Juan Fernandez and Galapagos species, in *Antarctic pinnipedia, Antarctic Research Series 18*, Burt, W.H., Ed.,1971, 1–34.

Retainal, M.A., Quintana, R., Neira, F., Analysis cauliy cuantitatiro de las communidades benthonicus on Bahia Foster (Isla Deception) (xxxv Expedition Antarctica Chileno, enero 1981), *Publ. Inst. Ant. Chileno Ser. Cientifica*, 29, 5–15, 1982.

Riaux-Gobin, C., Bourgoin, P., Microphytic standing stocks at Kerguelen Islands (Subantarctic, Indian Ocean), annual variations to environmental factors, II: Intertidal and subtidal microphytobenthos, *Polar Biol.*, 27, 133–141, 2001.

Riaux-Gobin, C., Treguer, P., Poulton, M., Vetion, G., Nutrients, algal biomass, and communities in land-fast ice and seawater off Adélie Land (Antarctica), *Antarc. Sci.*, 12, 160–171, 2000.

Riaux-Gobin, C., Poulin, M., Prodon, R., Treguer, P., Land-fast ice microalgae and phytoplanktonic communities (Adélie Land, Antarctica) in relation to environmental factors during the ice breakup, *Antarc. Sci.*, 15, 353–364, 2003.

Ribec, C.A., Ainley, D.G., Consistency of seabird assemblages: An exploratory look, *Biol. Oceanogr.*, 6, 175–202, 1988.

Ribec, C.A., Ainley, D.G., Fraser, W.R., Habitat selection by marine mammals in the marginal ice zone, *Antarc. Sci.*, 3(2), 181–186, 1991.

Richardson, M.D., Benthic studies in the Antarctic, *Antarc. J. U.S.*, 7, 185–186, 1972.

Richardson, M.G., The dietary composition of some Antarctic fish, *Br. Antarc. Surv. Bull.*, 41/42, 113–120, 1979.

Richardson, M.D., Hedgpeth, J.W., Antarctic soft-bottom macrobenthic community adaptation to a cold, stable, highly productive, glacially-affected environment, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 181–186.

Richardson, M.G., Whitaker, T.M., An Antarctic fast-ice food chain: Observations on the interaction of the amphipod *Pontogeneia antarctica* Chevreux with ice-associated microalgae, *Br. Antarc. Surv. Bull.*, 47, 107–115, 1979.

Richdale, L.E., Biology of the sooty shearwater, *Puffinus griseus*, *Proc. Zool. Soc. Lond.*, 141, 1–117, 1963.

Ricker, W.E., *Methods for Assessment of Fish Production in Fresh Waters*, IGP Handbook No. 3, 1968, 1–313.

Ridgeway, S.H., Harrison, R.J., *Handbook of Marine Mammals, Volumes 1 and 2*, Academic Press, London, 1981.

Ridoux, V., Offredo, C., The diets of five summer breeding seabirds in Adélie Land, Antarctica, *Polar Biol.*, 9, 137–145, 1989.

Riebesell, U., Comparison of sinking and sedimentation rate measurements in a diatom winter/spring bloom, *Mar. Ecol. Prog. Ser.*, 54, 109–119, 1989.

Riebesell, U., Schloss, I., Smetacek, V., Aggregation of algae released from melting sea ice: Implications for seeding and sedimentation, *Polar Biol.*, 11, 239–248, 1991.

Riley, G.A., Theory of food chain relations in the ocean, in *The Sea, Volume 2*, Hill, M.N., Ed., Wiley Interscience, New York, 1963, 438–463.

Riseborough, R.W., Transfer of organochlorine pollutants to Antarctica, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 1203–1210.

Risebrough, R.W., Walker, H., Schmidt, T., de Lappe, B., Connors, C.W., Transfer of chloirinated biohenyls to Antarctica, *Nature (Lond.)*, 264(5888), 738–739, 1976.

Rivkin, R.B., Seasonal pattern of planktonic production in McMurdo Sound, Antarctica, *Am. Zool.*, 31, 5–16, 1991.

Rivkin, R.B., Putt, M., Heterotrophy and photoheterotrophy by Antarctic microalgae: Light-dependent incorporation of amino acids and glucose, *J. Phycol.*, 23, 442–452, 1987.

Rivkin, R.B., Putt, M., Alexander, S.P., Meritt, D., Gander, L., Biomass and production of polar plankton and sea ice microbial communities: A comparative study, *Mar. Biol.*, 101(2), 273–283, 1989.

Rivkin, R.B., Anderson, M.R., Gustafson, D.E., Jr., Seasonal pattern of bacterial and net nano- and picophytoplankton in McMurdo Sound, Antarctica, *Antarct. J. U.S.*, 25, 195–196, 1990.

Robertson, A.I., On the relationship between annual production: Biomass ratios and life spans of marine invertebrates, *Oecologia*, 38, 193–202, 1979.

Robertson, G., Gales, R., Eds., *Albatross Biology and Conservation*, Beatty and Sons, Surrey, Norton, Australia, 1998.

Robertson, G., Williams, R., Green, K., Robertson, I., Diet composition of emperor penguin chicks, *Aptenodytes forsteri*, at two Mawson coast colonies, Antarctica, *Ibis*, 136, 19–31, 1994.

Robin, G.deQ., Antarctic ice sheet: Its history and response to sea-level and climate changes over the past 100 million years, *Palaeogeogr., Palaeoclimateol., Palaeoecol.*, 67, 31–50, 1988.

Robinson, S.A., Hindell, M.A., Foraging ecology of gentoo penguins, *Pygoscelis papua*, at Macquarie Island during period of chick care, *Ibis*, 138, 722–731, 1996.

Robinson, P.H., Kolber, Z., Sullivan, C.W., Photophysiology and photoacclimation in surface sea ice algae from McMurdo Sound, *Mar. Ecol. Prog. Ser.*, 143, 243–256, 1997.

Robinson, C., Archer, S.D., Williams, P.T.leB., Microbial dynamics in coastal waters off East Antarctica: Plankton production and respiration, *Mar. Ecol. Prog. Ser.*, 180, 23–26, 1999.

Rodhouse, P.G., Cephalopod fauna of the South Scotia Sea at South Georgia: Potential for commercial exploitation and possible consequences, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin/Heidelberg, 1990, 289–298.

Rodhouse, P.G., Population structure of *Martialia hyadesi* (Cephalopoda: Ommastrephidae) at the Antarctic Polar Front and the Patagonian Shelf, South Atlantic, *Bull. Mar. Sci.*, 49, 404–418, 1991.

Rodhouse, P.G., Prince, P.A., Cephalopod prey of the black-browed albatross, *Diomedea melanophrys*, *Polar Biol.*, 13, 373–376, 1993.

Rodhouse, P.G., Yeatman, J., Redescription of *Martilia hyadesi* Rochbrunne and Mabile, 1889 (Mollusca: Cephalopoda), *Bull. Br. Museum Nat. His. (Zool.)*, 56, 135–140, 1990.

Rodhouse, P.G., Olsson, O., Anker-Nilsson, P., Murry, A.W.A., Cephalopod predation by the king penguin, *Aptenodytes patagonicus*, from South Georgia, *Mar. Ecol. Prog. Ser.*, 168, 13–19, 1987.

Rodhouse, P.G., Croxall, J.P., Prince, P.A., Towards an assessment of the stock of ommastrephid squid *Martialia hyadesi* in the Scotia Sea: Data from predators, in *Recent Advances in Cephalopod Fishes Biology*, Okutani, T., O'Dor, R.K., Kubodera, T., Eds., Tokai University Press, Tokyo, 1993, 433–440.

Rodhouse, P.G., Arnbom, T.R., Fedak, M.A., Yeatman, G.A., Murray, A.W.A., Cephalopod prey of the wandering albatross, *Diomedea exulans*, *Mar. Biol.*, 96, 1–10, 1997.

Roe, H.S.J., Seasonal formation of laminae in the ear plug of the fin whale, *Discov. Rep.*, 35, 1–36, 1967.

Roed, L.P., O'Brien, J.J., A coupled ice-ocean model of upwelling in the marginal ice zone, *J. Geophys. Res.*, 88, 2863–2872, 1983.

Ronan, T.E., Jr., Lipps, J.A., Delaca, T.E., Sediments and life under the Ross Ice Shelf, *Antarc. J. U.S.*, 13, 141–142, 1978.

Ronner, U., Sorenson, F., Holm-Hansen, O., Nitrogen assimilation by phytoplankton in the Scotia Sea, *Polar Biol.*, 2, 137–147, 1983.

Roper, C.E.F., Systematics and zoogeography of the worldwide bathypelagic squid *Bathyteuthis (Cephalopoda: Oregopsida), United States National Museum Bulletin* 291, Smithsonian Institution Press, Washington, DC, 1969.

Roper, C.E.F., Cephalopods of the Southern Ocean region: Potential resources and bibliography, in *BIOMASS, Volume II*, El-Sayed, S.Z., Ed., SCAR, SCOR, Scott Polar Research Institute, Cambridge, UK, 1981, 99–105.

Roper, C.E.F., Systematics and zoogeography of the worldwide bathypelagic squid *Bathyteuthis* (Cephalopoda: Oregopsida), *United States National Museum Bulletin* 291, Smithsonian Institution Press, Washington, DC, 2001.

Ropert-Condert, Y., Kato, A., Baudet, J., Bost, C.-A., Le Maho, Y., Naito, Y., Feeding strategies of free-ranging Adélie Penguins, *Pygoscelis adeliae*, analysed by multiple data recording, *Polar Biol.*, 24(6), 460–466, 2001.

Rosenberg, A.A., Beddington, J.R., Basson, M., Growth and longevity of krill during the first decade of pelagic whaling, *Nature (Lond.)*, 324, 152–153, 1986.

Ross, R.M., Energetics of *Euphausia pacifica*: Complete carbon and nitrogen budgets at 8° and 12°C throughout the life-span, *Mar. Biol.*, 68, 15–23, 1982.

Ross, R.M., Quetin, L.B., *Euphausia superba*: Fecundity and the physiological ecology of its eggs and larvae, *Antarc. J. U.S.*, 17, 166–167, 1983.

Ross, R.M., Quetin, L.B., Spawning frequency and fecundity of the Antarctic krill, *Euphausia superba*, *Mar. Biol.*, 77, 201–205, 1983.

Ross, R.M., Quetin, L.B., How productive are Antarctic krill?, *BioScience*, 36, 264–269, 1986.

Ross, R.M., Quetin, L.B., Ecological physiology of larval euphausiids, *Euphausia superba* (Euphausiacea), *Mem. Queensl. Mus.*, 31, 321–333, 1991.

Ross, R.M., Quetin, L.B., Amsler, M.O., *Euphausia superba*: A preliminary report on three areas of investigation, *Antarc. J. U.S.*, 19, 153–155, 1985.

Ross, R.M., Quetin, L.B., Baker, K.S., Vernet, M., Smith, R.C., Growth limitation in young *Euphausia superba* under field conditions, *Limnol. Oceanogr.*, 45, 31–43, 2000.

Ross, R.M., Quetin, L.B., Newberger, T., Oakes, S.A., Growth and behaviour of krill (*Euphausia superba*) under the ice in late winter 2001 west of the Antarctic Peninsula, *Deep-Sea Res.*, 51, 2169–2184, 2004.

Rott, H., Skavarca, P., Nagler, T., Recent changes of Larsen Ice Shelf, Antarctic Peninsula, unveiled by ERS-1, *Revista SELPER*, 11(1–2), 46–50, 1995.

Rott, H., Rack, W., Naglaer, T., Skavarca, P., Climate-induced retreat and collapse of the Northern Larsen Ice Shelf (Antarctic Peninsula), *Ann. Glaciol.*, 17, 628–632, 1998.

Rounesvell, D.E., Periodic eruption of itinerant leopard seals within the Australian sector of the Southern Ocean, 1976–1986, *Pap. Royal Society of Tasmania*, 122, 189–191, 1988.

Rounsevell, D.E., Eberhard, I., Leopard seals, *Hydrurga leptonyx* (Pinnipedia), at Macquarie Island, *Aust. J. Mar. Freshwat. Res.*, 7, 403–415, 1980.

Rowedder, U., Feeding ecology of the myctophid *Electrona antarctica* (Günther, 1878) (Teleostei), *Meeresforschung*, 27, 252–263, 1979a.

Rowedder, U., Some aspects of the biology of *Electrona antarctica* (Günther 1878) (Family Myctophidae), *Meeresforschung*, 4, 244–251, 1979b.

Rudd, J.T., On the biology of the Euphausiidae, *Hvalradets Skr.*, 2, 1–105, 1932.

Russek, J.T., Kaspryzk, Z., Szostak, S., Preliminary economic evaluation of commercial kill catches, *Stud. Mater. Morsk. Inst. Ryb. Gdynia*, 42, 1981. In Polish.

Ryan, K.G., UV radiation and photosynthetic properties of sea ice microalgae, *J. Photochem. Photobiol.*, 13, 25–31, 1992.

Ryan, K.G., Beaglehole, D., Ultraviolet radiation and bottom ice algae: Laboratory and field studies from McMurdo Sound, Antarctica, in *Ultraviolet Radiation in Antarctica: Measurements and Environmental Effects, Antarctic Research Series 62*, Weller, C.S., Penhale, P.A., Eds., American Geophysical Union, Washington, DC, 1994, 229–242.

Ryther, J.H., Photosynthesis and fish production in the sea, *Science*, 166, 72–76, 1969.

Sabourenkov, E., Mesopelagic fishes of the Southern Ocean—Summary results of recent Soviet studies, in *Selected Scientific Papers, Scientific Committee of CCAMLR*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 433–457 pp, 1990.

Sadiq, M., *Toxic Chemistry in Marine Environments*, Marcel Dekker, New York, 1992.

Sadlier, M.F.S., Lay, K.M., Foraging movements of Adélie Penguins (*Pygoscelis adeliae*) in McMurdo Sound, in *Penguin Biology*, Davis, L.S., Darby, J.T., Eds., Academic Press, London, 1990, 157–180.

Saggiomo, V., Garrada, G.C., Magoni, O., Marino, D., Ribera d'Alcala, M., Ecological and physiological aspects of primary production in the Ross Sea, in *Ross Sea Ecology*, Faranda, F.M., Guglielmo, L., Ianora, A., Eds., Springer, New York, 2000, 247–258.

Sahrhage, D., Length-weight correlation in Antarctic krill *Euphausia superba*, *Meeresforschung*, 26, 47–49, 1978.

Sahrhage, D., Some indications for environmental and krill resources variability in the Southern Ocean, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin/ Heidelberg, 1988a, 33–40.

Sahrhage, D., Ed., *Antarctic Ocean and Resources Variability*, Springer, Berlin/Heidelberg, 1988b.

Saijo, Y., Kawashi, T., Primary production in the Antarctic Ocean, *J. Oceanogr. Soc. Jap.*, 19(4), 190–196, 1964.

Sakshaug, E., Holm-Hansen, O., Factors governing pelagic production in polar oceans, in *Marine Phytoplankton and Productivity*, Holm-Hansen, O., Bolis, O.L., Gilles, R., Eds., Springer, Berling/Heidelberg, 1984, 1–18.

Sakshaug, E., Holm-Hansen, O., Photoadaptation in Antarctic phytoplankton: Variations in growth rate, chemical composition, and *P* vs *I* curves, *J. Plankton Res.*, 8, 459–573, 1986.

Sakshaug, E., Skjodal, H.R., Life at the ice edge, *Ambio*, 18, 60–67, 1989.

Sakshaug, E., Slagstad, D., Light and productivity of phytoplankton in polar marine systems: A physiological view, in *Pro Mare Symposium on Polar Marine Ecology*, Trondheim, Sakshaug, E., Hopkins, C.C.E., Eds., Polar Research, 69–85, 1991.

Sampson, D.B., Pregnancy rates versus length in southern fin whales, *Int. Whaling Committee Rep.*, 20, 255–265, 1989.

Samyshev, E.Z., Bacterioplankton of Antarctic coastal waters: Concentration, production and bacterial destruction, *Oceanology*, 26, 508–515, 1986.

Sanders, H.L., Benthic marine diversity and the stability-time hypothesis: Diversity and stability in ecological systems, *Proc. Brookhaven Symp. Biol.*, 22, 71–81, 1969.

Sanders, H.L., Evolutionary ecology and life-history patterns in the deep sea, *Sarsia*, 64, 1–7, 1979.

Sarmiento, J.L., Le Quéré, C., Oceanic carbon dioxide uptake in a model of century-scale global warming, *Science*, 274, 1346–1350, 1996.

Sasaki, H., Distribution of nano- and microplankton in the Indian Sector of the Southern Ocean, *Mem. Natl Inst. Polar Res., Spec. Issue*, 2, 38–50, 1984.

Sasaki, H., Hoshiai, T., Sedimentation of microalgae under Antarctic fast ice in summer, *Mem. Natl Inst. Polar Res., Spe. Issue*, 40, 45–55, 1986.

Sasaki, H., Watanabe, K., Underwater observations of ice-algae in Lützow-Holm Bay, Antarctica, *Antarc. Rec.*, 81, 1–8, 1984.

Sato, T., Hatanaka, H., A review of assessment of Japanese distant-water fisheries for cephalopods, in *Advances in Assessment of World Cephalopod Resources*, FAO Fisheries Technical Paper No. 231, Caddy, J.F., Ed., FAO Fisheries, Rome, 1983, 145–203.

Satoh, H., Watanabe, K., Kanda, H., Takahashi, E., Seasonal changes of chlorophyll *a* standing stocks and oceanographic conditions under fast ice near Syowa Station, Antarctica, *Antarc. Rec.*, 30, 19–32, 1986.

Satoh, H., Fukami, K., Watanabe, K., Takahashi, E., Seasonal changes in heterotrophic bacteria under fast ice near Syowa Station, Antarctica, *Can. J. Microbiol.*, 35, 329–333, 1989.

Savidge, G., Harbour, D., Gilpin, L.C., Boyd, P.W., Phytoplankton distribution and production in the Bellinghausen-Laurev Sea, austral spring 1992, *Deep-Sea Res.*, 42, 1201–1217, 1995.

Savidge, G., Priddle, J., Gilpin, L.C., Bathmann, U., Murphy, E.J., Owens, N.J.P., Pollard, R.T., Turner, D.R., Veth, C., Boyd, P.W., An assessment of the role of the marginal ice zone in the carbon cycle of the Southern Ocean, *Antarc. Sci.*, 8, 349–358, 1996.

Saville, A., Survey methods of appraising resources, *FAO Fisheries Technical Paper*, 1977, 171.

SCAR Bird Biology Subcommittee, Minutes of meeting 22 and 23 August 1983, Hobart, Tasmania, *Cormorant*, 16, 138–145, 1983.

SCAR/SCOR, Meeting of the SCAR Group of Specialists of Southern Ocean Ecosystems and Their Living Resources, BIOMASS Report Series No. 35, 1983a.

SCAR/SCOR, First Meeting of the *ad hoc* Group on Squid Biology, BIOMASS Report Series No. 33, 1983b.

SC-CCAMLR, Report of the Seventh Meeting of the Scientific Committee (SC-CAMLR-VII), Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1988.

SC-CCAMLR, Fish stock assessment—Report of the Working Group, in *Report of the Ninth Meeting of the Scientific Committee*, Annex 6, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1990a, 281–286.

SC-CCAMLR, Report of the Ninth meeting of the Scientific Committee (SC-CCAMLR-IX). Nitrogen assimilation by phytoplankton in the Scotia Sea, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 1990b.

Schalk, R., Brey, T., Bathman, U., Arntz, W., Gerdes, D., Dieckmann, G., Ekau, W. et al., Towards a conceptual model for the Weddell Sea ecosystem, in *Trophic Models of Aquatic Ecosystems*, Christense, V., Pauly, D. et al. Eds., International Center for Living Aquatic Resources Management, Manila, 1993, 323–327.

Scheffer, V.B., *Seals, Sea Lions and Walrusses: A Review of the Pinnepedia*, Stanford University Press, Stanford, CA, 1958.

Scheffer, M., Carpenter, S., Foley, J.A., Walker, B., Catastrophic shifts in ecosystems, *Nature (Lond.)*, 413, 591–696, 2001.

Schlosser, P., Helium: A new tracer in Antarctic oceanography, *Nature (Lond.)*, 321(6067), 233–235, 1986.

Schmitz, W.J., On the interbasin-scale thermohaline circulation, *Rev. Geophys.*, 33, 151–173, 1995.

Schnack, S.B., A note on the sedimentation of particulate matter in Antarctic waters during summer, *Meeresforschung*, 30, 306–315, 1985a.

Schnack, S.B., Feeding of *Euphausia superba* and copepod species in response to varying concentrations of phytoplankton, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985b, 311–323.

Schnack, S.B., Smetacek, V., von Bodungen, B., Utilization of phytoplankton by copepods in Antarctic waters during spring, in *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*, Gray, J.S., Christiansen, M.E., Eds., Wiley, Chichester, 1985, 65–81.

Schnack-Schiel, S.B., The macrobiology of sea ice, in *Sea Ice: An Introduction to its Physics, Biology and Geology*, Thomas, D.N., Dieckmann, G.S., Eds., Blackwell Science, Oxford, 2003, 211.

Schnack-Schiel, S.B., Hagen, W., Life cycle strategies and seasonal variations in distribution and population structure of four dominant copepod species in the easten Weddell Sea, Antarctica, *J. Plankton Res.*, 65, 1543–1552, 1994.

Schnack-Schiel, S.B., Mujica, A., The zooplankton of the Antarctic Peninsula, in *Southern Ocean Ecology: The BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, UK, 1996, 79–92.

Schnack-Schiel, S.B., Dieckmann, G.S., Eicken, H., Weissenbeger, J., Mizdalski, E., Beyer, K., Thomas, D., Gradinger, R., Spindler, M., Life cycle strategy of the Antarctic calanoid copepod *Stephos longipes*, *Prog. Oceanogr.*, 36, 45–75, 1995.

Schnack-Schiel, S.B., Thomas, D., Dahms, H.-U., Haas, C., Mizdaski, E., Copepods in Antarctic sea ice, *Antarct. Rec. Ser.*, 73, 173–182, 1998.

Schnack-Schiel, S.B., Dieckmann, G.S., Gradinger, R., Melnikov, I.A., Spindler, M., Thomas, D.N., Meiofauna in sea ice of the Weddell Sea (Antarctica), *Polar Biol.*, 24, 724–728, 2001.

Schneppenheim, R., Concentration of fluoride in Antarctic animals, *Meeresforschung*, 28, 179–182, 1980.

Schneppenheim, R., MacDonald, C.M., Genetic variation and population structure of krill (*Euphausia superba*) in the Atlantic sector of Antarctic waters and off the Antarctic Peninsula, *Polar Biol.*, 3, 19–28, 1984.

Schröder, A., Lombarte, A., Olaso, I., Knust, R., Demersal fish fauna, *Ber. Polarforsch.*, 301, 124–135, 1999.

Schulenberger, E., Wormuth, J.H., Loeb, V.J., A large swarm of *Euphausia superba*: Overview of patch structure and composition, *J. Crust. Biol.*, 4, 75–95, 1984.

Schwarzbacher, W., Die Fischfauna des östlichen und südlichen Weddellmeers, Nahrung und trophrishe Stekkung, Fischarten, *Ber. Polarforsch.*, 54, 1084–1093, 1988.

Sciermammano, F., Jr., Observations of Antarctic polar front motions in a deep water expression, *J. Phys. Oceanogr.*, 9, 221–226, 1989.

Scolaro, J.A., Censo de elefantes marinos (*Mirounga leonina* L.) en el territorio continental Argentino, *Informes Técnicos del Centro Nacional Patagónico*, 1.4.1, 1–12, 1976.

Scott, F.J., Davidson, A.T., Marchant, H.J., Grazing by the Antarctic sea ice ciliate Pseudocalanus embus, *Polar Biol.*, 24, 127–131, 2001.

Seddon, P.J., van Heezik, Y., Diving depths of the yellow-eyed penguin, *Megadyptes antipodes*, *Emu*, 90, 53–57, 1990.

Seebacher, F., Davison, W., Lowe, C.J., Franklin, C.E., A falsification of the thermal specialization paradigm: Compensation for elevated temperatures in Antarctic fishes, *Biol. Lett.*, 1, 151–154, 2005.

Segawa, S., Kato, M., Murano, M., Growth, moult and filtering rate of krill in laboratory conditions, *Mem. Natl Inst. Polar Res., Spec. Issue*, 27, 93–103, 1983.

Selph, K.E., Landry, M.R., Allen, C.B., Calbet, A., Christensen, S., Bidigare, R.R., Microbial community composition and growth dynamics of the Antarctic polar front and seasonal ice zone during late spring, *Deep-Sea Res.*, 48, 4059–4080, 2001.

Seno, J., Komaki, Y., Takeda, A., Reports on the biology of the *Umitaka-Maru* expedition: Plankton collected by the *Umitaka-Maru* in the Antarctic and adjacent water, with special reference to copepods, *J. Tokyo Univ. Fish.*, 49, 53–62, 1963.

Sergeant, D.E., Feeding rates of cetacea, *Fiskeridirektorastets Skrifter Serie Havunderskelser*, 15, 246–258, 1969.

Sergeant, D.E., Feeding, growth and productivity of northwest Atlantic harp seals (*Pagophilus groenlandicus*), *J. Fish. Res. Board Can.*, 30, 17–29, 1973.

Servais, P., Billen, G., Vives Rojo, J., Rate of bacterial mortality in aquatic environments, *Appl. Environ. Microbiol.*, 40, 1440–1455, 1985.

Seventy, D.L., The banding programme of *Puffinus tenuirostris* (Temminck), *CSIRO Wildl. Res.*, 6, 42–55, 1957.

Shabica, S.V., Tidal zone ecology at Palmer Station, *Antarc. J. U.S.*, 7, 184–191, 1977.

Shackleton, N.J., Kennett, J.P., Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: Oxygen and carbon isotope analysis in DSDP sites 277, 279, and 281, *Initial Rep. Deep Sea Drilling Proj.*, 29, 743–755, 1975.

Shaughnessy, P.D., Kerry, K.R., Crabeater seals (Lobodon carcinophagus) during the breeding season: Observations on five groups near Enderby Land, Antarctica, *Mar. Mamm. Sci.*, 5(1), 68–77, 1989.

Shaw, E., Schooling fishes, *Am. Sci.*, 66, 166–175, 1978.

Sheldon, R.W., Prakash, A., Sutcliffe, W.H., Size distribution of particles in the ocean, *Limnol. Oceanogr.*, 17, 327–340, 1972.

Sheppard, D.S., Deely, J.M., Edgerley, W.H.L., Heavy metal content of meltwater for the Ross Dependency, *NZ J. Mar. Freshwat. Res.*, 31, 313–318, 1997.

Sherman, K., Ryan, A.F., Antarctic marine living resources, *Oceanus*, 31, 59–63, 1988.

Sherman, K., Jones, C., Sullivan, L., Smith, W., Berrien, P., Ejsymont, L., Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems, *Nature (Lond.)*, 291, 486–489, 1981.

Sherr, B.F., Sherr, E.B., Role of heterotrophic protozoa in carbon and energy flow in aquatic systems, in *Current Perspectives in Microbial Ecology*, Klug, M.J., Reddy, C.A., Eds., American Society for Microbiology, Washington, DC, 1984, 412–423.

Sherr, E.B., Sherr, B.F., Fallon, R.D., Newell, S.Y., Small aloricate ciliates as a major component of the marine heterotrophic nanoplankton, *Limnol. Oceanogr.*, 31, 177–183, 1986.

Sherr, E.B., Rassoulzadegan, F., Sherr, B.F., Bacterivory by pelagic choreotrichous ciliates in coastal waters of the NW Mediterranean Sea, *Mar. Ecol. Prog. Ser.*, 55, 235–240, 1989.

Shevchenko, V., The nature of interrelationships between killer whales and other cetaceans. Fisheries and Marine Series Translation Series No. 3839. Original title: Kharakter vzaimootnoshenii kasahiki i drugikh kitoobraznykh, *Morsk Mleikopitayushchie Chast*, 23, 173–175, 1975.

Shick, J., Dunlap, W., Mycosporine-like amino acids and related gadusols: Biosynthesis, accumulation and UV-protective function in aquatic organisms, *Annu. Rev. Physiol.*, 54, 223–262, 2002.

Shick, J., Dunlop, W., Buettner, G., Ultraviolet (UV) protection in marine organisms. II. Biosynthesis, accumulation, and sunscreening function of micosporine-like amino acids, in *Free Radicals in Chemistry, Biology and Medicine*, Yoshikawa, T., Toyokuri, S., Yamamoto, Y., Naito, Y., Eds., OICA International, London, 2000, 215–228.

Shimadzu, Y, A brief summary of Japanese fishing activity in relation to Antarctic krill, 1972/73 to 1982–83, in *Selected Papers Presented to the Scientific Committee of CCAMLR, 1982–1984: Part I*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 439–471 pp, 1984a.

Shimadzu, Y, A review of Antarctic ecosystem models, in *Selected Papers Presented to the Scientific Committee of CCAMLR, 1982–1984: Part II*, Commission for the Conservation of Antarctic Marine Living Resources, Hobart, 221–246, 1984b.

Shirakihara, K., Nakayama, K., Komaku, Y., Acoustic estimation of krill biomass in R.V. *Kaiyo-Maru* SIBEX I Survey area (Indian Ocean sector of the Southern Ocean), *Mem. Natl Inst. Polar Res., Tokyo*, 190, 140–152, 1986.

Shlibanov, V.I., Growth and natural mortality of Patagonian rock cod (*Patagonotothen guntheri shagensis*) from Shag Rocks, *SC-CAMLR Selected Scientific Papers, 1989*, 1–11, 1990.

Showers, W.J., Jr., Daniels, R.A., Laine, D., Marine biology at Palmer Station, 1975 austral winter, *Antarc. J. U.S.*, 12, 22–25, 1977.

Shust, K.V., Visual observations on Antarctic krill made on board the factory ship *Akademik Knipovich*, *Trudy Vsesoyiuznogo Nauchoissledovatel'skogo Instituta Morskogo Rybnogo Khnopvich (Trudy VNIRO)*, 66, 223–250, 1969, MAAF Translation No. RTS 5588.

Shust, K.V., Brief communications on the distribution and biology of members of the genus *Micromesistius* (Family Gadidae), *J. Ichthyol.*, 18, 490–492, 1978.

Sicrachi, M.E., Siebruth, J.McN., Sunlight-induced decay of planktonic marine bacteria in filtered seawater, *Mar. Ecol. Prog. Ser.*, 33, 19–27, 1986.

Siebruth, J.McN., Microbiology of Antarctica, in *Biogeography and Ecology of Antarctica*, van Miegham, J., van Oye, P., Eds., Dr. W. Junk, The Hague, 1967, 267–295.

Siebruth, J.McN., Studies on algal substances in the sea. III. Glebstoff (humic material) in terrestrial and marine waters, *J. Exp. Mar. Biol. Ecol.*, 2, 174–184, 1969.

Siebruth, J.McN., *Sea Microbes*, Oxford University Press, New York, 1979.

Siebruth, J.McN., Grazing of bacteria by protozooplankton in pelagic marine waters, in *Heterotrophic Activity in the Sea*, Hobbie, J., Williams, A.J.LeB., Eds., Plenum Press, New York, 1984, 405–444.

Siebruth, J.McN., Davis, P.G., The role of heterotrophic nanoplankton in the grazing of planktonic bacteria in the Sargasso and Caribbean Seas, *Ann. Inst. Oceanogr.*, 58, 285–290, 1982.

Siebruth, J.McN., Smetacek, V., Lenza, J., Pelagic ecosystem structure: Heterotrophic compartments and their relationship to plankton site functions, *Limnol. Oceanogr.*, 23, 1256–1263, 1978.

Siegel, V., Relationships of various length measurements of *Euphausia superba* Dana, *Meeresforschung*, 29, 114–117, 1982.

Siegel, V., On the fecundity of the Antarctic krill *Euphausia superba* (Euphausiacea), *Arch. Fischereiwiss.*, 36, 185–193, 1985.

Siegel, V., Structure and composition of the Antarctic krill stock in the Bransfield Strait (Antarctic Peninsula) during the Second International BIOMASS Experiment (SIBEX), *Arch. Fischereiwiss.*, 37, 51–72, 1986a.

Siegel, V., Untersuchungen zur Biologie des antarkischen Krill, *Euphausia superba*, im Bereich der Bransfield Strabe und angrenzender Gebiete, *Mitt. Inst. Seefischerei, Hamburg*, 38, 1–224, 1986b.

Siegel, V., Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions, *Mar. Biol.*, 96, 483, 1987.

Siegel, V., Winter and spring distribution and status of the krill stock in Antarctic Peninsula waters, *Arch. Fischereiwiss.*, 39, 45–72, 1989.

Siegel, V., Assessment of krill (*Euphausia superba*) spawning off the Antarctic Peninsula, *Arch. Fischereiwiss.*, 41, 101–130, 1992.

Siegel, V., Krill (Euphausiacea) life history and aspects of population dynamics, *Can. J. Fish. Aquat. Sci.*, 57(Supplement), 130–150, 2000a.

Siegel, V., Krill (Euphausiacea) demography and variability in abundance and distribution, *Can. J. Fish. Aquat. Sci.*, 57(Supplement), 151–167, 2000b.

Siegel, V., Distribution and population dynamics of *Euphausia superba*: Summary of recent findings, *Polar Biol.*, 29, 1–22, 2005.

Siegel, V., Kalinowski, J., Krill demography and small-scale processes: A review, in *Southern Ocean Ecology: The BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, UK, 1996, 145–163.

Siegel, V., Loeb, V., Recruitment of Antarctic krill, *Euphausia superba*, and possible causes of its variability, *Mar. Ecol. Prog. Ser.*, 123, 45–56, 1995.

Siegel, V., Bergstrom, B., Strobens, J.O., Schalk, P.H., Distribution, size frequencies and maturity stages of krill, *Euphausia superba*, in relation to sea-ice in the northern Weddell Sea, *Polar Biol.*, 10, 549–557, 1990.

Siegel, V., Shibowski, A., Harm, U., Community structure of the epipelagic zooplankton community under the sea ice in the northern Weddell Sea, *Polar Biol.*, 12, 15–24, 1992.

Siegel, V., Loeb, V., Groger, J., Krill (*Euphausia superba*) density, proportional and absolute recruitment and biomass in the Elephant Island region (Antarctic Peninsula) during the period 1977 to 1997, *Polar Biol.*, 19, 393–398, 1998.

Siegel, V., Bergstrom, B., Muhlenherdt-Siegel, M., Demography of krill in the Elephant Island area during summer 2000 and its significance for stock recruitment, *Antarct. Sci.*, 14, 162–170, 2002.

Siegfried, W.R., Birds and mammals—Oceanic birds of the Antarctic, in *Key Environments—Antarctica*, Bonner, W.N., Walton, D.W.H., Eds., Pergamon Press, Oxford, 1985, 242–265.

Siegfried, W.R., Williams, A.J., Burger, A.E., Berruti, A., Mineral and energy contributions of eggs of selected seabirds to the Marion Island terrestrial ecosystem, *S. Afr. J. Antarc. Res.*, 8, 75–87, 1978.

Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., *Antarctic nutrient cycles and food webs*, Symposium on Antarctic Biology, Wilderness, South Africa 12–16 September 1983, Springer, Berlin, 1985.

Sievers, H.A., Nowlin, W.D., Jr., Upper ocean characteristics in Drake Passage and adjourning areas of the Southern Ocean, 39° W-95° W, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin/Heidelberg, 1988, 57–80.

Silver, M.W., Alldredge, A.L., Bathypelagic marine snow: Deep sea algal and detrital community, *J. Mar. Res.*, 39, 501–530, 1981.

Silver, M.W., Mitchell, J.G., Ringo, D.L., Siliceous nanoplankton, II. Newly discovered cysts and abundant choanoflagellates in the Weddell Sea, Antarctica, *Mar. Biol.*, 58, 211–217, 1980.

Silver, M.W., Gowing, M.M., Brownlee, D.C., Corless, J.O., Ciliated protozoa associated with oceanic sinking debris, *Nature (Lond.)*, 309, 246–248, 1984.

Simmonds, I., Modelling of the reaction of Antarctica to climate change at its periphery, in *Impact of Climate Change on Antarctica-Australia*, Australian Government Publishing Service, Canberra, 1992, 16–23.

Simon, V., Sarano, F., Concentrations en sels nutritifs de l'eau de surface dans le secteur Indian de l'Ocean Austral (compagne Apsara II Antipod III 1984), in *Characteristiques biologiques, chemiques et sedimentalogiques du Secteur indian de l'Ocean Austral (Plateu des Kerguelen), Rapp. Comp. Mer. TAAF*. 84-01, 8–103, 1978.

Simon, M., Glockner, F.O., Amann, R., Different community structure and temperature optima of heterotrophic picoplankton in various regions of the Southern Ocean, *Aquat. Microb. Ecol.*, 68, 275–284, 1999.

Simpson, R.D., The shore environment of Macquarie Island, *A.N.A.R.E. Report, Series B*, 125(1), 1–41, 1976a.

Simpson, R.D., Physical and biotic factors limiting the distribution and abundance of littoral molluscs on Macquarie Island (Sub-Antarctic), *J. Exp. Mar. Biol. Ecol.*, 21, 11–19, 1976b.

Simpson, R.D., The reproduction of some littoral molluscs from Macquarie Island, *Mar. Biol.*, 44, 125–142, 1977.

Siniff, D.B., Seal population dynamics and ecology, *J. Royal Soc. N. Z.*, 11, 317–327, 1982.

Siniff, D.B., An overview of the ecology of Antarctic seals, *Am. Zool.*, 31, 143–152, 1991.

Siniff, D.B., Bengtson, J.L., Observations and hypotheses concerning the interactions among crabeater seals, leopard seals, and killer whales, *J. Mammal.*, 58(3), 414–416, 1977.

Siniff, D.B., Stone, S., The role of the leopard seal in the trophodynamics of the Antarctic marine ecosystem, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 555–560.

Siniff, D.B., Cline, D.R., Erickson, A.W., Population densities of seals in the Weddell Sea, Antarctica, in 1968, in *Antarctic Ecology, Volume I*, Holdgate, W.M., Ed., Academic Press, London, 1970, 377–394.

Siniff, D.B., Tester, J.R., Kuechle, V.B., Some observations on the activity patterns of Weddell seals as recorded by telemetry, in *Antarctic Pinnipedia, Antarctic Research Series 18*, Burt, W.H., Ed., 1971, 173–180.

Siniff, D.B., DeMaster, D.P., Hofman, R.J., Eberhart, L.L., An analysis of the dynamics of a Weddell seal population, *Ecol. Monogr.*, 47, 319–335, 1977.

Siniff, D.B., Stirling, I., Bengtson, J.L., Reichle, R.A., Biota of the Antarctic pack ice: R/V *Hero* Cruise 1976–77, *Antarc. J. U.S.*, 15, 160–165, 1977.

Siniff, D.B., Stirling, I., Bengtson, J.L., Reichle, R.A., Social and reproductive behaviour of crabeater seals (*Lobodon carcinophagus*) during austral spring, *Can. J. Zool.*, 57, 2243–2256, 1979.

Siniff, D.B., Stone, S., Reichle, D., Smith, T., Aspects of leopard seals (*Hydrurga leptonyx*) in the Antarctic Peninsula pack ice, *Antarc. J. U.S.*, 15, 160–161, 1980.

Sissenwinw, M.P., Modelling the application of a recent tool in Antarctic marine living resources, in *Selected Papers Presented to the Scientific Committee of CCAMLR, Part IV*, CCAMLR, Hobart, 1985, 369–390.

Skavarca, P., Fast recession of the northern Larsen ice Shelf monitored by space images, *Ann. Glaciol.*, 17, 317–321, 1993.

Skavarca, P., Rack, W., Pott, H., Ibarzabal y Donangelo, T., Climatic trend and the retreat and disintegration of ice shelves on the Antarctic Peninsula: An overview, *Polar Rec.*, 18, 151–157, 1999.

Skottsberg, C.J.F., Communities of marine algae in subantarctic and Antarctic waters, *Konglia svenska Veteetenskapsa kademions Handlinger*, 19(4), 1–92, 1941.

Skottsberg, C.J.F., Antarctic phycology, in *Biologie Antarctique*, Carrick, R., Holdgate, M.W., Prevost, J., Eds., Herman, Paris, 1964, 147–154.

Sladen, W.J.L., Menzie, C.M., Reichel, W.L. *Nature (Lond.)*, 200, 670, 1963.

Slattery, P.N., Oliver, J.S., Scavenging and other feeding habits of lysanianassid amphipods (*Orchomene* spp.) from McMurdo Sound, *Polar Biol.*, 8, 181–190, 1986.

Slawyk, G., ^{13}C and ^{15}N uptake by phytoplankton in the Antarctic upwelling area: Results from the Antiopd 1 cruise in the Indian Ocean sector, *Aust. J. Mar. Freshwat. Res.*, 30, 431–448, 1979.

Slijper, E.J., Whales, Hutchinson, London, 1982.

Slosarczyk, W., Juvenile *Trematomus bernacchii* (Boulenger, 1982) and *Pagothenia brachysoma* (Proppenheim, 1962) (Pisces: Nototheniidae) in krill concentrations off Balleney Island (Antarctica), *Pol. Polar Res.*, 4, 57–69, 1983.

Slosarczyk, W., Rembiszewski, J.M., The occurrence of juvenile Notothenioidea (Pisces) within krill concentrations in the region of the Bransfield Strait and the southern Drake Passage, *Pol. Polar Res.*, 4, 299–312, 1982.

Smetacek, V.S., The annual cycle of protozooplankton in the Kiel Bight, *Ophelia Suppl.*, 63, 1–11, 1980.

Smetacek, V.S., Annual cycle of sedimentation in relation to plankton ecology in the western Kiel Bight, *Ophelia Suppl.*, 1, 65–76, 1981a.

Smetacek, V.S., The annual cycle of protozooplankton in the Kiel Bight, *Mar. Biol.*, 63, 1–11, 1981b.

Smetacek, V.S., Passow, U., Spring bloom initiation and Sverdrup's critical-depth model, *Limnol. Oceanogr.*, 35, 228–233, 1990.

Smetacek, V.S., Scharek, R., Gordon, L.I., Eicken, H., Fahrbach, E., Rohardt, G., Moore, S., Early spring phytoplankton blooms in ice platelet layers of the southern Weddell Sea, Antarctica, *Deep-Sea Res.*, 39, 153–168, 1992.

Smetacek, V.S., Scharek, R., Nöthig, E.-M., Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin/Heidelberg, 1990, 103–114.

Smetacek, V.S., Klaas, C., Menten-Deuers, S., Rynearson, T.A., Mesoscale distribution of dominant diatom species relative to the hydrographic field along the Antarctic Polar Front, *Deep-Sea Res.II*, 49/18, 3835–3848, 2002.

Smetacek, V.S., Assmy, P., Henjes, J., The role of grazing in structuring Southern Ocean pelagic ecosystems and biogeochemical cycles, *Antarc. Sci.*, 16(4), 541–558, 2004.

Smith, M.S.R., Seasonal movements of the Weddell seal in McMurdo Sound, Antarctica, *J. Wildl. Manage.*, 29, 464–470, 1965.

Smith, V.R., A quantitative description of energy flow and nutrient cycling in the Marion Island terrestial ecosystem, *Polar Rec.*, 18, 361–370, 1977.

Smith, P.E., Biological effects of ocean variability: Time and space scales of biological response, *Rapp. P. v. Reun. Cons. Int. Explor. Mer.*, 173, 117–122, 1978.

Smith, W.O., Jr., Phytoplankton dynamics in marginal ice zones, *Oceanogr. Mar. Biol. Ann. Rev.*, 25, 1–38, 1990a.

Smith, W.O., Jr., Ed., *Polar Oceanography, Part A: Physical Science*, Academic Press, London, 1990b.

Smith, W.O., Jr., Ed., *Polar Oceanography, Part B: Chemistry, Biology and Geology*, Academic Press, London, 1990c.

Smith, R.C., Baker, K.S., Assessment of the influence of enhanced UV-B on marine primary productivity, in *The Role of Ultraviolet Radiation In Marine Ecosystems*, Watkins, J., Ed., Plenum Press, New York, 1982, 509–537.

Smith, E.A., Burton, R.W., Weddell seals of Signy Island, in *Antarctic Ecology, Volume I*, Holdgate, M.W., Ed., Academic Press, London, 1970, 415–428.

Smith, W.O., Jr., Gordon, L.I., Hyperproductivity of the Ross Sea (Antarctica) polyna during austral spring, *Geophys. Res. Lett.*, 24, 233–236, 1997.

Smith, M.A.K., Haschemeyer, A.E.V., Protein metabolism and cold adaptation in Antarctic fishes, *Physiol. Zool.*, 53, 373–382, 1980.

Smith, W.O., Jr., Kettner, G., Inorganic nitrogen uptake by phytoplankton in the marginal ice zone of the Fram Strait, *Rapports et Proces-Verbaux des Reuniones Conseil Permanent International pour l'Exploration de la Mer*, 188, 90–97, 1989.

Smith, W.O., Jr., Lancelot, C., Bottom-up versus top-down control in phytolankton of the Southern Ocean, *Antarct. Sci.*, 16, 531–539, 2004.

Smith, W.O., Jr., Nelson, D.M., Phytoplankton biomass near a receding ice-edge in the Ross Sea, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985a, 70–77.

Smith, W.O., Jr., Nelson, D.M., Phytoplankton bloom produced by a receding ice edge in the Ross Sea: Spatial coherence with the density field, *Science*, 227, 163–166, 1985b.

Smith, W.O., Jr., Nelson, D.M., The importance of ice edge phytoplankton production in the Southern Ocean, *BioScience*, 36, 251–257, 1986.

Smith, W.O., Jr., Nelson, D.M., Phytoplankton growth and new production in the Weddell Sea marginal ice zone during austral spring and autumn, *Limnol. Oceanogr.*, 35, 909–921, 1990a.

Smith, W.O., Jr., Sakshaug, E., Polar phytoplankton, in *Polar Oceanography, Part B: Chemistry, Biology and Geology*, Smith, W.O., Jr., Ed., Academic Press, San Diego, CA, 1995, 477–525.

Smith, S.L., Schnack-Schiel, S.B., Polar zooplankton, in *Polar Oceanography, Part B: Chemistry, Biology and Geology*, Smith, W.O., Jr., Ed., Academic Press, London, 1990, 521–528.

Smith, J.M.B., Simpson, R.D., Biotic zonation on rocky shores of Heard Island, *Polar Biol.*, 4, 89–94, 1985.

Smith, S.P.A., Simpson, R.D., Effect of the *Nella Dan* oil spill on the fauna of *Durvillaea antarctica* holdfast, *Mar. Ecol. Prog. Ser.*, 121, 73–89, 1995.

Smith, R.C., Stammerjohn, S.E., Variation of surface air temperarture and sea ice extent in the western Peninsula region, *Ann. Glaciol.*, 33, 493–498, 2001.

Smith, V.R., Steenkamp, M., Climate change and its ecological implications at a subantarctic island, *Oecologia*, 85, 14–24, 1990.

Smith, M.A.K., Mathews, R.W., Hudson, A.P., Haschemeyer, A.E.V., Protein metabolism of tropical reef and pelagic fish, *Comp. Biochem. Physiol.*, 65B, 415–418, 1980.

Smith, G.A., Nichols, P.D., White, D.C., Fatty acid composition and microbial activity of benthic marine sediment from McMurdo Sound, Antarctica, *FEMS Microb. Ecol.*, 38, 219–231, 1986.

Smith, W.O., Jr., Baunmann, M.E., Wilson, D.L., Aletsee, L., Phytoplankton biomass and productivity in the marginal ice zone of the Fram Strait during summer 1984, *J. Geophys. Res.*, 92, 6777–6786, 1987.

Smith, W.O., Jr., Keene, N.K., Comiso, J.C., Interannual variability in estimated primary productivity of the Antarctic marginal ice zone, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin/Heidelberg, 1988, 131–139.

Smith, G.A., Nichols, P.D., White, D.C., Benthic nearshore microbial communities of McMurdo Sound. Paper presented at the Fifth SCAR Symposium on Antarctic Biology, Hobart, Australia, 29 August–3 September, 1988, 1989a.

Smith, G.A., Davis, J.D., Muscat, A.M., Moe, R.L., White, D.C., Lipid composition and metabolic activities of benthic near-shore microbial communities of Arthur Harbour, Antarctic Peninsula: Comparisons with McMurdo Sound, *Polar Biol.*, 9, 517–524, 1989.

Smith, W.O., Jr., Kelly, H.P., Rich, J.H., Chlorophyll distribution and primary production in the Ross Sea, austral summer, *Antarct. J. U.S.*, 25, 179–182, 1990.

Smith, D.C., Steward, G.F., Azam, F., Virus and bacteria abundances in the Drake Passage during January and August 1991, *Antarc. J. U.S.*, 27, 125–127, 1992.

Smith, R.C., Prézelin, B.B., Baker, K.S., Bidigare, R.R., Boucher, N.P., Coley, T., Karentz, D., Macintyre, S., Matlick, H.A., Menzies, D., Ondrusek, M., Wan, Z., Waters, K.J., Ozone depletion—ultraviolet radiation and phytoplankton biology in Antarctic waters, *Science*, 255, 952–959, 1992.

Smith, W.O., Jr., Nelson, D.M., Tullio, G.R., Leventer, A.R., Temporal and spatial patterns in the Ross Sea: Phytoplankton biomass, elemental composition, productivity and growth, *J. Geophys. Res.*, 101, 18455–18465, 1996.

Smith, R.C., Ainley, D., Baker, K. et al. Marine ecosystem sensitivity to climate change, *BioScience*, 49, 393–404, 1999.

Snape, I., Cole, C.M., Riddle, M.J., Gore, D.G., Duquesne, S., Stark, J.S., Management and remediation of contaminated sites at Casey Station, Antarctica, *Polar Rec.*, 37, 199–214, 2001.

Soevik, T., Braekholm, O.R., Fluoride in Antarctic krill (*Euphausia superba*) and the Atlantic krill (*Meganyctiphanes norvegica*), *J. Fish. Res. Board of Can.*, 36, 1414–1416, 1979.

Solomon, S., Stratospheric ozone depletion: A review of concepts and history, *Rev. Geophys.*, 17, 275–316, 1999.

Solyanik, G.A., An interesting ichthyological find, *Soviet Antarctic Expedition Information Bulletin* No. 42, 78–80, 1963.

Solyanik, G.A., Experiment in marking seals from small ships, *Sov. Antarc. Exped. Info. Bull.*, 5, 212–217, 1964.

Solyanik, G.A., Distribution and nutrition of bathypelagic fish *Notolepis coatsi* (Paralepidae family), *Sov. Antarct. Exped. Info. Bull.*, 5, 365–366, 1965.

Solyanik, G.A., The food of the Antarctic fish (*Electrona antarctica* Günther), *Sov. Antarc. Exped. Info. Bull.*, 6, 443–447, 1967.

Somero, G.N., Enzyme mechanisms of temperature compensation: Immediate and evolutionary effects of temperature on enzymes of aquatic poikilotherms, *Am. Nat.*, 103, 517–530, 1969.

Somero, G.N., Giese, A.C., Wohlschlag, D.E., Cold adaptation in the Antarctic fish *Trematomus bernacchii*, *Comp. Biochem. Physiol.*, 26, 223–232, 1968.

Somero, G.N., Fields, P.A., Hofmann, C.E., Weinstein, R.B., Kawall, H., Cold adaptation and stenothermy in Antarctic Notothenioid fishes: What has been gained and what has been lost?, in *Fishes of Antarctica: A Biological Overview*, di Prisco, G., Pascano, E., Clarke, A., Eds., Springer, Milan, 1998, 98–109.

Sommer, U., Maximal growth rates of Antarctic phytoplankton: Only weak dependence on cell size, *Limnol. Oceanogr.*, 34, 1109–1112, 1989.

SooHoo, J.B., Palmisano, A.C., Lizotte, M.P., Kottmeier, S.T., SooHoo, S.L., Sullivan, C.W., Spectral light absorption and quantum yield of photosynthesis in sea ice microalgae and a bloom of Phaeocystis pouchetii from McMurdo Sound, Antarctica, *Mar. Ecol. Prog. Ser.*, 39, 175–189, 1987.

Soot-Ryen, T., Antarctic pelecypods, *Sci. Res. Norwegian Antarct. Exped. 1927–1928*, 3, 1–46, 1951.

Sorokin, Yu.I., Microheterotrophic organisms in marine ecosystems, in *Analysis of Marine Ecosystems*, Longhurst, A.R., Ed., Academic Press, New York, 1981, 293–342.

Sorokin, Yu.I., Federov, V.K., Classification of bacterioplankton in Antarctic waters, *Trudy IOAN SSSR*, 112, 69–75, 1978.

Sorokin, Yu.I., Kogelschatz, J.E., Analysis of heterotrophic microplankton in an upwelling area, *Hydrobiologia*, 66, 195–208, 1979.

Sosinski, J., Kuranty, J., Morze Scotia-nowy nejon Polowow ryb Polskiego Rybolowstwa, *Technikai Gospodarka Morska*, 12, 23–29, 1979.

Sosinski, J., Sikora, K., Wyniki baden ichtiologicznych prowadzonych na MT *Gemini w czasie* II: Polskiej Ekspedycji Antarkycznei, *Biuletyn Morskiego Institutu Rybackiago*, 43, 23–29, 1977.

Soutar, A., Isaacs, J.D., Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediments off California, *Fish. Bull., NOAA/U.S. Dep. Commerce*, 72, 257–273, 1974.

South, G.R., Biogeography of benthic marine algae of the Southern Oceans, in *Proceedings of the International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere: Volume I*, N.Z. DSIR Information Series 137, Wellington, 85–108, 1979.

Southern Ocean Convention Workshop, Southern Ocean Convention Workshop on the Management of Antarctic Marine Living

Resources 1980 Report and Recommendations, Centre for Environmental Education—The Whale Protection Fund, Washington, DC, 1980.

Spies, A., Growth rates of Antarctic marine phytoplankton in the Weddell Sea, *Mar. Ecol. Prog. Ser.*, 41, 267–274, 1987.

Spindler, M., Dieckmann, G.S., Distribution and abundance of the planktic Foraminifera *Neogloboquadrina pachyderma* in sea ice of the Weddell Sea (Antarctica), *Polar Biol.*, 5, 185–191, 1986.

Spindler, M., Dieckmann, G.S., Das Meeres ab Lebensraum, *Spectrum der Wissenschaft*, 2/1991, 48, 1991.

Spindler, M., Dieckmann, G.S., Lange, M.A., Seasonal and geographic variations in sea ice community structure of the Weddell Sea, Antarctica, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin/Heidelberg, 1990, 129–135.

Spiridonov, V.A., Gruzov, E.N., Pushkin, A.F., Issledovaniia stai antarkicheskoi *Euphausia superba* (Crustacea: Euphausiacea) pod l'dom (Investigations of schools of Antarctic *Euphausia superba* under the ice), *Zoologicheskii Zhurnal*, 64, 1655–1660, 1985.

Spurr, E.B., The breeding of the Adélie Penguin *Pygoscelis adeliae* at Cape Bird, *Ibis*, 117, 324–338, 1975.

Squire, V.A., The physical oceanography and sea ice characteristics of the Southern Ocean, *Primer Symposium Español de Estudios Antarcticos, Pama de Mallorca, 30 June–July 1985*, 1–2, 1987.

Stachelin, J., Harris, N.R.P., Appenzeller, C., Eberhard, J., Ozone trends: A review, *Rev. Geophys.*, 39, 231–290, 2001.

Stahl, J.C., Jouventin, P., Mougin, J.L., Roux, J.P., Weimerskirch, H., The foraging zones of seabirds in the Crozet Islands sector of the Southern Ocean, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 478–486.

Stambler, N., Primary production, light absorption and quantum yields of phytoplankton from the Bellingshausen and Amundsen Seas (Antarctica), *Polar Biol.*, 26, 438–451, 2003.

Stammerjohn, S.E., Smith, R.C., Spatial and temporal variability of outer Antarctic Peninsula ice coverage, *Antarct. Res. Ser.*, 70, 81–104, 1996.

Stanwell-Smith, D.P., Barnes, P.K.A., Benthic community development in Antarctica: recruitment and growth in settlement panels at Signy Island, *J. Exp. Mar. Biol. Ecol.*, 212, 61–79, 1997.

Stark, J.S., The distribution and abundance of soft-sediment macrobenthos around Casey Station, East Antarctica, *Polar Biol.*, 23, 840–850, 2000.

Stark, J.S., Riddle, M.J., Human impacts in marine benthic communities at Casey Station: Description, determination and demonstration of impacts, in *Antarctic Biology in a Global Context*, Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backhuys Publishers, Leiden, The Netherlands, 2003, 278–284.

Starmans, A., Gutt, J., Arntz, W.E., Mega-epibenthic communities in Arctic and Antarctic shelf areas, *Polar Biol.*, 135, 269–280, 1999.

Steele, J.H., The Structure of Marine Ecosystems, Harvard University Press, Cambridge, MA, 1974.

Steeman-Nielsen, E., The use of radioactive carbon for measuring organic production in the sea, *Journal du Conseil International pour l'Exploration de la Mer*, 18(2), 117–140, 1952.

Steen, J.B., Berg, T., The gills of two species of haemoglobin-free fishes compared to those of other teleosts—with a note on severe anaemia in an eel, *Comp. Biochem. Physiol.*, 18, 517–526, 1966.

Stein, M, Variation of geostropic circulation off the Antarctic Peninsula and in the southwest Scotia Sea, in *Antarctic*, Springer, Berlin/Heidelberg, 81 pp, 1988.

Stein, M., Variability of local upwelling off the Antarctic Peninsula, 1986-1990, *Arch. für Fischereiwiss.*, 41(2), 131–158, 1992.

Stein, M., Heywood, R.B., Antarctic environment—physical oceanography: The Antarctic Peninsula and Southwest Atlantic region of the Southern Ocean, in *Southern Ocean Ecology: The BIOMASS Perspective*, El-Sayed, S.Z., Ed., Cambridge University Press, Cambridge, UK, 1994, 11–24.

Stenton-Dozey, J., Griffiths, C.L., The fauna associated with kelp stranded on a sandy beach, in *Sandy Beaches as Ecosystems*, McLachlan, A., Erasmus, T., Eds., Dr. W. Junk Publishers, The Hague, 1983, 441–447.

Stepnik, R., All-year population studies of Euphausiacea (Crustacea) in Admiralty Bay (King George Island, South Shetland Islands, Antarctica), *Pol. Polar Res.*, 3, 49–68, 1982.

Stewardson, C.L., *Mammals of the Sea*, Sedolna Publishing, Braddon, 1997.

Stewart, B.S., Yochem, P.K., Gelatt, T.S., First-year movements of Weddell Seals (*Leptonychotes weddellii*) in the Ross Sea, Antarctica, during the first year of life, *N.Z. Nat. Sci.*, 23, 195, 2000.

Stewart, B.S., Yochem, P.K., Gelatt, T.S., Siniff, D.B., The pack ice niche of Weddell seals in the Ross Sea, *N.Z. Nat. Sci.*, 23(Supplement), 114, 1998a.

Stewart, B.S., Yochem, P.K., Gelatt, T.S., Siniff, D.B., Dispersal and habitat use of Weddell seals (*Leptonychotes weddelli*) in the Ross Sea, Antarctica, during their first year of life, *N.Z. Nat. Sci.*, 23, 195–206, 1998b.

Stewart, B.S., Yochem, P.K., Gelatt, T.S., Siniff, D.B., The pack ice niche of Weddell seals in the Ross Sea, in *Antarctic Biology in a Global Context*, Huskies, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backhuys Publishers, Leiden, The Netherlands, 2003, 224–229.

Steyeart, J., Distribution of planktonic diatoms along an African–Antarctic transect, *Invest. Pesq.*, 37, 295–328, 1973.

Stirling, I., The seals at White Island: A hypothesis on their origin, *Antarctica*, 4, 310–313, 1965.

Stirling, I., Ecology of the Weddell Seal in McMurdo Sound, Antarctica, *Ecology*, 50, 573–586, 1969a.

Stirling, I., Tooth wear as a mortality factor in the Weddell seal *Leptonychotes weddelli*, *J. Mammal.*, 50, 559–565, 1969b.

Stirling, I., Distribution and abundance of the Weddell seal in the western Ross Sea, Antarctica, *N.Z. J. Mar. Freshwat. Res.*, 3, 191–200, 1969c.

Stirling, I., Population dynamics of the Weddell seal (*Leptonychotes weddelli*) in McMurdo Sound, in *Antarctic Pinnipedia, Antarctic Research Series 18*, Burt, W.H., Ed., American Geophysical Society, Washington, DC, 1971a, 141–161.

Stirling, I., Population aspects of Weddell seal harvesting at McMurdo Sound, Antarctica, *Polar Rec.*, 15, 653–667, 1971b.

Stirling, I., Regulation of numbers of an apparently isolated population of Weddell seals (*Leptonychotes weddelli*), *J. Mammal.*, 53, 107–115, 1972.

Stirling, I., Factors affecting the evolution of social behaviour in the pinnipedia, *Rapports et Preces-Verbaux des Reunios Conseil Permanent International pour l'Exploration de la Mer*, 169, 205–212, 1975.

Stirling, I., The biological significance of polynas in the Canadian Arctic, *Arctic*, 33, 303–312, 1980.

Stirling, I., Cleator, H., *Polynas in the Canadian Arctic*, Canadian Wildlife Service Occasional Paper No. 45, Canadian Wildlife Service, Ottawa, 1981.

Stockner, J.G., Phototrophic picoplankton: an overview from marine and freshwater ecosystems, *Limnol. Oceanogr.*, 33, 765–775, 1988.

Stockner, J.C., Anita, N.J., Algal picoplankton from marine and freshwater systems: a multidisciplinary perspective, *Can. J. Fish. Aquat. Sci.*, 43, 2472–2503, 1986.

Stockton, W., An intertidal assemblage at Palmer Station, *Antarc. J. U.S.*, 8, 305–307, 1973.

Stockton, W., The intertidal zone at Palmer Station, Anvers Island, Antarctic Peninsula, in the wake of the *Bahia Paraiso* spill, *Antarc. J. U.S.*, 25, 203–207, 1990.

Stoeckner, D.K., Michaels, E., Davis, L.H., Large proportion of marine planktonic ciliates found to contain functional chloroplasts, *Nature (Lond.)*, 326, 790–792, 1987.

Stoeckner, D.K., Buck, H.R., Putt, M., A flagellate- and ciliate-dominated microbial community in the land-fast ice, *Antarc. J. U.S.*, 25, 197–199, 1990.

Stoeckner, D.K., Buck, H.R., Putt, M., Changes in the sea-ice brine community during spring–summer transition, McMurdo Sound, Antarctica. I. Photosynthetic protists, *Mar. Ecol. Prog. Ser.*, 84, 265–278, 1992.

Stoeckner, D.K., Buck, H.R., Putt, M., Changes in sea-ice brine community during the spring–summer transition in McMurdo Sound, Antarctica. II. Phagotrophic protists, *Mar. Ecol. Prog. Ser.*, 95, 103–113, 1993.

Stoeckner, D.K., Putt, M., Moisan, T., Nano- and microplankton dynamics during the spring *Phaeocystis* sp. bloom in McMurdo Sound, Antarctica, *J. Mar. Biol. Assoc. U.K.*, 75, 815–832, 1995.

Stone, H.S., Siniff, D.B., Leopard seal feeding and food consumption in Antarctic spring and summer, in *Proceedings of the Fourth Biennial Conference on Biology of Marine Mammals*, *December 14–18, 1983*, 14–18, 1983.

Stonehouse, B., Bird life, in *Antarctic Research*, Adie, R.J., Robin, G. deQ., Eds., Butterworth, London, 1964, 219–239.

Stonehouse, B., The general ecology and thermal balance of penguins, *Adv. Ecol. Res.*, 4, 131–196, 1967.

Stonehouse, B., Adaptation in polar and subpolar penguins, in *Antarctic Ecology, Volume I*, Holdgate, M.W., Ed., Academic Press, London, 1970, 526–541.

Stonehouse, B., Birds and mammals—penguins, in *Key Environments—Antarctica*, Bonner, W.W., Ed., Pergamon Press, Oxford, 1985, 223–241.

Stonehouse, B., Monitoring shipborne visitors in Antarctica: A preliminary field study, *Polar Rec.*, 28, 213–218, 1992.

Stout, W.E., Shabica, S.V., Marine ecological studies at Palmer Station and vicinity, *Antarc. J. U.S.*, 5, 134–135, 1970.

Strand, S.W., Hamner, W.M., Schooling behaviour of Antarctic krill (*Euphausia superba*) in laboratory aquaria: Reactions to chemical and visual stimuli, *Mar. Biol.*, 105, 355–359, 1990.

Strange, I.J., The thin-billed prion, *Pachyptila belcheri*, at New Island, Falkland Islands, *Gerfaut*, 70, 411–445, 1980.

Stretch, T.J., Hamner, P.P., Hamner, W.M., Michel, W.C., Cook, J., Sullivan, C.W., Foraging behaviour of Antarctic krill *Euphausia superba* on sea-ice microalgae, *Mar. Ecol. Prog. Ser.*, 44, 131–139, 1988.

Sukuromato, K., Kato, H., Tanaka, S., A simulation study about several factors influencing the estimates of a trend in age at sexual maturity of the Antarctic minke whale, *Rep. Int. Whal. Commun.*, 35, 285–2990, 1985; 36, 231–235, 1980.

Sullivan, C.W., Sea ice bacteria: Reciprocal interactions of the organisms and their environment, in *Sea Ice Biota*, Horner, R.A., Ed., CRC Press, Boca Raton, FL, 1985, 22–79.

Sullivan, C.W., Palmisano, A.C., Sea-ice microbial communities in McMurdo Sound, *Antarc. J. U.S.*, 16, 128–130, 1981.

Sullivan, C.W., Palmisano, A.C., Sea ice microbial communities: Distribution, abundance and diversity of ice bacteria in McMurdo Sound, Antarctica in 1980, *Appl. Environ. Microbiol.*, April 1984, 788–795, 1984.

Sullivan, C.W., Palmisano, A.C., Kottmeier, S., Moe, R., Development of the sea ice microbial community in McMurdo Sound, *Antarc. J. U.S.*, 18, 155–157, 1982.

Sullivan, C.W., Palmisano, A.C., Soohoo, J.B., Influence of sea ice and sea ice biota on downwelling irradiance and spectral composition of light in McMurdo Sound, *Int. Soc. Opt. Eng. Proc., 489, Ocean Optics*, 7, 159–165, 1984.

Sullivan, C.W., Palmisano, A.C., Kottmeier, S., Grossi, S.McG., Moe, R., The influence of light on growth and development of the sea-ice microbial community of McMurdo Sound, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 78–83.

Sullivan, C.W., McClain, C.R., Comiso, J.C., Smith, W.O., Jr., Phytoplankton standing crops in an Antarctic ice edge assessed by satellite remote sensing, *J. Geophys. Res.*, 93, 12487–12498, 1988.

Sullivan, C.W., Cota, G.F., Krempin, G.W., Smith, W.O., Jr., Distribution and activity of bacterioplankton in the marginal ice zone of the Weddell-Scotia Sea during austral spring, *Mar. Ecol. Prog. Ser.*, 63, 239–252, 1990.

Sullivan, C.W., Arrigo, K.R., McLain, C.R., Comiso, J.C., Firestone, J., Distribution of phytoplankton blooms in the Southern Ocean, *Science*, 262, 1832–1837, 1993.

Sun, L.G., Liu, X.D., Yin, X.B., Zhu, R.B., Xie, Z.Q., Wang, Y.H., A 1500-year record of Antarctic seal populations in response to climate change, *Polar Biol.*, 25, 495–501, 2004.

Suskin, V.A., Planktonnye soobshcjestva antarkticheskoi chasti Atlantiki, in *Biologicheskie osnovy promyslovogo osvoeniia otkrytykh rainov okeana*, Vinogradov, M.E., Flint, M.V., Eds., Nauka, Moscow, 1985, 29–39.

Sverdrup, H.U., On conditions for the vernal blooming of phytoplankton, *Journal du Conseil, Conseil Permanent International pour l'Exploration de la Mer*, 18, 287–295, 1953.

Sverdrup, H.U., Johnson, M.W., Fleming, R.H., The Oceans: Their Physics, Chemistry and General Biology, Prentice-Hall, Englewood Cliffs, NJ, 1942.

Svetlov, M.F., The porbeagle *Lamma nasus* in Atlantic waters, *J. Ichthyol.*, 18, 850–851, 1978.

Swadling, K.M., Population structure of two Antarctic ice-associated copepods, *Drescheriella glacialis* and *Paralabidocera antarctica*, in winter sea ice, *Mar. Biol.*, 139, 597–603, 2001.

Swadling, K.M., Gibson, J.A.E., Ritz, D.A., Nichols, P.D., Horizontal patchiness in sympagic organisms of the Antarctic fast ice, *Antarc. Sci.*, 9, 399–406, 1997.

Swadling, K.M., Gibson, J.A.E., Ritz, D.A., Nichols, P.D., Grazing of phytoplankton by protozoa in eastern Antarctic waters, *Mar. Biol.*, 128, 39–48, 1997.

Swithinbank, C., McClain, P., Little, P., Drift tracks of Antarctic icebergs, *Polar Rec.*, 18, 495–561, 1977.

Takahasi, E., Loricate and scale-bearing protists from Lutzow–Holm Bay, Antarctica. I. Species of Acanthoecidae and Centrohelida found at a site selected on fast ice, *Antarct. Rec.*, 73, 1–22, 1981.

Takahashi, M., Trophic ecology of demersal fish community north of the South Shetland Islands, with note on the ecological role of krill, *Mem. Natl Inst. Polar Res., Spec. Issue*, 27, 183–192, 1983.

Takahashi, E., Loricate and scale-bearing protists from Lützow-Holm Bay, Antarctica. II. Four marine species of *Paraphysomonas* (Chrysophyceae), including two new species from the fast-ice-covered coastal area, *Jap. J. Phycol.*, 35, 155–166, 1987.

Takahashi, M., Bienfang, P.K., Size structure of phytoplankton in subtropical waters, *Mar. Biol.*, 76, 203–211, 1983.

Takahashi, M., Nemoto, T., Food of some Antarctic fish in the Western Ross Sea in the summer of 1979, *Polar Biol.*, 3, 237–239, 1984.

Takeda, S., Influence of iron availability on nutrient consumption ratio of diatoms in oceanic waters, *Nature (Lond.)*, 393, 774–777, 1998.

Takeda, S., Watanabe, K., Growth response of Antarctic phytoplankton to iron enrichment, *Proc. NIPR Symp. Antarct. Biol.*, 10, 14–24, 1997.

Taljaard, J.J., van Loon, H., Crutcher, H.L., Jenne, R.L., *Climate of the Upper Air. Part 1. Southern Hemisphere*, U.S. National Center for Atmospheric Research, Washington, DC, 1969, 140.

Tanabe, S., Tatsukawa, R., Chlorinated hydrocarbons in the Southern Ocean, in *Proceedings of the BIOMASS Collection in 1982*, Nemoto, T., Matsuda, T., Eds., National Institute for Polar Research, Tokyo, 1983, 64–76.

Tande, K.S., Bamstedt, U., On the trophic fate of *Phaeocystis pouchetii*. I. Copepod feeding rates on solitary cells and colonies of *P. pouchetii*, *Sarsia*, 72, 313–320, 1987.

Taniguchi, A., Hamada, E., Okazaki, M., Naito, Y., Distribution of phytoplankton chlorophyll continuously recorded in JARE-25 cruise to Syowa Station, Antarctica (SIBEX I). Proceedings of the Eighth Symposium on Polar Biology, 1985, *Mem. Natl Inst. Polar Res., Spe. Issue*, 44, 3–14, 1986.

Tanimura, A., Distribution of chlorophyll *a* along the course of the *Fuji* to and from Antarctica in 1979–1980, *Antarct. Rec.*, 72, 35–48, 1981.

Tanimura, A., Minoda, T., Fukuchi, M., Hoshiai, T., Ohtsuka, H., Swarm of *Paralabidocera antarctica* (Calanoida: Copepoda) under sea ice near Syowa Station, Antarctica, *Antarc. Rec.*, 82, 12–19, 1984.

Tanimura, A., Fukuchi, M., Hoshiai, T., Seasonal changes in the abundance and species composition of copepods in the ice-covered sea near Syowa Station, Antarctica, *Mem. Natl Inst. Polar Res., Spe. Issue*, 40, 212–220, 1986.

Tanimura, A., Hoshiai, T., Fukuchi, M., The life cycle of the ice-associated copepod *Paralabidocera antarctica* (Calanoida: Copepoda) at Syowa Station, Antarctica, *Antarc. Sci.*, 8, 257–266, 1996.

Tanoue, E., Organic chemical composition of fecal pellet of the krill *Euphausia superba* Dana, I: Lipid composition, *Trans. Tokyo Univ. Fish.*, 6, 43–57, 1985.

Tanoue, E., Handa, N., Vertical transport of organic nutrients in the northern Pacific as determined by sediment trap experiments, Part 1: Fatty acid composition, *J. Oceanogr. Soc. Japan*, 36, 231–245, 1980.

Tanoue, E., Hara, S., Ecological implications of fecal pellets produced by the Antarctic krill *Euphausia superba* in the Antarctic Ocean, *Mar. Biol.*, 91, 359–369, 1986.

Tanoue, E., Handa, N., Sakugawa, H., Difference of the chemical composition of organic matter between fecal pellet of *Euphausia superba* and its feed, *Dunaliella tertiolecta*, *Trans. Tokyo Univ. Fish.*, 5, 189–196, 1982.

Targett, T., Trophic ecology and structure of coastal Antarctic fish communities, *Mar. Ecol. Prog. Ser.*, 4, 243–263, 1981.

Tarling, G.A., Ward, P., Sheader, M., Williams, J.A., Symon, C., Distribution patterns of macrozooplankton assemblages in the Southwest Atlantic, *Mar. Ecol. Prog. Ser.*, 120, 29–40, 1995.

Tarpy, C., Killer whale attack, *Nat. Geograph. Mag.*, 155, 542–545, 1979.

Tarverdiyera, M.I., The food consumption, daily ration and feeding habits of the ice fish *Champsocephalus gunnari* Lönnberg of the South Orkneys, in *Characteristics of the Pelagic Community from the Sea of Scotia and Adjacent Waters*, Trudy VNIRO, Moscow, 69–76 pp, 1982. In Russian.

Tarverdiyera, M.I., Pinskaya, I.A., The feeding of fishes of the families Nototheniidae and Channichthyidae on the shelves of the Antarctic Peninsula and the South Shetland Islands, *J. Ichthyol.*, 20, 50–69, 1980.

Tatian, M., Sahade, R.T., Fuentes, V., Mecuri, G., Use of a wide spectrum of particle food by suspension feeders: Adaptation to low phytoplankton availability, *IX SCAR Biol. Symp. Abstr.*, 63, 2005.

Taylor, G.T., The role of pelagic heterotrophic protozoa in nutrient cycling: A review, *Ann. de l'Institut Oceanographique*, 58, 227–241, 1982.

Taylor, R.H., Wilson, P.R., Recent increase and southern expansion of Adélie Penguin populations in the Ross Sea, Antarctica, related to climate warming, *N.Z. J. Ecol.*, 14, 25–29, 1990.

Taylor, G.T., Iturriaga, R., Sullivan, C.W., Interactions of bacterivorous grazers and heterotrophic bacteria with dissolved organic matter, *Mar. Ecol. Prog. Ser.*, 23, 129–141, 1985.

Taylor, R.H., Wilson, P.R., Thomas, B.W., Status and trends of Adélie Penguin populations in the Ross Sea Region, *Polar Rec.*, 26, 293–304, 1990.

Tayor, R.J.F., An unusual record of three species of whale being restricted to pools in Antarctic sea ice, *J. Zool.*, 129, 325–331, 1957.

Tchernia, P., Etude de la derive antarctique Est-Quest au moyen d'icebergs suivi par la satellite, *Comptes Rendus Academie des Sciences (Paris)*, 278, 667–670, 1974.

Tchernia, P., Descriptive Physical Oceanography, Pergamon Press, Oxford, 1980.

Tchernia, P., Jeannin, P.F., Circulation in Antarctic waters as revealed by iceberg tracks, 1972–83, *Polar Rec.*, 22, 263–269, 1984.

Tenaza, R., Behaviour and nesting success relative to nest location in Adélie Penguins (*Pygoscelis adeliae*), *Condor*, 73, 81–92, 1971.

Terazaki, M., Wada, M., Euphausiids collected from the Australian Sector of the Southern Ocean during BIOMASS SIBEX Cruise KH-83-4, *Mem. Natl Inst. Polar Res., Spe. Issue*, 40, 97–109, 1986.

Tererry, L.J., McMinn, A., Ryan, K.G., *In situ* oxygen microelectrode measurements of bottom ice algal production in McMurdo Sound, Antarctica, *Polar Biol.*, 25, 72–80, 2002.

Testa, J.W., Siniff, D.B., Population dynamics of Weddell seals (*Leptonychotes weddelli*) in McMurdo Sound, *Ecol. Monogr.*, 57, 141–161, 1987.

Testa, J.W., Siniff, D.B., Ross, M.J., Winter, J.D., Dynamics of Weddell seal/Antarctic cod interactions in McMurdo Sound, Antarctica, in

Antarctic Nutrient Cycles and Food Webs, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, *Polar Biology* 5, 1985, 561.

Testa, J.W., Oehlert, G., Ainley, D.G., Bengtson, J.L., Siniff, D.B., Laws, R.M., Rounsevelle, D., Temporal variability in Antarctic marine ecosystems: Periodic fluctuations in the phocid seals, *Can. J. Fish. Aquat. Sci.*, 48, 631–639, 1987.

Texido, N., Garrabau, J., Gutt, J., Arntz, W.E., Recovery in Antarctic benthos after iceberg disturbance: Trends in benthic composition and growth forms, *Mar. Ecol. Prog. Ser.*, 278, 1–16, 2004.

Theriot, F., Fryxell, G.A., Multivariate statistical analysis of net diatom species distribution in the southwestern Atlantic and Indian Oceans, *Polar Biol.*, 5, 23–36, 1985.

Thomas, G., The food and feeding ecology of the light-mantled sooty albatross at South Georgia, *Emu*, 82, 92–100, 1982.

Thomas, D.N., Dieckmann, G.S., Antarctic sea ice: A habitat for extreme places, *Science*, 295, 641–652, 2002.

Thomas, D.M., Dieckman, G., Sea Ice: An Introduction to its Physics, Chemistry, Biology and Geology, Blackwell Science, Oxford, 2003.

Thomas, P.B., Green, K., Distribution of *Euphausia crystallorophias* within Prydz Bay and its importance to inshore the marine ecosystem, *Polar Biol.*, 8, 327–331, 1988.

Thomas, P.B., Jiang, J., Epiphytic diatoms of the inshore marine areas near Davis Station, *Hydrobiologia*, 140, 193–198, 1986.

Thomas, D.N., Baumann, M.E., Gleitz, M., Efficiency of carbon assimilation and photoacclimation in *Chaetoceros* species from the Weddell Sea (Antarctica)—influence of temperature and irradiance, *J. Exp. Mar. Biol. Ecol.*, 157, 195–209, 1992.

Thomas, D.N., Lara, R.J., Haas, C., Schnack-Schiel, S.B., Dieckmann, G.S., Kattner, G., Nöthig, E.-M., Mizdalski, E., Biological soup within decaying summer sea ice in the Amundsen Sea, Antarctica, in *Antarctic Sea Ice: Biological Processes, Interactions and Variability, Antarctic Research Series 73*, Lizotte, M., Arrigo, K., Eds., American Geophysical Union, Washington, DC, 1998, 161–171.

Thomas, D.N., Kattner, G., Engbrodt, R., Gannelli, V., Kennedy, H., Haas, C., Dieckmann, G.S., Dissolved organic matter in Antarctic sea ice, *Ann. Glaciol.*, 33, 297–303, 2001.

Thomas, D.N., Kennedy, H., Kattner, G., Gerdes, D., Gough, C., Dieckmann, G.S., Biogeochemistry of platelet ice: Influence on particle flux under land-fast sea ice during summer at Drescher Inlet, Weddell Sea, Antarctica, *Polar Biol.*, 24, 486–496, 2001.

Thompson, R.B., Effects of human disturbance on an Adélie Penguin rookery and measures to control it, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 1177–1180.

Thompson, P.M., Ollason, J.C., Lagged effects of ocean climate change on fulmar population dynamics, *Nature (Lond.)*, 413, 417–420, 2001.

Thorson, G., Reproductive and larval ecology of marine bottom invertebrates, *Biol. Rev.*, 25, 1–45, 1950.

Throndsen, J., Motility in some marine nanoplankton flagellates, *Norwegian J. Zool.*, 21, 193–200, 1973.

Thurston, M.H., The Crustacean Amphipoda of Signy Island, South Orkney Islands, *Br. Antarct. Surv. Sci. Rep.*, 71, 1972.

Tickell, W.L.N., Movements of the black-browed and grey-headed albatrosses in the South Atlantic, *Emu*, 66, 357–367, 1967.

Tickell, W.L.N., *Albatrosses*, Pica Press, East Sussex, 2000.

Tikhomirov, E.A., Biology of the ice forms of seals in the Pacific section of the Antarctic, *Rapports Proces-Verboux des Renunions Conceil International Pour l'Exploration de la Mer*, 169, 409–512, 1975.

Tilzer, M.M., Dubinsky, Z., Effects of temperature and day length on the mass balance of Antarctic phytoplankton, *Polar Biol.*, 7, 35–42, 1987.

Tilzer, M.M., von Bodungen, B., Smetacek, V., Light-dependence of photosynthesis in the Antarctic Ocean: Implications for regulatory productivity, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 61–69.

Tilzer, M.M., Elbracher, M., Gieskes, W.W.C., Beeze, B., Light-temperature interactions in the control of photosynthesis in Antarctic phytoplankton, *Polar Biol.*, 5, 105–111, 1986.

Timmermans, K.R., van Leeuwe, M.A., de Jong, J.T.M., McKay, R.M.L., Nolting, R.P., Witte, H.J., van Ooyen, J., Swagerman, M.J.W., Kloosterhuis, H., de Baar, H.J.W., Iron stress in the Pacific region of the Southern Ocean: Evidence from enrichment bioassays, *Mar. Ecol. Prog. Ser.*, 166, 27–41, 1998.

Timmermans, K.R., Garringa, L.T.A., de Baar, H.J.W., Vander Wagt, B., Veldhuis, M.J.W., de Jong, J.T.M., Croot, P.L., Boye, M., Growth rates of large and small Southern Ocean diatoms in relation to availability of iron in natural seawater, *Limnol. Oceanogr.*, 46, 260–266, 2001.

Tizler, M.M., Gieskes, W.W.C., Heusel, R., Fenton, N., The impact of phytoplankton on the spectral water transparency in the Southern Ocean: Implications for primary production, *Polar Biol.*, 14, 127–136, 1994.

Toharczyk, R., Annual cycle of chlorophyll *a* in Admiralty Bay 1981–1982 (King George Island, South Shetlands), *Pol. Arch. Hydrobiol.*, 33, 177–188, 1986.

Tomlin, A.G., Cetacean Mammals of the USSR and Adjacent Countries, *Isr. Prog. Sci. Transl.*, Jerusalem, 1967.

Torres, J.J., Somero, G.N., Metabolism, enzyme activities and cold adaptation in Antarctic mesopelagic fish, *Mar. Biol.*, 98, 169–180, 1988.

Torres, J.J., Lancraft, T.M., Weigle, B.L., Hopkins, T.L., Distribution and abundance of fishes and salps in relation to the marginal ice zone of the Scotia Sea, November and December 1983, *Antarct. J. U.S.*, 19(5), 117–119, 1984.

Torres, J.J., Aarset, A.V., Donnelly, J., Hopkins, T.L., Lancraft, T.M., Ainley, D.G., Proximate composition and overwintering strategies of Antarctic micronekton crustacea, *Mar. Ecol. Prog. Ser.*, 113, 221–232, 1994.

Tortell, P.D., Evolutionary and ecological perspectives on carbon acquisition in phytoplankton, *Limnol. Oceanogr.*, 45, 744–750, 2000.

Totten, A.K., Siphonophora of the Indian Ocean, together with systematic and biological notes on related species from other areas, *Discov. Rep.*, 27, 1–162, 1954.

Townsend, C.H., The distribution of certain whales as shown by logbook records of American whale ships, *Zoologica (New York)*, 19(1), 1–50, 1935.

Tranter, D.J., Interlinking of physical and biological processes in the Antarctic Ocean, *Oceanogr. Mar. Biol.: Ann. Rev.*, 20, 11–35, 1982.

Tratham, P.N., Croxall, J.P., Murphy, E.J., Dynamics of Antarctic penguin populations in relation to interannual polar variability in sea ice distribution, *Polar Biol.*, 16, 321–330, 1996.

Tréguer, P., Silica and the cycle of carbon in the sea, *Geoscience*, 334, 2002.

Tréguer, P., Jacques, G., Dynamics of nutrient and phytoplankton and fluxes of carbon, nitrogen and silica in the Antarctic Ocean, *Polar Biol.*, 12, 149–162, 1992.

Tréguer, P., van Bennekom, A.J., The annual production of biogenic silica in the Antarctic Ocean, *Mar. Chem.*, 35, 477–487, 1991.

Treguer, P., Gueneley, S., Zeyons, C., The distribution of biogenic and lithogenic silica and the composition of particulate matter in the Scotia Sea and Drake Passage during autumn, 1987, *Deep-Sea Res.*, 37, 783–791, 1990.

Trehen, P., Vernon, P., Peuplement dipterologie d'une île subantarctique la Possession (41° S, 51° E, Îles Crozet), *Rev. Ecol. Biol. Sol.*, 18, 105–120, 1982.

Tremblay, Y., Cherel, Y., Benthic and pelagic dives: A new foraging behaviour in rockhopper penguins, *Mar. Ecol. Prog. Ser.*, 204, 257–267, 2000.

Tremblay, J.E., Lucas, M.I., Kattner, G., Pollard, R., Strauss, V.H., Bathmann, U., Bracher, A., Significance of the Polar Frontal Zone for large sized diatoms and new production during summer in the Atlantic sector of the Southern Ocean, *Deep-Sea Res. II*, 49, 3793–3811, 2002.

Trenerry, L.J., McMinn, A., Ryan, K.G., *In situ* oxygen electrode measurements of bottom-ice algal production in McMurdo Sound, *Polar Biol.*, 25, 72–80, 2002.

Treshnikov, A.F., Alekseyev, G.V., Sarukanyan, E.I., Smirnov, N.P., Water circulation in the southern Ocean, *Trudy Arktichskii Naucho-issle-dovatel'skii Institut*, 345, English translation: Scripton Publishing Co., Washington, DC, 21–35 pp, 1978.

Tressler, W.L., Ommundsen, A.M., Seasonal oceanographic studies in McMurdo Sound, Antarctica. U.S. Navy Hydrographic Office Technical Report, 1–141, 1962.

Trillmich, F., Feeding territories and breeding success of South Polar skuas, *The Auk*, 95, 23–33, 1978.

Trillimich, F., Oho, K.A., Pinnipeds and El Niño: Responses to environmental stress, in *Ecological Studies*, Ed., Springer, Berlin/Heidelberg, 1983, 1–62.

Trimble, A.M., Harris, G.P., Phytoplankton population dynamics of a small reservoir: Use of sediment traps to quantify the loss of diatoms and recruitment of summer bloom-forming blue-green algae, *J. Plankton Res.*, 6, 897–917, 1984.

Trivelpiece, W.Z., Fraser, W.R., The breeding biology and distribution of Adélie Penguins: Adaptations to environmental variability, *Antarct. Res. Ser.*, 70, 273–286, 1996.

Trivelpiece, W.Z., Volkman, N.J., Feeding strategies of sympatric polar (*Catharacta maccormicki*) and brown skuas (*C. lönnbergi*), *Ibis*, 124, 50–54, 1980.

Trivelpiece, W.Z., Butler, R.G., Volkman, N.J., Feeding territories of brown skuas (*Catharacta lönnbergi*), *The Auk*, 97, 669–676, 1980.

Trivelpiece, W.Z., Bengtson, J.L., Trivelpiece, S.G., Volkman, N.J., Foraging behaviour of Gentoo and Chinstrap Penguins as determined by radiotelemetry techniques, *The Auk*, 103, 777–781, 1986.

Trivelpiece, W.Z., Ainley, D.G., Fraser, W.R., Trivelpiece, S.G., Skua survival, *Nature (Lond.)*, 345, 211, 1990.

Trivelpiece, W.Z., Trivelpiece, S.G., Guepel, G.R., Kjelmyr, J., Volkman, N.J., Adélie and Chinstrap Penguins: Their potential as monitors of Southern Ocean marine ecosystems, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin, 1990, 191–202.

Truesdale, R.S., Kellog, T.B., Ross sea diatoms: Modern assemblage distributions and their relationship to ecologic, oceanographic, and sedimentary conditions, *Mar. Micropaleontol.*, 4, 13–31, 1979.

Tucker, M.J., Burton, H.R., Seasonal and spatial variations in the zooplankton community of an eastern Antarctic coastal location, *Polar Biol.*, 10, 571–579, 1990.

Tupas, L.M., Koike, I., Simultaneous uptake and regeneration of ammonium by mixed assemblages of heterotrophic bacteria, *Mar. Ecol. Prog. Ser.*, 70, 273–282, 1991.

Tupas, L.M., Koike, I., Karl, D.M., Holm-Hansen, O., Nitrogen metabolism by heterotrophic bacterial assemblages in Antarctic coastal waters, *Polar Biol.*, 14, 195–204, 1994.

Turbott, E.G., Seals of the southern ocean, in *Antarctica Today*, Simpson, F.A., Ed., Reed, Wellington, 1952, 195–215.

Turkiewicz, M., Gales, E., Kalinowski, H., Collagenolytic activity of the serine proteinase from *Euphausia superba* Dana. *19th FEBS Meeting Rome, Abstracts*, MO214, 1989.

Turner, J.T., Sinking rates of fecal pellets from marine copepod *Pontella meadii*, *Mar. Biol.*, 40, 249–259, 1977.

Turner, J., The El Niño-Southern Oscillation and Antarctica, *Int. J. Climatol.*, 24, 1–31, 2004.

Twelves, E.L., Blood volumes of two Antarctic fishes, *Br. Antarct. Surv. Bull.*, 31, 85–92, 1960.

Tyler, J.C., Erythrocyte counts and haemoglobin determinations for two Antarctic Nototheniid fishes, *Stanford Ichthyol. Bull.*, 7, 199–201, 1960.

UNEP. Regionally-Based Assessment of Persistent Toxic Substances: Antarctic Regional Report. (2002), United Nations Environment Programme, Geneva, 2002.

Urban-Rich, J., Dagg, M.J., Peterson, T., Copepod grazing on phytoplankton in the Pacific sector of the Antarctic Polar Front, *Deep-Sea Res.*, 48, 4223–4246, 2001.

Uribe, E., Influence of the phytoplankton and primary production of the Antarctic waters in relationships with the distribution and behaviour of krill, *Serie Científico del Instituto Antártico Chileno*, 28, 147–163, 1982.

Ushakov, P.V., Quelques particularites de al bionomie benthique de l'Antarctique del'Es, *Cash. Biol. Mar.*, 4, 81–89, 1963.

van Aarde, R.J., Pascel, M., Marking southern elephant seals on Isles Kerguelen, *Polar Rec.*, 20, 62–65, 1980.

van Andel, T.H., Moore, T.C., Jr., Cenozoic calcium carbonate distribution and calcite compensation depth in the central equatorial Pacific ocean, *Geology*, 2, 87–92, 1974.

van Franeker, J., Top predators as indicators for ecosystem events in the confluence zone and marginal ice zone of the Weddell and Scotia Seas, Antarctica, *Polar Biol.*, 12, 93–102, 1992.

van Loon, H., Shea, D.J., The Southern Oscillation, Part VI: Anomalies of sea-level pressure on the southern Hemisphere and on Pacific sea surface temperature during the development of Warm Event, *Monthly Weather Review*, 115, 370–379, 1987.

van Woert, M.L., Wintertime expansion and contraction of the Terra Nova Bay polyna, in *Oceanography of the Ross Sea*, Spezie, G., Manzella, G.M.R., Eds., Springer, Milan, 1999, 145–164.

Vanhoeffen, E., Van der deutschen Südpolar expedition Fischereiversuche, *Petermans geographische Mitteilungen Erganzungschaft*, 47, 19–20, 1902.

Vanhove, S., Wittoeck, J., Desmet, G., van den Berghe, B., Herman, R.L., Bak, R.P.M., Nieuwland, G., Vosjan, J.H., Boldrin, A., Rabitti, S., Vincx, M., Deep-sea meiofauna communities in Antarctica: Structural analysis and relation with the environment, *Mar. Ecol. Prog. Ser.*, 127, 65–76, 1995.

Vanhove, S., Lee, H.J., Beghyn, M., van Gansgeke, D., Brockington, S., Vincx, M., The metazoan meiofauna in its biochemical environment: The case of an Antarctic coastal sediment, *J. Mar. Biol. Assoc. U.K.*, 78, 411–434, 1998.

Vanhove, S., Beghyn, M., van Gansbehe, D., Bullough, L.W., Vinex, M., A seasonally varying biotope at Signy Island, Antarctica: Implications for meiofaunal structure, *Mar. Ecol. Prog. Ser.*, 201, 13–25, 2000.

Vanucci, S., Bruni, V., Ultraviolet phytoplankton community structure in the Ross Sea during the Austral Spring 1994, in *Ross Sea Ecology*, Faranda, F.M., Guglielmo, L., Ianora, A., Eds., Springer, Berlin, 1998, 181.

Vaque, D., Durate, C.M., Marrasse, C., Phytoplankton colonization by bacteria; encounter probability as a limiting factor, *Polar Biol.*, 5, 241–247, 1989.

Vargo, G.A., Fanning, K., Heil, C., Bell, L., Growth rates and the salinity response on an Antarctic ice microflora community, *Polar Biol.*, 5, 241–247, 1986.

Veit, R.R., Braun, B.M., Hydrographic fronts and marine bird distribution in the Antarctic and sub-Antarctic, *Antarct. J. U.S.*, 19, 165–167, 1984.

Veith, C., Lancelot, C., Obst, S., On processes determining the vertical stability of surface waters in the marginal ice zone of the northwestern Weddell Sea and their relationship with phytoplankton bloom development, *Polar Biol.*, 12, 237–243, 1992.

Veit-Köhler, G., Meiofauna study in Potter Cove: Sediment situation and resource availability for small crustaceans (Copepoda and Peracarida), *Berichte zur Polarforschung*, 299, 132–136, 1998.

Veldhuis, M.J.W., Admiraal, W., Transfer of photosynthetic products in gelatinous colonies of *Phaeocystis pouchetii* (Haptophyceae) and its effect on the measurement of excretion rate, *Mar. Ecol. Prog. Ser.*, 26, 301–304, 1985.

Verity, P.G., Grazing of phytotrophic nanoplankton by microzooplankton in Narragansett Bay, *Mar. Ecol. Prog. Ser.*, 29, 105–115, 1986.

Vernet, M., Brody, E.A., Holm-Hansen, O., Mitchell, B.G., The response of Antarctic phytoplankton to ultraviolet radiation: Absorption, photosynthesis, and taxonomic composition, in *Ultraviolet Radiation in Antarctica: Measurements and Biological Effects, Antarctic Research Series 62*, Weiler, C.S., Penhale, P.A., Eds., American Geophysical Union, Washington, DC, 1994, 143–158.

Vervoot, W., Copepods from Antarctic and sub-Antarctic plankton samples, *Reports of the B.A.N.Z. Antar. Res. Exped.*, 3, 1–160, 1957.

Villafãne, V.E., Helbling, E.W., Holm-Hansen, O., Phytoplankton around Elephant Island, Antarctica, *Polar Biol.*, 13, 183, 1993.

Villafãne, V.E., Helbling, E.W., Holm-Hansen, O., Spatial and temporal variability of phytoplankton biomass and taxonomic composition around Elephant Island, Antarctica, during summers of 1990–1993, *Mar. Biol.*, 123, 677–686, 1995.

Villafãne, V.E., Helbling, E.W., Holm-Hansen, O., Distribution of phytoplankton organic carbon in the vicinity of Elephant Island, Antarctica, during the summers of 1990–1993, *Antarct. Res. Ser.*, 7, 70–77, 1996.

Vincent, W.F. Microbial Ecosystems of Antarctica, Cambridge University Press, Cambridge, UK, 1988.

Vincent, W.F., Ray, S., Solar ultraviolet-B radiation and aquatic primary production: Damage protection and recovery, *Environ. Rev.*, 1, 1–12, 1993.

Vincent, W.F., Belzile, C., Biological UV exposure in polar oceans: Arctic–Antarctic comparisons, in *Antarctic Biology in a Global Context*, Huskies, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J., Eds., Backhuys Publishers, Leiden, The Netherlands, 2003, 176–181.

Vinex, M., Seasonal fluctuations and production of nematode communities in the Belgian coastal zone of the North Sea, in *Verhandelingen van het Symposium 'Invertebraten van Belgie', 25–28 Nov., 1988*, Koninkhjk Belgisch Institut voor Naturwetenschappen, Brussels, 1989, 25–26.

Vinogradov, M.E., Naumov, A.G., Quantitative distribution of plankton in Antarctic waters of the Indian and Pacific oceans, *Inf. Bull. Soviet Antarc. Exped.*, 1, 110–112, 1958.

Virtue, P., Nichols, P.D., Hosie, G., Reproductive trade-off in male Antarctic krill, *Euphausia superba*, *Mar. Biol.*, 126, 521–527, 1996.

Vo, J., Macrozoobenthos und Gemeinschaftsanlagse des östlichen Weddellmeeres (Antarktis), *Berichte zur Polarforschung*, 39, 123, 1988.

Voisin, J.-F., Notes on the behaviour of the killer whale, *Orcinus orca* (L.), *Nytt Magasin Zool.*, 20, 93–96, 1972.

Voisin, J.-F., On the behaviour of the killer whale, *Orcinus orca* (L.), *Nytt Magasin Zool*, 24, 69–71, 1976.

Volkman, N.J., Trivelpiece, W.Z., Nest-site selection among Adélie, chinstrap and gentoo penguins in mixed species rookeries, *Wilson Bulletin*, 93(2), 243–248, 1981.

Volkman, N.J., Presler, P., Trivelpiece, W., Diets of pygoscelid penguins at King George Island, Antarctica, *Condor*, 82, 373–378, 1980.

Volkovinskii, V.V., Studies on primary production in the waters of the Southern Ocean, Abstracts of Papers Presented at the Second International Oceanology Congress (Moscow) 1966, 386–387, 1966.

von Bennekom, J., Burma, A., Geoyens, L., Linder, L., Morvan, J., Nöthig, R., Panouse, M., Sorensson, F., Treguer, P., Uptake and regeneration of nitrogen, silica and phosphorus, *Berichte zur Polarforschung*, 65, 56–67, 1989.

von Bodungen, B., Phytoplankton growth and krill grazing during spring in the Bransfield Strait, Antarctica—Implications for sediment trap collection, *Polar Biol.*, 6, 153–161, 1986.

von Bodungen, B., von Brockel, K., Smetacek, V., Zeitzschel, B., Growth and sedimentation of the phytoplankton spring bloom in the Bornholm Sea (Baltic Sea), *Kieler Meeresforschung, Sondheim*, 5, 49–60, 1981.

von Bodungen, B., Smetacek, V.S., Tilzer, M.M., Zietschel, B., Primary production and sedimentation during the spring in the Antarctic Peninsula region, *Deep-Sea Res.*, 33, 177–194, 1986.

von Bodungen, B., Fischer, G., Nöthig, E.-M., Wefer, G., Sedimentation of krill faeces during spring development of phytoplankton in the Bransfield Strait, Antarctica, in *Particle Flux in the Ocean*, Vol. 62, Degens, E.T., Honjo, S., Izdar, E., Eds., SCOPE UNEP Sonderband, Mitteilungen aus dem Geologisch-Palaeontologischen Institut der Universität Hamburg, Hamburg, 243–257 pp, 1987.

von Bodungen, B., Nöthig, E.-M., Sui, Q., New production of phytoplankton and sedimentation during summer 1985 in the South Eastern Weddell Sea, *Comp. Biochem. Physiol.*, 90B, 475–487, 1988.

von Brockel, K., The importance of nanoplankton within the pelagic Antarctic ecosystem, *Kieler Meeresforschung Sonderheft*, 5, 61–67, 1981.

von Brockel, K., Primary production data from the south-eastern Weddell Sea, *Polar Biol.*, 4, 75, 1985.

Voous, K.H., Antarctic birds, in *Biogeography and Ecology in Antarctica*, van Meighem, J., van Oye, P., Eds., Dr. W. Junk, The Hague, 1965, 659–689.

Vorinina, N.M., Distribution of zooplankton biomass in the Southern Ocean, *Oceanology*, 6, 834–836, 1960.

Vorinina, N.M., The distribution of zooplankton in the Southern Ocean and its dependence on the circulation of water, *Sarsia*, 34, 277–283, 1968.

Vorinina, N.M., Seasonal cycles of some common Antarctic copepod species, in *Antarctic Ecology, Volume 1*, Holdgate, M.W., Ed., Academic Press, London/New York, 1970, 162–172.

Vorinina, N.M., Annual cycle of Antarctic plankton, in *Fundamentals of the Biological Productivity of the Ocean and its Exploitation*, Beklemishev, V., Ed., Nauka, Moscow, 1971, 64–71. In Russian.

Vorinina, N.M., Vertical structure of a pelagic community in the Antarctic, *Oceanology (Okeanologiya)*, 12, 415–420, 1972.

Vorinina, N.M., An attempt at a functional analysis of the distributional range of *Euphausia superba*, *Mar. Biol.*, 24, 347, 1974.

Vorinina, N.M., Variability of ecosystems, in *Advances in Oceanography*, Charnock, H., Deacon, G.E.R., Eds., Plenum Press, New York, 1978, 221–243.

Voronina, N.M., Memshutkin, V.V., Tseytlin, V.B., Production of an abundant species of copepod, *Calanus acutus*, *Oceanology (Okeanologiya)*, 20, 137, 1980.

Voronina, N.M., Memshutkin, V.V., Tseytlin, V.B., Model investigations of an annual cycle of the abundant species *Rhincalanus gigas* and an estimate of its production in the Antarctica, *Oceanology (Okeanologiya)*, 20, 709–713, 1980.

Voronina, N.M., Memshutkin, V.V., Tseytlin, V.B., Secondary production in the pelagic layer of the Antarctic, *Oceanology (Okeanologiya)*, 20, 714–715, 1981.

Vosjan, J.H., Olaniczuk-Neyman, K.M., Influence of temperature on respiration, ETS activity of micro-organisms from Admiralty Bay, King George Island, Antarctica, *Neth. J. Sea Res.*, 28, 221–225, 1991.

Voss, G.L., Cephalopod resources of the world, *F.A.O. Fisheries Circular*, 149, 1973.

Voytek, M.A., Addressing the biological effects of decreased ozone on the Antarctic environment, *Ambio*, 19, 52–61, 1990.

Vranken, G., Heip, C., The productivity of marine nematodes, *Ophelia*, 26, 429–442, 1986.

Wada, E., Hatton, A., *Nitrogen in the Sea: Abundance and Processes*, CRC Press, Boca Raton, FL, 1990.

Wada, E., Tarazaki, M., Kabaya, Y., Nemoto, T., ^{15}N and ^{13}C abundance in the Antarctic Ocean, with emphasis on the biogeochemical structure of the food web, *Deep-Sea Res.*, 34, 829–841, 1987.

Wadhams, P., A mechanism for the formation of ice edge bands, *J. Geophys. Res.*, 88, 2813–2818, 1983.

Wadhams, P., *Ice in the Oceans*, Gordon and Breach Science Publishers, London, 1992.

Wadhams, P., Squire, V., An ice-water vortex at the edge of the East Greenland Current, *J. Geophys. Res.*, 88, 2770–2780, 1983.

Waghorn, E.J., Two new species of copepoda from White Island, Antarctica, *N.Z. J. Mar. Freshwat. Res.*, 13, 459–470, 1979.

Waghorn, E.J., Knox, G.A., Summer tide-crack zooplankton at White Island, McMurdo Sound, Antarctica, *N.Z. J. Mar. Freshwat. Res.*, 22, 557–563, 1988.

Wagle, J.W., Buto, T.A., Die sublittorale Faun der maritimen Antartkis: Erste Unterwassenbeobachtungen in der Admiralitätsbacht, *Nature Museum*, 120, 269–282, 1990.

Wakatsuchi, M., Seasonal variations in water structure under the fast ice near Syowa Station, *Antarct. Rec.*, 74, 85–105, 1982.

Walls, N.W., Bacteriology of Antarctic region waters and sediments, *Antarct. J. U.S.*, 2, 192–193, 1967.

Walsh, J.J., Relative importance of habitat variables in predicting the distribution of phytoplankton at the ecotone of the Antarctic upwelling ecosystem, *Ecol. Monogr.*, 41, 291–309, 1971.

Ward, P., Atkinson, A., Murray, A.W.A., Wood, A.G., Williams, R., Poulet, S.A., The summer zooplankton community at South Georgia: Biomass, vertical migration and grazing, *Polar Biol.*, 15(3), 195–208, 1995.

Wassman, P., Vernet, M., Mitchell, B.G., Rey, F., Mass sedimentation of *Phaeocystis pouchetii* in the Barents Sea during spring, *Mar. Ecol. Prog. Ser.*, 66, 183–195, 1990.

Watanabe, K., Centric diatom communities found in Antarctic sea ice, *Antarc. Rec.*, 74, 119–126, 1982.

Watanabe, K., Sub-ice microalgal strands in the Antarctic coastal fast ice near Syowa Station, *Jap. J. Phycol.*, 36, 221–229, 1988.

Watanabe, K., Nakajima, Y., Vertical distribution of chlorophyll *a* along 45° E in the southern ocean, 1981, *Mem. Natl Inst. Polar Res., Spe. Issue*, 23, 73–86, 1982.

Watanabe, K., Satoh, H., Seasonal variations of ice algal standing crop near Syowa Station, East Antarctica, in 1983/84, *Bull. Plankton Soc. J.*, 34, 143–164, 1987.

Watanabe, K., Nakajima, Y., Naito, Y., Higashi-Onguru-tô engan de no hyôka-sensui chôsa hôkoku (SCUBA ice diving along the coast of East Ongul Island, Antarctica), *Nankyoku Shiryô (Antarct. Rec.)*, 75, 75–92, 1982. In Japanese with English abstract.

Watanabe, K., Satoh, H., Hoshiai, T., Seasonal variation in ice algal assemblages in the fast ice near Syowa Station in 1983/84, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Heidelberg, 1990, 136–142.

Watanuki, Y., Kato, A., Naito, Y., Robertson, G., Robison, S., Diving and foraging behaviour of Adélie Penguins in areas with and without fast sea-ice, *Polar Biol.*, 17, 296–304, 1997.

Waters, T.F., The turnover ratio in production ecology of freshwater invertebrates, *Am. Nat.*, 103, 173–185, 1969.

Watkins, J.L., Variations in the size of Antarctic krill, *Euphausia superba* Dana, in small swarms, *Mar. Ecol. Prog. Ser.*, 31, 67–73, 1986.

Watkins, J.L., A composite recruitment index to describe interannual changes in the population structure of Antarctic krill at South Georgia, *CCAMLR Science*, 6, 71–84, 1999.

Watkins, J.L., Murray, A.W.A., Layers of Antarctic krill, *Euphausia superba*: Are they just long krill swarms?, *Mar. Biol.*, 131, 237–247, 1998.

Watkins, J.L., Morris, D.J., Rickets, C., Priddle, J., Differences between swarms of Antarctic krill and some implications for sampling krill populations, *Mar. Biol.*, 93, 137–146, 1986.

Watkins, J.L., Morris, D.J., Ricketts, C., Priddle, J., Differences between swarms of Antarctic krill and some implications for sampling krill populations, *Mar. Biol.*, 93, 137–146, 1986.

Watkins, J.L., Morris, D.J., Ricketts, C., Murray, A.W.A., Sampling biological characteristics of krill: Effects of heterogeneous nature of krill swarms, *Mar. Biol.*, 107, 409–415, 1990.

Watkins, J.L., Buchholz, F., Priddle, J., Morris, D.J., Ricketts, C., Variation in reproductive status of Antarctic krill swarms: Evidence for a size-related sorting mechanism?, *Mar. Ecol. Prog. Ser.*, 82, 163–174, 1992.

Watson, G.E., Angle, J.P., Harper, P.C., Birds of the Antarctic and Subantarctic, *Antarct. Res. Ser.*, 32, 1–12, 1971.

Watson, R.T., Zinyowera, M.C., Moss, R.H., IPCC Special Report on the Regional Impacts of Climate Change: An assessment of Vulnerability, Intergovernmental Panel on Climate Change, Geneva, 1997.

Watson, R.T., Zinyowera, M.C., Moss, R.H*., IPPC Special Report on the Regional Impacts of Climate Change: An Assessment of Vulnerability, Intergovernment Panel on Climate Change*, Cambridge University Press, Cambridge, 2001.

Waugh, S.M., Weimerskirch, H., Cherel, Y., Shankar, U., Prince, P.A., Sagar, P.M., Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean, *Mar. Ecol. Prog. Ser.*, 177, 243–254, 1999.

Weber, L.H., Spatial variability of phytoplankton in relation to the distributional patterns of krill (*Euphausia superba*), Ph.D. Thesis, Texas A&M University, College Station, Texas, 1984.

Weber, L.H., El-Sayed, S.Z., Spatial variability of phytoplankton and the distributions and abundance of krill in the Indian Sector of the Southern Ocean, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985, 284–293.

Weber, L.H., El-Sayed, S.Z., Size-fractionated phytoplankton standing crop and primary productivity in the west Indian sector of the Southern Ocean (R.S.S.A. *Agulhas* Cruise; February–March 1985), Technical Report, Texas A&M University, College Station, TX, 1986a.

Weber, L.H., El-Sayed, S.Z., Phytoplankton data from the November–December 1984 cruise of the *Polarstern* to the Bransfield Strait/Elephant Island region of the Southern Ocean, Technical Report, Texas A&M University, College Station, TX, 1986b.

Weber, L.H., El-Sayed, S.Z., Contribution of net-, nano-, and pico-plankton to the phytoplankton standing crop and primary productivity of the Southern Ocean, *J. Plankton Res.*, 9, 973–994, 1987.

Weber, L.H., El-Sayed, S.Z., Hampton, I., Variance spectra of phytoplankton, krill and water temperature in the Atlantic Ocean south of Africa, *Deep-Sea Res.*, 33, 1327–1343, 1986.

Weeks, W.F., Ackley, S.F., The growth, structure, and properties of sea ice. *CCREL Monograph* 82-1, United States Army Cold Regions Research and Engineering Laboratory, Hanover, NH, 1982.

Weeks, W.F., Lee, O.S., The salinity distribution in young sea ice, *Arctic.*, 15, 92–109, 1982.

Wefer, G., Fischer, G., Annual primary production and export flux in the Southern Ocean sediment trap data, *Mar. Chem.*, 35, 597–614, 1991.

Wefer, G., Suess, E., Balzer, W., Liebezeit, G., Müller, P.J., Ungerer, C.A., Zenk, W., Fluxes of biogenic components from sediment trap deployment in circumpolar waters of the Drake Passage, *Nature (Lond.)*, 299(5879), 145–147, 1982.

Wefer, G., Fischer, G., Fuetterer, D., Gersonde, R., Seasonal particle flux in the Bransfield Strait, Antarctica, *Deep-Sea Res.*, 35, 891–898, 1988.

Wefer, G., Fischer, G., Futterer, D.K., Gersonde, R., Honjo, S., Osterman, D., Particle sedimentation and productivity in Antarctic waters of the Atlantic sector, in *Geological History of Polar Oceans: Arctic versus Antarctic*, Bleil, U., Thiede, J., Eds., Kluwer Academic Publishers, Dordrecht, 1990, 363–379.

Weimerskirch, H., La stratégie de reproduction de l'albatros fuligineux à dos sombre, *Comité National Français des Recherches Antarctique*, 51, 437–447, 1982.

Weimerskirch, H., Wilson, R.P., When do wandering albatrosses (*Diomedea exulans*) forage?, *Mar. Ecol. Prog. Ser.*, 86, 297–300, 1992.

Weimerskirch, H., Mougey, T., Hindermeyer, X., Foraging and provisioning strategies of black-browed albatrosses in relation to requirements of chick: Natural variation and experimental study, *Behav. Ecol.*, 8(6), 635–643, 1997.

Weimerskirch, H., Catard, A., Prince, P.A., Cherel, Y., Croxall, J.P., Foraging white-chinned petrels, *Procellaria aequinoctialis*, at risk from the tropics to Antarctica, *Biol. Conserv.*, 87, 273–275, 1999.

Weimerskirch, H., Inchausti, P., Guinet, C., Barbraud, C., Trends in bird and seal populations as indicators of a system shift in the Southern Ocean, *Antarct. Sci.*, 15, 249–256, 2003.

Weimerskirch, H., Jenouvrier, S., Barbraud, C., Climate and population dynamics of Southern Ocean seabirds, *Abstracts SCAR Science Conference, Bremen, 2004*, 2004, 130.

Weincke, C., Notes on the development of some benthic marine macroalgae of King George Island, Antarctica, *Serie Científico del Instituto Antártico Chileno*, 37, 23–47, 1988.

Weincke, C., Seasonality of brown macroalgae from Antarctica—a long-term culture study under fluctuating Antarctic daylengths, *Polar Biol.*, 10, 589–600, 1990.

Weincke, C., Recent advances in the investigation of Antarctic macroalgae, *Polar Biol.*, 16, 231–240, 1996.

Weller, C.S., Penhale, P.A., Ultraviolet radiation and biological research in Antarctica, *Antarct. Res. Ser.*, 62, 1–311, 1994.

Wells, R.M.G., Respiration of Antarctic fishes from McMurdo Sound, *Comp. Biochem. Physiol.*, 88, 417–424, 1987.

Wells, R.M.G., Ashby, M.D., Duncan, S.J., McDonald, J.A., Comparative study of the erythrocytes and haemoglobins in nototheniid fishes from Antarctica, *Journal of Fish Biology*, 17, 517–527, 1980.

Wells, R.M.G., MacDonald, J.A., Di Prisco, G., Thin-blooded Antarctic fishes: A rheological comparison of the haemoglobin-free ice fishes *Chionodraco kathbleenae* and *Cryodraco antarcticus* with the red-blooded nototheniid *Pagothenia bernacchii*, *J. Fish Biol.*, 36, 595–609, 1990.

Wetzel, R.G., Detrital dissolved and particulate organic carbon functions in aquatic systems, *Bull. Mar. Sci.*, 35, 503–509, 1984.

Weyman, G., Wiencke, C., Seasonal photosynthetic performance of the endemic Antarctic alga *Palmaria deicpiens* (Reinsch) Ricker, *Polar Biol.*, 16, 357–361, 1996.

Whitaker, T.M., Sea ice habitats of Signy Island (South Orkneys) and their primary productivity, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977a, 75–87.

Whitaker, T.M., Plant production in inshore waters of Signy Island, Antarctica, Ph.D. thesis, University of London, 1977b.

Whitaker, T.M., Primary production of phytoplankton off Signy Island, South Orkneys, the Antarctic, *Proc. Rl. Soc. Lond.*, B214, 169–189, 1982.

Whitaker, T.M., Richardson, M.G., Morphology and chemical composition of a natural population of an ice-associated diatom, *Navicula glacei*, *J. Phycol.*, 16, 256–263, 1980.

White, M.G., Oxygen consumption and nitrogen excretion by the giant Antarctic isopod *Glyptonotus antarcticus* Eights in relation to cold-adapted metabolism in marine polar poikilotherms, *Proceedings of the 9th European Marine Biology Symposium*, 707–724, 1975.

White, M.G., Ecological adaptations by Antarctic poikilotherms to the polar marine environment, in *Adaptations within Antarctic Ecosystems*, Llano, G.A., Ed., Smithsonian Institution, Washington, DC, 1977, 197–208.

White, M.G., Marine benthos, in *Antarctic Ecology, Vol 2*, Laws, R.M., Ed., Academic Press, London, 1984, 421–461.

White, M.G., Conroy, J.W.H., Aspects of competition between pygoscelid penguins at Signey Island, South Orkney Islands, *Ibis*, 117, 371–373, 1975.

White, M.G., Robins, M.W., Biomass estimates from Borge Bay, South Orkney Islands, *Bull. Br. Antarct. Surv.*, 3, 45–56, 1972.

White, M.G., North, A.W., Twelves, E.L., Jones, S., Early development of *Notothenia neglecta* from the Scotia Sea, Antarctica, *Cybium*, 6, 43–51, 1982.

White, D.C., Smith, G.A., Stanton, G.R., Biomass community structure, and metabolic activity of the microbiota in benthic marine sediments and sponge spicule mats, *Antarc. J. US*, 19, 125–156, 1984.

White, D.C., Smith, G.A., Nichols, P.D., Stanton, G.R., Palmisano, A.C., Lipid composition and microbial activity of selected recent Antarctic benthic marine sediments and organisms: A mechanism for monitoring and comparing microbial populations, *Antarct. J. U.S.*, 19, 130–132, 1985.

White, D.C., Smith, G.A., Guckert, T.B., Nichols, P.D., Nearshore benthic marine sediments, in *Antarctic Microbiology*, Friedman, E.I., Ed., Wiley-Liss, New York, 1993, 235–240.

Whitehead, M.D., Johnstone, G.W., Burton, H.R., Annual fluctuations in productivity and breeding success of Adélie Penguins and fulmarine petrels in Prydz Bay, East Antarctica, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin/Heidelberg, 1990, 214–223.

Whitehouse, M.J., Veit, R.R., Distribution and abundance of seabirds and fur seals near the Antarctic Peninsula during the austral winter, 1986, *Polar Biol.*, 14, 325–330, 1994.

Whitehouse, M.J., Priddle, J.P., Symon, C., Seasonal and annual changes in seawater, temperature, salinity, nutrient and chlorophyll *a* distribution around South Georgia, *CCAMLR Science*, 6, 71–79, 1996.

Wiebe, W.J., Pomeroy, L.R., Microorganisms and their association with aggregates and detritus in the sea: A microscopic study, *Memories de l'Institut Italiano di Idriobiologia*, 24(Suppl.), 325–352, 1972.

Wiencke, C., Stolpe, U., Lehmann, H., Morphogenesis of the brown alga *Desmarestia antarctica* cultivated under seasonally fluctuating daylengths, *Serie Científico del Instituto Antártico Chileno*, 41, 65–78, 1991.

Wiencke, C., Rahmel, J., Karsten, U., Weykam, G., Kirst, G.O., Photosynthesis of marine macroalgae from Antarctica: Light and temperature requirements, *Botanica Acta*, 106, 78–87, 1993.

Wiencke, C., Bartsch, I., Bishoff, B., Peters, A.F., Breeman, A.M., Temperature requirements and biogeography of Antarctic, Arctic and amphiequatorial seaweeds, *Botanica Marina*, 37, 247–259, 1994.

Wiencke, C., Gómez, I., Pakker, H., Flores-Moya, A., Altamirano, M., Hanelt, D., Bischof, K., Figueroa, F.L., Impacts of UV radiation on viability, photosynthetic characteristics and DNA of brown algal zoospores: Implications for depth zonation, *Mar. Ecol. Prog. Ser.*, 197, 217–229, 2000.

Wigley, R.L., MacIntyre, A.D., Some quantitative comparisons of offshore meiobenthos and macrobenthos south of Martha's Vineyard, *Limnol. Oceanogr.*, 9, 485–493, 1964.

Williams, P.J.LeB., in *Biological and chemical aspects of dissolved organic compounds in sea water*, Riley, J.P., Shirrow, G., Eds. 2nd edition *Chemical Oceanography*, Vol. 2, Academic Press, London, 1975, 301–363.

Williams, P.J.LeB., Incorporation of microheterotrophic processes into classical paradigm of the plankton food web, *Kieler Meeresforschung Sonderheft*, 5, 1–28, 1981.

Williams, R., The inshore fishes of Heard and Macquarie Islands, Southern Indian Ocean, *J. Fish Biol.*, 23, 283–292, 1983.

Williams, A.J., The status and conservation of sea birds on some islands in the African sector of the Southern Ocean, in *The Status and Conservation of the World's Seabirds*, ICBP Technical Publication No. 2, Croxall, J.P., Evans, P.G.H., Schreiber, R.W., Eds., International Council for Bird Preservation, Cambridge, UK, 627–636 pp, 1984.

Williams, R., Potential impact of a krill fishery upon pelagic fish in the Prydz Bay area of Antarctica, *Polar Biol.*, 5, 1–4, 1985a.

Williams, R., Trophic relationships between pelagic fish and euphausiids in Antarctic waters, in *Antarctic Nutrient Cycles and Food Webs*, Siegfried, W.R., Condy, P.R., Laws, R.M., Eds., Springer, Berlin, 1985b, 452–459.

Williams, A.J., Siegfried, W.R., Foraging ranges of krill-eating penguins, *Polar Rec.*, 20, 159–162, 1980.

Williams, P.J.leB., Berman, T., Holm-Hansen, O., Amino acid uptake and respiration by marine heterotrophs, *Mar. Biol.*, 35, 41–47, 1976.

Williams, A.J., Siegfried, W.R., Berger, A.E., Berruti, A., The Prince Edward Islands: A sanctuary for seabirds in the Southern Ocean, *Biological Conservation*, 15, 59–71, 1979.

Williams, R., Kirkwood, J.M., O'Sullivan, D., FIBEX cruise zooplankton data, *Aust. Natl Antarc. Res. Exped. Notes*, 7, 1–163, 1983.

Williams, R., Kirkwood, J.M., O'Sullivan, D., AbdEX 1 cruise zooplankton data, *Aust. Natl Antarc. Res. Exped. Notes*, 31, 1–9, 1986.

Williamson, G.R., Minke whales off Brazil, *Sci. Rep. Whales Res. Inst. Tokyo*, 27, 37–59, 1975.

Wilson, E.A., *Stenorhincus leptonyx*, the sea leopard, *National Antarctic Expedition, 1901–1904, Natural History and Zoology*, 2, 26–30, 1907.

Wilson, G.J., Distribution and abundance of Antarctic and sub-Antarctic penguins: a synthesis of current knowledge, *BIOMASS Sci. Ser.* 4, 1981.

Wilson, K.J., Fluctuations in populations of Adélie Penguins at Cape Bird, Antarctica, *Polar Rec.*, 26, 305–308, 1990.

Wilson, R.P., Preliminary assessment of depth utilization by Adélie and Gentoo Penguins at Esperanza, Antarctica. *Cormorant* 17, 1–8, 19.

Wilson, E.O., Bossert, W.H. *A Primer of Population Biology*, Sinauer Associates, Sunderland, MA, 1971.

Wilson, W.H., Mann, N.H., Lysogenic and lyric viral production in marine microbial communities, *Aquat. Microbial Ecol.*, 13, 95–103, 1997.

Wilson, D.L., Smith, W.O., Jr., Nelson, D.M., Phytoplankton bloom dynamics of the western Ross Sea ice edge, I: Primary productivity and species-specific production, *Deep-Sea Res.*, 33, 1375–1387, 1986.

Wilson, K.J., Taylor, R.H., Barton, K.H., The impact of man on Adélie Penguins at Cape Hallett, Antarctica, in *Antarctic Ecosystems: Ecological Change and Conservation*, Kerry, K.R., Hempel, G., Eds., Springer, Berlin/Heidelberg, 1990, 183–190.

Wilson, R.P., Culik, B.M., Darnfield, R., Adelung, D., People in Antarctica: How much do Adélie Penguins (*Pygoscelis adeliae*) care?, *Polar Biol.*, 11, 363–470, 1991.

Wilson, R.P., Pútz, K., Grémillet, D., Culik, B.M., Kierspel, M., Regel, M., Bost, J., Lage, C.A., Cooper, J., Reliability of stomach temperature changes in determining feeding characteristics of seabirds, *J. Exp. Biol.*, 198, 1115–1135, 1995.

Wilson, R.P., Ainley, D.G., Nur, N. et al., Adélie Penguin population changes in the Pacific sector of Antarctica: Relation to sea-ice extent and the Antarctic Circumpolar Current, *Mar. Ecol. Prog. Ser.*, 213, 301–318, 2001.

Witek, Z., Koronkeiwicz, A., Soszka, G.J., Certain aspects of the early life history of krill, *Euphausia superba* Dana (Crustacea), *Pol. Polar Res.*, 1, 97–115, 1980.

Witek, Z., Grelowski, A., Wolnomiejski, N., Studies in aggregations of krill (*Euphausia superba*), *Meeresforschung*, 28, 228–243, 1981.

Witek, Z., Pastuzak, M., Grelowski, A., Net-phytoplankton abundance in western Antarctic and its relationship to environmental conditions, *Meeresforschung*, 29, 166–180, 1982a.

Witek, Z., Grelowski, A., Kalinowsky, J., Formation of Antarctic krill concentrations in relation to hydrodynamic processes and social behaviour, *ICES CM 1982/L*, 59, 16–22, 1982b.

Witek, Z., Kittel, W., Czkieta, H., Zmijewoska, M.I., Presler, E., Macrozooplankton in the Southern Drake Passage and the Bransfield Strait during BIOMASS-SIBEX (December 1983–January 1984), *Pol. Polar Res.*, 6, 95–115, 1985.

Witek, Z., Kalinowski, J., Grelowski, A., Formation of Antarctic krill concentrations in relation to hydrodynamic processes and social behaviour, in *Antarctic Ocean and Resources Variability*, Sahrhage, D., Ed., Springer, Berlin/Heidelberg, 1988, 237–244.

Woehler, E.J., *The Distribution and Abundance of Antarctic and Subantarctic Penguins*, Scientific Committee for Antarctic Research, Cambridge, UK, 1993.

Woehler, E.J., Concurrent decreases in five species of Southern Ocean seabirds in Prydz Bay, *Polar Biol.*, 16, 379–382, 1995.

Woehler, E.J., Seabird abundance, biomass and energy consumption within Prydz Bay, Antarctica, 1980/81–1992/93, *Polar Biol.*, 17, 371–383, 1997.

Woehler, E.J., Bergstrom, D., The impacts of climate change on Heard Island during the 20th century, Abstracts of the SCAR Science Conference, Bremen, 95, 2004.

Woehler, E.J., Green, K., Consumption of marine resources by seabirds and seals at Heard Island and the McDonald Islands, *Polar Biol.*, 12, 659–665, 1992.

Woehler, E.J., Perry, R.L., Creet, S.M., Burton, H.R., Impacts of human visitors on breeding success and long-term population trends in Adélie Penguins at Casey, Antarctica, *Polar Biol.*, 14, 269–274, 1994.

Woehler, E.J., Slip, D.J., Robertson, L.M., Fullabar, P.J., Burton, H.R., The distribution, abundance and status of Adélie Penguins (*Pygoscelis adeliae*) in the Windmill Islands, Wilkes Land, Antarctica, *Mar. Ornithol.*, 19, 1–18, 1997.

Woehler, E.J., Cooper, J., Croxall, J.P., Fraser, W.R., Kooyman, G.L., Miller, G.D., Nel, D.C., Patterson, D.L., Peter, H.-U., Ribic, C.A., Salwicka, K., Trivelpiece, W.Z., Weimerskirch, H., A statistical assessment of the status and trends of Antarctic and subantarctic seabirds, *SCAR, NSF, CCAMLR* 2001.

Wohlschlag, D.E., Respiratory metabolism and ecological characteristics of some fishes in McMurdo Sound, Antarctica, *Antarct. Res. Ser.*, 1, 11–62, 1964.

Wohrmann, A.P.A., Freezing resistance in Antarctic fish, in *Antarctic Communities: Species, Structures and Survival*, Valencia, J., Walton, D.W.H., Eds., Cambridge University Press, Cambridge, UK, 1997, 209–211.

Wolnomiejski, N., Chlapowski, K., Porebski, J., Gorbacik-Wesolowka, A., Obserwacje nad ekologia antarktyczrego kryala (*Euphausia superba* Dana), *Studi i Materialy MIR, Gdynia, A23*, 1978. In Polish.

Wommack, K.E., Colwell, R.R., Viroplankton: Viruses in aquatic ecosystems, *Microbiology and Molecular Biology Review*, 64, 69–114, 2000.

Woodley, J.D., Chornesky, E.A., Clifford, P.A., Jackson, J.B.C., Kaufman, L.S., Knowlton, N., Lang, J.C., Pearson, M.P., Porter, J.W., Rooney, M.C., Rylaarsdam, K.W., Tunnicliffe, V.J., Wahle, C.M., Wulff, J.L., Curtis, A.S.G., Dallmeyer, M.D., Jupp, B.P., Koehl, M.A.R., Neigel, J., Sides, E.M., Hurricane Allen's impact on Jamaican coral reefs, *Science*, 214, 749–755, 1991.

Wormuth, J.H., Interannual variability in Antarctic zooplankton populations round the tip of the Antarctic Peninsula (abstract), *Intergovernmental Oceanographical Committee Reports*, 50, 10–19, 1987.

Worrest, R.C., Wolniaowski, K.U., Scott, J.D., Brooker, D.L., Thomson, B.E., van Dyke, H., Sensitivity of marine phytoplankton to UV-B radiation: Impact upon a model ecosystem, *Photochem. Photobiol.*, 33, 223–227, 1981.

Wright, R.T., Coffin, R.B., Measuring microzooplankton grazing on planktonic marine bacteria by its impact on bacterial production, *Microbial Ecol.*, 10, 137–149, 1984.

Wyanski, D.M., Targett, T.E., Feeding biology of fishes in the endemic Antarctic Harpagiferidae, *Copeia*, 3, 686–693, 1981.

Xavier, J.C., Croxall, J.P., Tratham, P.N., Rodhouse, G.R., Inter-annual variability in the cephalopod component of the diet of wandering albatross, *Diomedea exulans*, breeding at Bird Island, South Georgia, *Mar. Biol.*, 142, 611, 2003.

Xiuren, N., Zilin, L., Genhai, Z., Junxian, S., Size-fractionated biomass and productivity of phytoplankton and particulate organic carbon in the Southern Ocean, *Polar Biol.*, 16, 1–11, 1996.

Yamada, S., Kawamura, A., Some characteristics of the zooplankton distribution in the Prydz Bay region of the Indian sector of the Antarctic Ocean in the summer of 1983/84, *Mem. Natl. Inst Polar Res.*, 44, 86–95, 1986.

Yamaguchi, Y., Shibata, Y., Standing stock and distribution of phytoplankton chlorophyll in the Southern Ocean south of Australia, *Trans. Tokyo Univ. Fish.*, 5, 111–128, 1982.

Yamanaka, I., Interaction among krill, whales and other mammals in the Antarctic ecosystem, *Mem. Natl Inst. Polar Res., Spe. Issue*, 27, 220–232, 1983.

Yeates, G.W., Studies on the Adélie Penguin at Cape Royds, 1964–65 and 1965–66, *N.Z. J. Mar. Freshwat. Res.*, 2, 472–496, 1968.

Yeates, G.W., Microclimate, climate and breeding success in Antarctic penguins, in *The Biology of Penguins*, Stonehouse, B., Ed., MacMillan, London, 1975, 397–409.

Young, E.C., The breeding behaviour of the South Polar skua, *Catharacta maccormicki*, *Ibis*, 105, 205–232, 1963.

Young, E.C., Feeding habits of the South Polar skua, *Catharacta maccormicki*, *Ibis*, 105, 301–318, 1963.

Yukov, V.I., *The Antarctic Toothfish*, Nauka, Moscow, 1982.

Zacher, K., Wulff, A., Hanelt, D., Wiencke, C., Campana, G., Quartino, L., Impact of UV radiation on succession of benthic primary producers in Antarctica, *Information Leaflet*, Alfred Wegner Institute for Polar and Marine Research, Bremerhaven, 2005.

Zaneveld, J.S., The occurrence of benthic marine algae under shore-fast ice in the western Ross Sea, Antarctica, *Proceedings of the 5th International Seaweed Symposium, Halifax, 1965*, Pergamon Press, London, 217–231, 1966a.

Zaneveld, J.S., Vertical zonation of Antarctic and sub-Antarctic benthic marine algae, *Antarct. J. U.S.*, 1, 211–213, 1966.

Zaneveld, J.S., Benthic marine algae, Ross Island, *Antarctic Map Folio Series*, Vol. 10, American Geographical Society, Washington, DC, 9–10 pp, 1968.

Zemsky, V.A., *Whales of the Antarctic*, Karlingrad, 1962. In Russian.

Zenkovitch, B.A., Whales and plankton, in *Food and Feeding Behaviour of Whales*, Asenev, V.A., Zenkovich, B.A., Chalskii, K.K., Eds., Izdatel'stro Nauka, Moscow, 1969, 150–152. In Russian.

Zenkovitch, B.A., Whales and plankton in Antarctic waters, in *Antarctic Ecology, Volume 1*, Holdgate, M.W., Ed., Academic Press, London, 1970, 183–185.

Zielinski, K., Bottom macrobenthic of the Admiralty bay (King George Island, South Shetland Islands, Antarctica), *Pol. Polar Res.*, 11, 95–131, 1990.

Zink, M., Observations of seabirds during a cruise from Ross Island to Anvers Island, Antarctica, *Wilson Bulletin*, 93, 1–20, 1977.

Zinova, A.D., Composition and character of the algal flora near the shores of the Antarctic Continent in the vicinity of Kerguelen and Macquarie Islands, *Inf. Bull. Soviet Antarc. Exped.*, 3, 47–49, 1958.

Zmijewska, M.I., Copepoda in the southern part of the Drake Passage and in Bransfield Strait during early summer 1983–1984 (BIOMASS-SIBEX, December–January), *Pol. Polar Res.*, 6, 79–83, 1985.

Zmijewska, M.I., Yen, J., Seasonal and diel changes in the abundance and vertical distribution of Antarctic copepod species *Calanoides acutus, Calanus propinquus, Rhincalanus gigas, Metridia gerlachei* and *Euchaeta antarctica* (Calanoida) in Croker Passage (Antarctic Peninsula), *Oceanology*, 35, 73–100, 1993.

Zumberge, J.H., Swithinbank, C., The dynamics of ice shelves, *Antarc. Res., Geophys. Monogr.*, 7, 197–218, 1962.

Zurr, R., The age and growth of *Trematomus bernacchi* and *Trematomus centronotus* at White Island, Antarctica, B.Sc. (Hons) thesis in Zoology, University of Canterbury, Christchurch, 1977.

Zvreva, Zh. A., Ed., Seasonal changes of Antarctic plankton in the Molodezhnaya and Mirny region. Geographical and seasonal variations of marine plankton, *Explor. Mar. Fauna* 12, 248–262, 1975.

Zwally, H.T., Comiso, J.C., Parkinson, C.L., Campbell, W.J., Carsey, F.D., Gleorsen, P., Antarctic sea ice, 1973–1976: Satellite passive-microwave observations. NASA Special Publication SP 459, 1983a.

Zwally, H.J., Parkinson, C.L., Comiso, J.C., Variability of Antarctic sea ice and changes in carbon dioxide, *Science*, 220, 1005–1012, 1983b.

Zwally, H.T., Comiso, K., Gordon, A.L., Antarctic offshore leads and polynas and oceanographic effects, *Antarc. Res. Ser.*, 43, 203–226, 1985.

Appendix A
Approaches to Systems Modelling

CONTENTS

Organizing and understanding the complexity of marine ecosystems can best be carried out by the construction of models which have the potential for stimulation. The two approaches adopted in this book are compartmental approaches and the energy analysis approach.

A.1 COMPARTMENTAL SYSTEMS APPROACH

Investigators using this approach are usually interested in the gross dynamics of whole ecosystems as energy processing or nutrient cycling units. Ecosystems are seen as consisting of compartments (or pools) of energy or nutrients. Each pool represents a species population or trophic level comprising the aggregated species populations at that level. For the purposes of the model, the complicated processes associated with populations making up each pool are assumed to counterbalance one another, resulting in simple behaviour of the pool as a whole. Figure 15.6, Figure 15.12, and Figure 15.16 are examples of such compartmental models.

A.2 ENERGY ANALYSIS APPROACH

The principal approach adopted in this book to constructing models in Odum's (1983) energy analysis. Energy circuit diagramming is a visual mathematics which uses models of chemical, physical, biologic and geologic subsystems. The first step in energy analysis is the construction of an overview of the system being studied using energy language diagrams. Symbols representing units and processes within the system are connected by pathways representing flows of energy (or materials) from sources outside the system, through the web of the system, and finally out as degraded energy. Figure A.1 presents the symbols that are used with a little explanation.

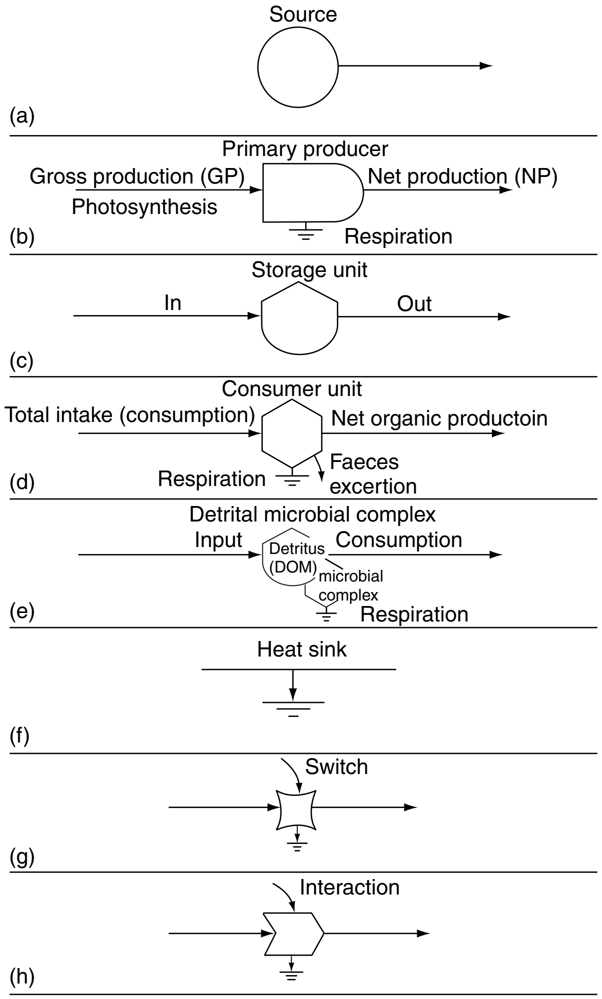


FIGURE A.1 Basic energy symbols. (a) *Source*. Outside energy source delivering forces according to a programme controlled from outside; a forcing function. (b) *Producer*. Units that collect and transform low-quality solar energy. (c) *Storage*. A compartment of energy storage within the system that stores a quantity of energy as a balance of inflows and outflows; a state variable. (d) *Consumer*. Unit that transforms energy, stores it and feeds it back autocatalytically to improve inflow. (e) *Detrital–microbial complex*. A particulate organic matter (POM) storage unit with its associated microbial community. (f) *Heat sink*. Dispersion of potential energy into heat; loss of potential energy from further use by the system. (g) *Switch*. A symbol that indicates ore or more switching actions. (h) *Interaction*. Interactive intersection of two pathways coupled to produce an outflow in proportion to a function of both; a work gate.