Impacts of Global Warming on Polar Ecosystems

Carlos M. Duarte (Ed.)

Fundación BBVA
CSIC
INTERNATIONAL POLAR YEAR 2007-2008

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CATALOGUING-IN-PUBLICATION DATA

Impacts of Global Warming on Polar Ecosystems / edited by Carlos M. Duarte. — Bilbao : Fundación BBVA, 2008.
190 p. ; 18 x 26 cm
ISBN: 978-84-96515-74-1
1. Cambio climático 2. Impacto ambiental 3. Ártico 4. Antártida I. Duarte, Carlos M. II. Fundación BBVA, ed.
551.581.21

Impacts of Global Warming on Polar Ecosystems

PUBLISHED BY:

Plaza de San Nicolás, 4. 48005 Bilbao

DESIGN AND PRODUCTION:
José Manuel Reyero / Comunicación y Gestión Ambiental ALAIRE, S.L.

EDITOR: Karen Welch

PRINTED BY: V.A. Impresores, S.A.

BOUND BY: Ramos

ISBN: 978-84-96515-74-1
LEGAL DEPOSIT: M-37491-2008

Printed in Spain

This book is printed on totally chlorine-free paper in conformity with the environmental standards required by current legislation.

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INTRODUCTION:
GLOBAL WARMING AND POLAR ECOSYSTEMS

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THE POLAR REGIONS are the remotest on the planet, explored for the first time less than a century ago when expeditions led by Norwegian Roald Amundsen reached the geographic poles (South Pole, 1911; North Pole, 1926). But not even their isolation has saved them from ranking, in our days, among the zones worst threatened by human activity.

The dangers confronting polar ecosystems are especially disturbing, because these regions play a vital role in the Earth System. Not only do they intervene in the circulation of the atmosphere and oceans, they also help regulate the planet's climate and have a high ecological value.

Despite this, our understanding of how the polar climate operates and about the functioning of its ecosystems is in many respects still primitive. To fill some of these gaps, the International Council for Science and the World Meteorological Organisation have called the International Polar Year 2007-2008 (*www.ipy.org*); the fourth declared to date after polar years 1882-3, 1932-3 and 1957-8, with the peculiarity that the present initiative is not about exploring polar systems, but about the need to investigate the impacts and rapid changes that they are currently undergoing. To this end, thousands of scientists from over 60 countries will engage up to 1 March, 2009 in more than 200 research projects on the Arctic and Antarctic under international coordination. This is the first time Spain has participated in an International Polar Year, and it has done so with an array of research projects funded under the Ministry of Education and Science's National R&D Plan (*www.api-spain.es*). Besides scientific research, International Polar Year numbers among its main objectives to train a new generation of experts in the polar sciences and to raise social awareness around the problems facing the polar regions. This book aims to contribute to the achievement of these two objectives.

◀ **Photo 1: Polar bear (*Ursus maritimus*).** The largest of the terrestrial carnivores hunts its main prey, seals, on the pack ice of the Arctic. The acceleration of the ice melt due to global warming, and losses of the ice masses that it hunts on, have impaired its predation success and currently threaten its survival.

Photos 2 and 3: Researchers at work in the Arctic during the Spanish research expedition ATOS-Ártico

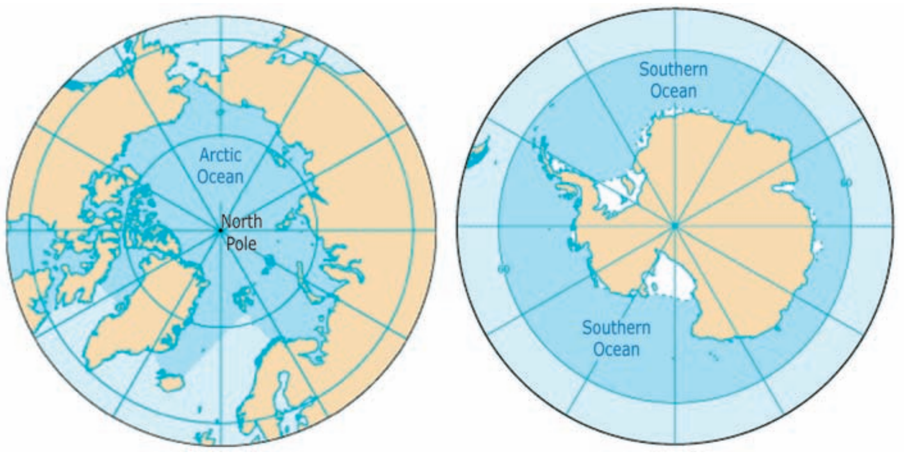
Polar ocean ecosystems are still dominated by a megafauna that has been decimated in other seas. The prevalence of large animals (cetaceans, pinnipeds, birds, etc.) in this kind of environment is due to a number of factors. These include the scant pressure of human activity (contrasting with the intense pressure exerted a few decades back by intensive whaling in the Antarctic, now regulated, and seal hunting in the Arctic, which still goes on), the short length of food chains, due to the presence of relatively large-sized primary producers and planktonic grazers compared to those dominating other oceans, their elevated summer production and the presence of large ice shelves that serve as a habitat for some of the native species. Polar ecosystems can be considered the planet's most inhospitable deserts. Their terrestrial primary production is minimal, meaning they rely almost entirely on the primary production of marine communities. Polar megafauna depend largely on the existence of large ice floes that serve as breeding grounds for key ecosystem organisms (for instance, the krill in the Antarctic), or as hunting, resting or transport platforms for penguins, fur seals and leopard seals in Antarctica and bears, seals, walruses and other animals, including humans, in the Arctic.

Arctic and Antarctic ecosystems have important differences between them, deriving from their geographical configuration, which entails striking contrasts in their functioning and their vulnerability to anthropogenic impact. The Antarctic ecosystem occupies a continent extending from the South Pole to 60º-80º south latitude, isolated from remaining continents by the Southern Ocean (map 1). It is accordingly remote from any territory with significant industrial activity. The Arctic, conversely, consists of a central ocean stretching from the North Pole to 70º-80º north latitude, mostly ice covered and encircled by continents with wide continental shelves, close to zones of intense industrial activity (for example, Canada, the United States, Russia, Norway; see map 1).

Antarctica then is surrounded by ice-free waters for most of the summer, while most of the Arctic polar ecosystem unfolds under a vast platform of ice. Further, periods of light and dark vary from the Arctic to the Southern oceans given the almost 20º difference in their latitude ranges in the corresponding hemispheres. And their connection with the global ocean is also different. The Southern Ocean connects with the Pacific, Atlantic and Indian oceans, whereas Arctic waters only mix significantly with the Atlantic Ocean through the Fram Strait, since exchanges with the Pacific through the Bering Strait are hindered by shallow-lying shelves (map 1).

Moreover, many populated cities with major industrial and commercial activities are found within the Arctic Polar Circle, which is not the case with the Antarctic. This proximity to inhabited continents and industrial centres is

Map 1: Area occupied by the polar oceans



Arctic **Antarctic**

important to remember, because it determines the pressure brought to bear on polar environments.

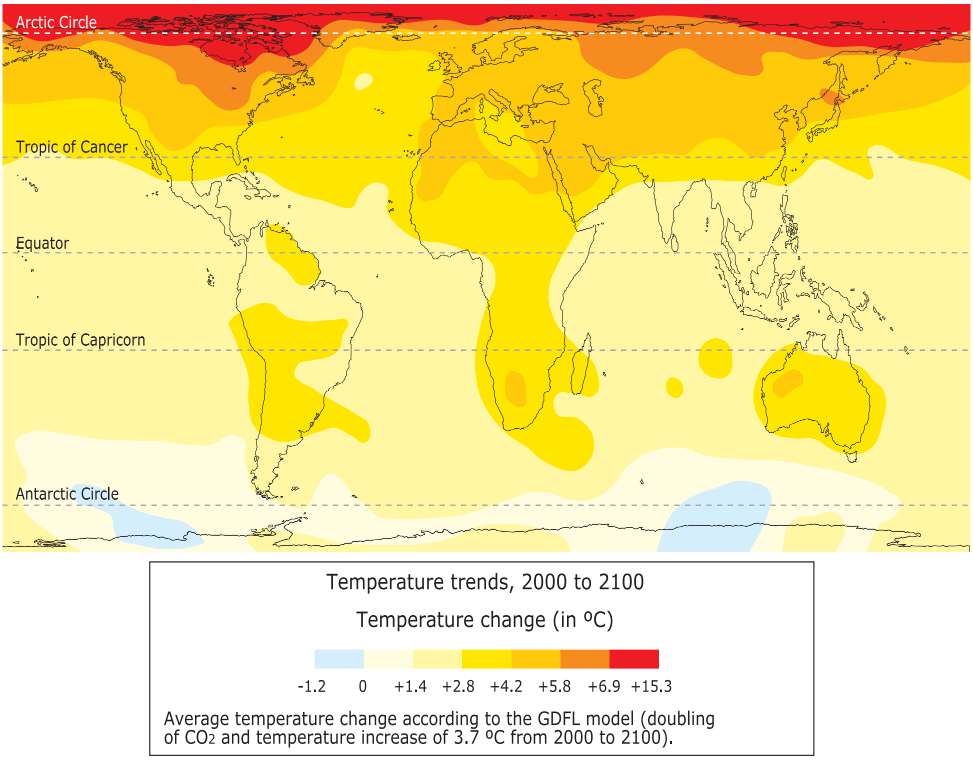
Polar ecosystems are currently experiencing a marked warming trend. This process has reached spectacular proportions in the case of the Arctic, where ice loss is rapid (Vinnikov et al. 1999; Serreze, Holland and Stroeve 2007) and apparently accelerating, to the extent that we can seriously posit an Arctic Ocean without its summer ice cover in the not too distant future (Serreze, Holland and Stroeve 2007). The Antarctic Peninsula is also experiencing significant warming and the disappearance of sea-ice masses (Rignot et al. 2004), albeit with losses much smaller and patchier than in the Arctic.

The effects of global warming on polar regions are already so evident and have such alarming consequences that they were the prime motivation behind the organisation of International Polar Year. Among the activities scheduled under its banner are studies of the polar ecosystem in order to more accurately predict its response to environmental changes, especially global warming. Another of its goals is to inform society better about the changes taking place in the polar regions; a goal shared by the authors of the present book.

Emissions of carbon dioxide and other greenhouse gases produced by human activity are causing a build-up of these substances in the atmosphere which threatens to push up the planet's global temperature by around 4 °C (IPCC 2001) in the course of the 21st century. The global circulation models used to predict future climate variations point to large regional differences in the speed of warming, with some zones suffering a drastic rise in temperature and others getting off relatively lightly. These models suggest that warming will be most intense in the Arctic zone, , where temperatures may rise by as much as 9 °C (map 2). In fact, records indicate that the Arctic is already heating up at a rate of 0.4 °C per decade, twice as fast as the rest of the planet (IPCC 2001). The Southern Hemisphere, in contrast, is projected to experience practically zero warming (map 2).

Other impacts deriving from human activity are, however, far greater in the Antarctic. For instance, the effects on the ozonosphere of volatile synthetic chemical compounds are magnified in the Southern Hemisphere, causing the appearance of a seasonal hole in the ozone layer which exposes the region to greatly increased levels of ultraviolet radiation (see chapter 1). Likewise, whaling has had an important aftermath in the world's southern waters, with implications for the Antarctic system that may run a lot deeper than suspected (see chapter 2).

Map 2: Predicted increase in average temperature of all world regions in the 21st century

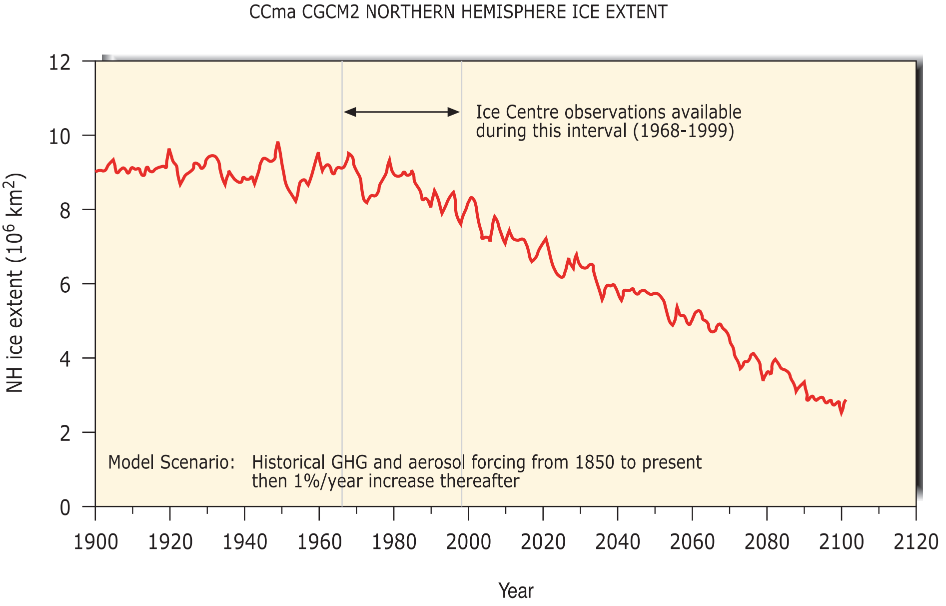


Average temperature change according to the GDFL model (doubling of CO_2 and temperature increase of 3.7 ºC from 2000 to 2100).

Source: Geophysical Fluid Dynamics Laboratory, Princeton University.

The first effect of global warming on polar ecosystems is the melting of the polar ice caps. Results published in 2006 reveal a sizeable loss of the planet's ice. On the one hand, the Antarctic ice sheet is losing 152 km^2 of ice a year. This equates to an annual increase in the global sea level of 0.4 ± 0.2 mm, and has also lost the Antarctic Peninsula around 8,000 km^2 of its ice shelves in the last 50 years, coinciding with an approximately 2 ºC rise in regional temperatures. On the other, the retreat of the Arctic ice sheet is accelerating, with recent data showing seasonal ice-cover losses up to 18 times higher than in past decades. This has been accompanied by an unprecedented decline in the Arctic ice, provoking an all-time low in winter ice cover in March 2006 (figure 1), followed by an abrupt melting event in the summer of 2007. Also, in August 2006, large cracks were observed, running hundreds of kilometres, in what was till now the Arctic's permanent ice cover, suggesting that the loss of mass may be about to quicken. In Greenland, meantime, the glaciers are melting at twice the rate of five years ago. The decline in the Greenland ice sheet

Figure 1: Changes observed over the 20th century in the Northern Hemisphere sea ice extent and predictions based on expected Arctic warming rates in the 21st century



Source: National Snow and Ice Data Centre, United States.

has increased fivefold to 239 ± 23 km^3 of ice a year, contributing a further 0.6 mm to the annual worldwide rise in sea level. And modellers are predicting a further jump in the warming rate, which in the Arctic, for instance, will increase to 1.2 °C per decade over the first part of the century, accelerating to 3 °C in the second half. Projections for global warming-induced changes in the Arctic ice sheet augur a rapid retreat to less than 3 million km^2 by the end of the 21st century (figure 1); three times less than its extension in the opening years of the 20th (see discussions in Rignot and Thomas 2002; Rignot et al. 2004; and Serreze, Holland and Stroeve, 2007). These estimates are being rapidly revised in the light of the abrupt ice loss of summer 2007.

All these losses have major climatic and geopolitical consequences, but they also threaten a unique "habitat"; the ice surface of the polar oceans. This publication sets out to examine the effects of global warming on polar ecosystems, until now only poorly investigated. In its pages, leading world experts in polar ecosystems discuss the impact of their waters being exposed to solar radiation—associated to loss of ice cover, with particular attention to the levels of ultraviolet radiation reaching the Antarctic ecosystem, and analyse how the marine ecosystem is responding to global warming along with the rich megafauna it sustains.

This book brings together the presentations delivered in the second cycle of debates organised by the Spanish Council for Scientific Research (CSIC) and the BBVA Foundation at the Cap Salines Lighthouse Coastal Research Station (Mallorca), in order to stimulate reflection on the latest scientific challenges and discoveries in marine biodiversity and to alert society to the need to conserve our oceans and coasts.

In its chapters, reputed international experts offer a prospective vision of the impact of climate change on polar ecosystems.

I wish, in closing, to thank the BBVA Foundation for its support and financial assistance in organising the event that gave rise to this book and facilitating its publication. My thanks also to José Manuel Reyero and his associates for their work on preparing the texts. This introductory text benefited from discussions to plan the Arctic Tipping Points project, funded by the European Commission.

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1. THE IMPACT OF INCREASING ULTRAVIOLET RADIATION ON THE POLAR OCEANS

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1.1. ULTRAVIOLET RADIATION AND THE TERRESTRIAL OZONE LAYER

MORE THAN 3,000 MILLION YEARS AGO, the cyanobacteria inhabiting the oceans changed the composition of the Earth's atmosphere by producing oxygen that accumulated in the atmosphere and became ozone when it reached the stratosphere. This is the current scientific explanation for the origin of the atmospheric ozone layer, which, given the capacity of this gas to absorb ultraviolet (UV) radiation, allowed life to develop on the surface of Planet Earth.

Once it reaches the stratosphere, oxygen is exposed to the intense solar radiation that impinges on the upper layers of the atmosphere. The high energy of the ultraviolet radiation reaching the stratosphere breaks down oxygen molecules (O_2) into oxygen atoms (O), which then react with oxygen molecules to form ozone (O_3). The same ultraviolet radiation dissociates the ozone into oxygen atoms, which can again react to form molecular oxygen and ozone, making ozone formation in the stratosphere a highly dynamic process. This process is expressed by the Chapman equations, which describe the phenomena associated with the formation and dissociation of ozone and oxygen molecules and atoms in the stratosphere. The outermost layer of the stratosphere, with the highest altitude, is dominated by atomic oxygen because solar radiation is much more intense and so produces greater dissociation. Within the stratosphere, however, solar radiation is absorbed to a greater degree, favouring the formation of ozone, which attains a maximum concentration at about 20 km above the Earth's surface. By contrast, in the lowest layer of the stratosphere, that closest to the Earth, ultraviolet radiation is very weak because it has largely been absorbed in its passage through the ozone layer. Molecular oxygen predominates here, since very little ozone is formed.

◀ **Photo 1.1: Icebergs and rainbow.** This rainbow spanning the Antarctic ice shows how solar radiation is composed of bands of different colours and energy. The least visible but most energetic of these is the ultraviolet band, whose intensity has increased in the polar regions due to depletion of the ozone layer.

Today, the ozone layer continues to protect the terrestrial and ocean surfaces of the planet from the high levels of ultraviolet radiation that strike the atmosphere by absorbing radiation in the 240-320 nm range. This band includes wavelengths of solar radiation of high energy that, were it not for the ozone layer, would pass through the atmosphere with harmful effects on living organisms. The ozonosphere is thinner above the equator, where ozone is found at a concentration of approximately 260 DU (Dobson units), and thickens towards higher latitudes. The greatest seasonal variation occurs at the poles, mostly because there is no solar radiation there during the polar winter, while during the long days of the polar summer they receive solar radiation for more hours.

The extent, thickness and seasonal dynamics of the ozone layer (see, for example, Solomon 1999; Staehelin et al. 2001) is an object of study for atmospheric chemists, who, amongst other tasks, have been taking regular measurements at different locations on the planet, such as Antarctica, the Arctic Ocean and, particularly, the Arosa station in Switzerland, with records dating back to 1926. The most widely used instruments for measuring ozone are the Dobson spectrophotometer and, more recently, balloons equipped with probes and sensors that are launched into the atmosphere and which calculate the change in ozone concentration with altitude. The TOMS (total ozone mapping spectrometers) satellites, of which the Earth Probe TOMS is currently in operation, and the OMI (ozone monitoring instrument) on board the AURA satellite are devices put into orbit by NASA in order to provide an overview of the distribution of ozone around our planet. The ozone maps plotted from the data sent by these satellites can be viewed online at the NASA website (jwocky.gsfc.nasa.gov/eptoms/ep.html and aura.gsfc.nasa.gov/ instruments/omi/index.html).

1.2. ATMOSPHERIC POLLUTION AND OZONE DECLINE

The equations describing the formation and destruction of ozone formulated by S. Chapman in 1930 included only oxygen and ultraviolet radiation (see, for example, Solomon 1999; Dahlback 2002), but other substances that are also naturally present in the atmosphere were subsequently discovered to combine actively with ozone (O) in the same way as Chapman described, dissociating thus: $X + O_3 \rightarrow XO + O_2$, where X may be H, NO, OH, Cl, I or Br. The natural occurrence of these compounds in the atmosphere and their role in ozone destruction processes helped explain why ozone values were lower than those predicted solely from the results of the oxygen and ultraviolet radiation interactions reported by Chapman.

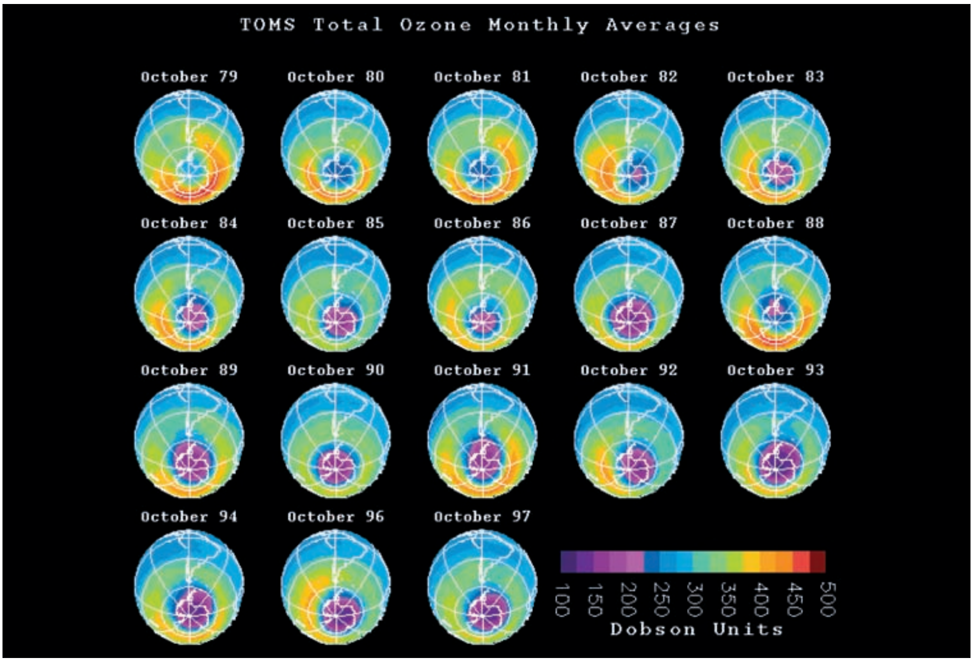
Photo 1.2: Icebergs in Antarctica. The most optimistic models predict that stratospheric ozone values will not recover until after 2050. In Antarctica, bright, sunny days are accompanied by high levels of ultraviolet radiation that may have negative effects on the development of life.

In 1970, Professor P. Crutzen not only described the NO-mediated ozone dissociation reactions, but also pinpointed a problem whereby emissions of nitrous oxide, a stable and long-lived gas produced by soil bacteria, had increased as a consequence of widespread fertilizer use and could cause an increase of NO in the atmosphere, leading to a reduction in the amount of ozone. Not long after, Crutzen and H. Johnston independently realised that supersonic aeroplane flights contributed to NO emissions. In 1974, Rowland and Molina described the role of atmospheric Cl in O_3 dissociation equations and also showed that organic chlorofluorocarbons (long-lived gases, such as the CFCs used in cooling systems) could be contributing to the reduction in the concentration of stratospheric ozone. When CFCs enter the stratosphere, they are dissociated by the action of UV radiation, forming free Cl that in turn reacts with ozone, destroying it. The Rowland-Molina theory met with fierce opposition from the aerosol and halocarbon industries, who branded it as “science fiction”. Nevertheless, laboratory evidence from other researchers and measurements of chlorine radicals in the atmosphere did link CFCs with the deterioration of the ozone layer. Predictions at that point were not optimistic: if CFC emissions continued, the ozone layer could decrease 30-50% by the year 2050.

1.2.1. An ozone hole over Antarctica

During the 1980s, scientists studying the ozone layer at the British Halley Station in Antarctica verified that the concentration of ozone was dropping fast; in fact, the decrease they measured was so large they thought it must be due to probe malfunction. Yet measurements taken with new instruments at the same station confirmed that the concentration of ozone over Antarctica had indeed fallen to alarmingly low levels. In 1985, the journal *Nature* reported the discovery by Farman, Gardiner and Shanklin of the Antarctic ozone hole, so called because of the huge fall in stratospheric ozone concentration. The decrease occurred at the end of winter and in the spring, with peak values reached in October (map 1.1). This discov-

Map 1.1: Distribution of ozone concentrations over Antarctica in the month of October from 1979 to 1997



The ozone hole above Antarctica is easily appreciable in the ozone maps (measured in Dobson units) plotted with data from the TOMS satellite launched by NASA. The minimum ozone concentrations over Antarctica are recorded in October, and have been declining notably since 1980.

Source: NASA.

ery was a wake-up call for the scientific community, who realised the far-reaching consequences that the loss of the ozone layer could have for life on our planet.

This drop in ozone levels was not only recorded in Antarctica (see, for example, Dahlback 2002). Satellite data making the same prediction were dismissed as incorrect, because the decrease in ozone concentration coincided with the placing in orbit of the new TOMS satellite. The chronological series of ozone layer measurements taken above Arosa (Switzerland), dating from 1926, also showed an unequivocal fall in ozone concentration as of 1980, which has continued at a rate of approximately 2.9% per decade. The conclusion was that the ozonosphere was deteriorating. Evidence from other latitudes helped confirm this realisation. The Arosa time series showed that ozone levels had held relatively stable in the stratosphere over long periods, so the recent depletion of the ozone layer was a global reality. A number of governments signed the Montreal Protocol in 1987, committing to a reduction in their CFC emissions and ushering in a period of severe restrictions. Crutzen, Molina and Rowland won the Nobel Prize for Chemistry in 1995 for their work on stratospheric ozone.

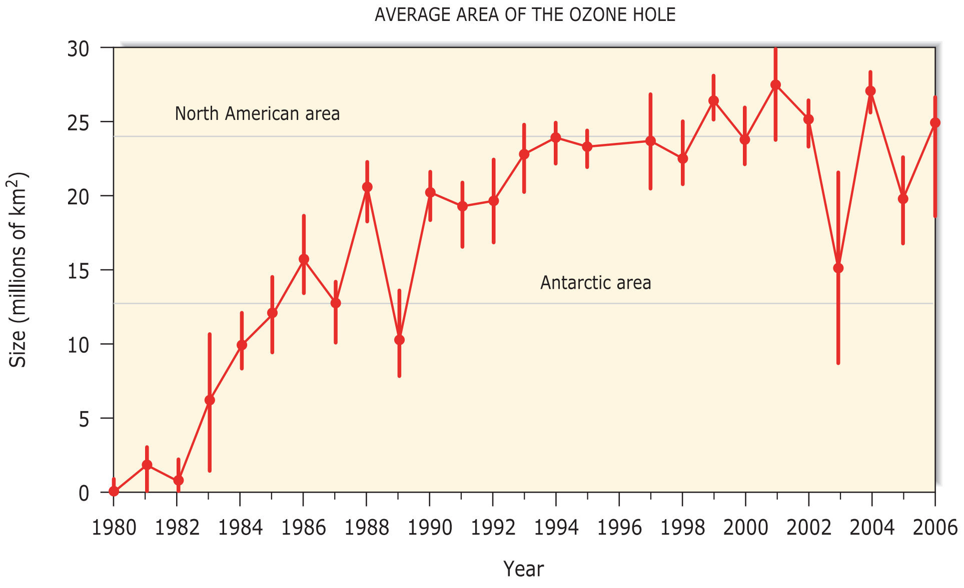
1.2.2. The current situation: predictions and global warming

The decline in stratospheric ozone concentration was arrested by the Montreal Protocol, but, so far, the gas has not recouped the levels recorded before the decline set in in the 1970s. Current predictions based on the rate of CFC disappearance from the atmosphere suggest that recovery of ozone to its 1960s and 1970s levels will not be achieved until 2050 (Weatherhead and Andersen 2006). If this is correct, the increased UV radiation reaching the terrestrial and marine surface will persist for at least 80 years from the onset of depletion, which may represent a significant impact with unforeseeable consequences. Recently, predictions about ozone recovery have been questioned (Shindell, Rind and Lonergan 1998; Weatherhead and Andersen 2006) on account of the considerable uncertainty that surrounds them; firstly, due to the continuing emission of polluting substances—such as nitrous oxide and new compounds that appear every year for various uses—that are prone to destroy ozone, and secondly, because the global warming generated by the accumulation of greenhouse gases in the atmosphere may also be hindering the recovery of the ozone layer. The warming of lower atmospheric strata has a deleterious effect on the ozone layer, because the temperature of the troposphere influences that of the stratosphere: the more heat accumulating in the troposphere the colder the stratosphere becomes, and the colder the stratosphere, the more ozone is lost from it (Shindell, Rind and Lonergan 1998).

Photo 1.3: Ice masses drifting in open waters. The increase in ultraviolet radiation reaching the poles, especially in Antarctica, is reducing the biological productivity of their waters.

The combination of these factors has prevented the polar areas and intermediate latitudes from recovering historical ozone concentrations; instead, the values recorded now are lower than those existing before CFC emissions began. In the polar regions, where ozone concentration is strongly seasonal, an ozone hole still forms every winter-spring; of immense proportions in the case of Antarctica. The rate of ozone decline and the size of the hole are greater over Antarctica than the Arctic Ocean, since the gas's natural concentration tends to be lower in the first case due to topographic differences. The Arctic is a frozen ocean surrounded by continents, while Antarctica is a frozen continent surrounded by oceanic waters. This essential difference is of prime importance for the atmospheric circulation—including that of the stratosphere—generated over the two poles. With the coming of winter, the lack of solar radiation at the poles causes a slowing of ozone production-destruction dynamics, exposing levels of the gas to the influence of the circulating air masses. The lack of solar radiation leads to a cooling of the air at the poles, creating a steep temperature gradient that sends it circulating vigorously in an east-west direction, encircling the area of the polar atmosphere. This whirlwind effect, known as the circumpolar vortex, prevents the ozone-rich air of lower latitudes from penetrating the interior, isolating the atmosphere above the poles. The vortex is much less powerful in the Arctic than over Antarctica, because the Arctic Ocean suffers frequent disturbances that

Figure 1.1: Changes in the size of the ozone hole over Antarctica from 1979, when it did not exist, up to the present day



The graph shows the average values in the size of the Antarctic ozone hole observed in successive months of October. The ozone hole is defined as the area where the concentration is equal to or less than 220 Dobson units. The vertical lines show the errors of the monthly averages. The horizontal lines are equivalent to the area of the Antarctic continent—surpassed by the ozone hole since 1990—and to the area of the North American land mass to which the ozone hole area is equivalent in the present time.

allow ozone-rich air to penetrate from lower latitudes. For this reason, although ozone concentration has diminished over the Arctic, an ozone hole does not always appear. In contrast, the Antarctic ozone hole persists to this day, with the lowest levels recorded in October, coinciding with the arrival of the southern spring. In effect, the hole reached its record minimum concentration in October 2006, according to measurements kept since the 1980s, before its existence (figure 1.1). This was accompanied, moreover by a recent-year low in ozone concentration, confirming that recovery is still far from sight.

Global warming is no longer a prediction but a reality. It is also having a dramatic effect on the polar areas; the most sensitive to global temperature changes, as we explain in other chapters of this book. Importantly, today's diminishing ozone values, with polar regions especially affected, mean that the impact of global warming and the melting of the polar ice is being felt in an environment subjected to high levels of UV radiation. The combined effects of high UV radiation, ice melt and increased ambient temperature are still very much an unknown quantity.

1.3. INCREASED UV RADIATION OVER THE POLAR REGIONS

The climatological conditions of the polar areas are inauspicious for the development of life, not only for their low temperatures, but also because the lack of liquid water means they are ice deserts devoid of vegetation. The polar oceans, on the other hand, are a less extreme environment and experience smaller temperature variations, between approximately +5 and –2.3ºC in polar waters, making them a more stable environment for life than the terrestrial habitat. In addition, polar waters are rich in nutrients that favour plankton proliferation. Life in the polar regions accordingly unfolds in the oceans, which serve as the source of food for their bird and large mammalian inhabitants. This is why any impacts on the polar oceans have serious consequences for the development and the maintenance of the system as a whole.

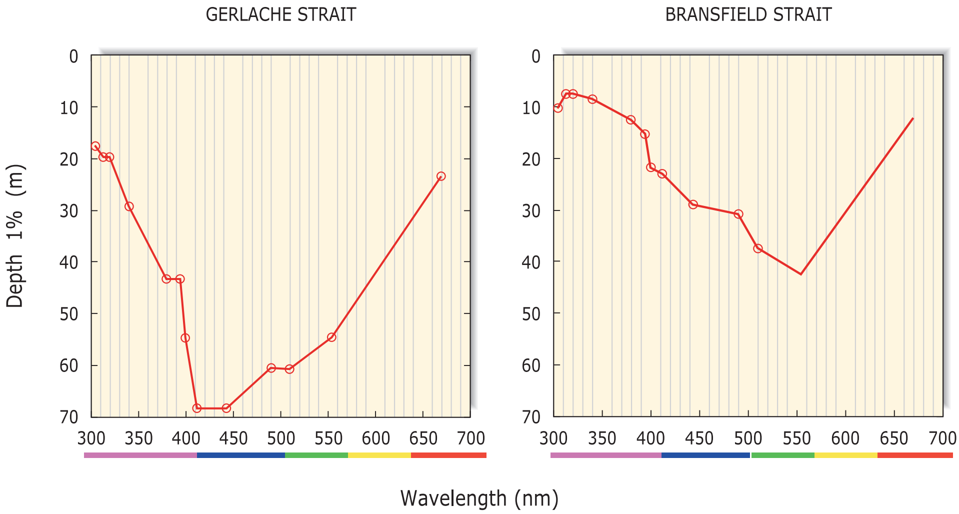
The evidence of increased UV radiation on polar ecosystems must be urgently checked and quantified. It is estimated that for every 1% reduction in stratospheric ozone, the transmission of ultraviolet B light to the surface of the Earth will increase by 1-2% (see, for example, Dahlback 2002). However, to assess the impact of UV radiation on these ecosystems, it is not enough just to consider the incident radiation, we also need to determine the effective doses organisms are receiving and how sensitive they are.

UV radiation absorption and reflection can operate through various processes, generating considerable variation in the doses received at a given place and by a particular organism. The intensity of this radiation varies according to the angle of the sun and therefore the latitude, the season of the year and the time of day (60% of total radiation is received between 10 a.m. and 2 p.m.). Cloud cover may influence the doses received since clouds absorb ultraviolet radiation, but only when cover is very dense does it provide an effective filter—90% of UV radiation can penetrate light cloud cover. The concentration of aerosols in the atmosphere is another factor, since these substances absorb UV radiation; and altitude too, with an extra 10-12% received for every 1,000 metres gained. Different surfaces have different capacities for reflecting ultraviolet radiation; so, while the Earth reflects around 25%, snow can reflect up to 80% of incident UV radiation. Finally, UV radiation penetrates water and can also have a significant effect on marine organisms.

Ultraviolet light, like visible light, is absorbed in the oceans by water, suspended particles and dissolved substances. Organic carbon compounds are the main agents of underwater attenuation of UV light. Wavelengths in the UVB band, despite containing more energy, are absorbed to a greater extent and do not penetrate as deeply as UVA band wavelengths. There are still few measurements of the penetrative capacity of UV light in ocean waters. The equipment required for its underwater quantification is novel and sophisticated, and in possession of only a handful of laboratories.

Measurements taken in polar waters show that UV radiation can penetrate down to significant depths, particularly in comparison with visible radiation. For instance, during the Spanish ICEPOS-2005 project in Antarctic waters in the southern summer of 2005, aboard the oceanographic research vessel *BIO Hespérides*, measurements were taken of underwater solar radiation in the Weddell and Bellingshausen seas and the Bransfield, Gerlache and Antarctic straits. The size of the illuminated layer, which, in oceanographic terms is calculated as the depth at which 1% of the light reaching the surface of the water is received, varied between 10 and 70 m in the waters sampled during the ICEPOS-2005 expedition. It was found that 1% of ultraviolet radiation penetrated to depths of 5 to 19 m for the UVB band (at 305 nm) and 45 m for the UVA band (380 nm) (figure 1.2). This means that ultraviolet radiation reaches considerable depths in the illuminated layer of Antarctic waters and is present in up to 50% of the photic layer, for which reason its impact on aquatic organisms may be significant.

Figure 1.2: Penetration depth (in metres) of solar radiation in two areas of the Southern Ocean, measured during the ICEPOS-2005 Spanish oceanographic expedition



The red line represents the depth reached by 1% of the solar radiation received at the ocean surface and shows how it varies as a function of the spectrum band (wavelength), each labelled with the corresponding colour of the visible spectrum. The colour violet (300-400 nm), for instance, represents radiation in the ultraviolet band.

Source: Data provided by S. Agustí and M. Llabrés.

1.4. DAMAGE INDUCED BY UV RADIATION AND PROTECTION MECHANISMS

The energy associated with a photon is inversely proportional to its wavelength; the higher the energy, the greater the capacity of UV radiation to cause damage. The UVC band (200-280 nm) has the highest energy, and is accordingly the most harmful; even so, if ozone concentration levels were to lower dramatically and the ozone layer to thin to a few centimetres, the atmosphere would still be capable of filtering out all the incident UVC solar radiation. The current loss of ozone, however, is sufficient to diminish absorption of UVB light (280-315 nm), which is the ultraviolet band mostly absorbed by ozone gas. This has given rise to an increase in the amount of UVB radiation received on the Earth's surface. Ozone absorbs little of bands of longer wavelength like the UVA band (315-400 nm), so changes in the ozonosphere do not greatly affect the amount of UVA radiation reaching the Earth. The difficulty in determining the scale of the increase in ultraviolet radiation striking the polar oceans and ecosystems is basically a lack of data, because records of UV radiation incidence prior to ozone layer depletion are practically non-existent.

UVB is a high-energy radiation that acts at the molecular level, denaturing many organic compounds that are essential for live organisms. UVA radiation is considered less harmful because it has less energy. It is also thought to play an important role in activating a range of photoprotection and repair mechanisms; nevertheless, at high doses, it can have the same harmful effects as UVB light.

The damages ultraviolet radiation causes living organisms are many and diverse (see, for example, Roy 2000; Vincent and Neale 2000; Buma, Boelen and Jeffrey 2003; Banaszak 2003). UV radiation denatures cellular DNA (a molecule particularly sensitive to ultraviolet light, given its capacity to absorb radiation in this band), causing transcription and replication errors, and is thus capable of producing mutations. It also denatures other compounds, such as proteins and pigments, destroys the cell membrane, inhibits nutrient absorption in photosynthesising plankton, affects the mobility and navigation systems of aquatic organisms, inhibits photosynthesis and the growth of unicellular plankton organisms and causes cell death in phytoplankton. All these effects indicate that UV radiation may be a direct cause of plankton population losses (Llabrés and Agustí 2006). In addition to the direct harm it causes, UV radiation reacts strongly with organic matter dissolved in the ocean and with other chemical compounds—such as nitrates—that are common in polar waters, forming so-called reactive oxygen species (ROS), like the hydroxyl radical (OH^-) and hydrogen peroxide (H_2O_2). Such substances are highly reactive and toxic to living organisms since they react with biomolecules (proteins, lipids, DNA, etc.), modifying or destroying them. ROS form in water and even inside the cells of organisms. UV radiation may also increase the toxicity of certain compounds. This is the case with some persistent polluting substances like aromatic polycyclic hydrocarbons, petroleum-derived compounds whose toxicity increases after exposure to UV radiation, in a process known as phototoxicity or photoactivation (Banaszak 2003).

Higher organisms have a greater capacity to generate protective structures against the damage caused by exposure to UV radiation, but this does not shield them completely from its harmful effects. Many marine invertebrates with shells and hard, highly protective exostructures lack such defences in the egg and larval stages, when they are as vulnerable to UV radiation as the larvae of aquatic vertebrates. UV radiation damage has also been documented in some aquatic vertebrates. For example, the eyes of some fish have developed cataracts due to exposure, and sunburn of the skin is common in fish living in high-altitude water bodies or confined in fish farm cages, since both are more exposed to UV rays. Although these burns are not lethal in themselves, they enormously increase the likelihood of the fish succumbing to infections, so may cause their death by indirect means (see, for example, Zagarese and Williamson 2000; Leech and Johnsen 2003).

Although currently exacerbated by diminishing ozone levels, exposure to certain levels of UV radiation has been a natural occurrence for the Earth's inhabitants since life first began. Millions of years of evolution have enabled species to develop mechanisms to minimise the harmful effects of UV radiation that are efficient for certain levels of radiation and exposure.

1.4.1. Avoiding exposure to UV radiation: plankton migrations

Only the surface layer of the oceans receives radiation, and this photic layer extends down to a maximum depth of 200 m in the planet's most transparent waters. The dark area of the ocean encompasses thousands of metres and provides a safe haven for organisms against UV radiation. Hence, one of the protection mechanisms available to aquatic species is directly to avoid exposure to UV radiation (see, for example, Leech and Johnsen 2003). Migrations through the water column and similar light-responsive behaviours are common in aquatic organisms. Zooplankton, for instance, migrate during the day to the dark region of the water column and only rise at night to feed in the surface layer, where photosynthetic plankton live. These daily migrations up and down the water column are so widespread that they have spawned new variants of predatory behaviour. Many aquatic species are equipped with sensors to detect light and ultraviolet radiation and react with negative or positive phototactic behaviour; some even have what is known as UV vision. And numerous organisms, fish amongst them, have vision within the UVA or UVB wavelength band, which is useful for navigation and communication and for identifying prey, especially those enriched by substances that protect against UV radiation, which are absorbed in large quantities in these bands. UV vision undoubtedly also helps to identify and avoid the depths to which the harmful wavelengths of UV light penetrate (Leech and Johnsen 2003).

1.4.2. Protection and repair systems

Not all aquatic organisms have the mobility or capacity to choose their position in the water column. A case in point are the photosynthetic plankton. These organisms (photo 1.4) have to absorb the light in the visible range to photosynthesise, and are forced to remain in the layer of the ocean lit by solar radiation and exposed to the UV spectrum. Their only defence is to develop protection mechanisms and, after years and years of evolution, these have become as many as they are varied (see, for example, Roy 2000; Banaszak 2003).

1.4.2.1. PROTECTIVE CELLULAR STRUCTURES OR "PARASOLS"

These are physical protection mechanisms involving the production of structures that act as barriers to prevent ultraviolet radiation from penetrating. One example is the mucus secreted by microalgae like *Phaeocystis pouchetii*, whose primary function is to bring cells together into colonies, but which also serves to reflect and prevent the penetration of UV radiation (Banaszak 2003). Other such structures are based on the creation of special cell walls or the formation of crystals on the outside of the cell. And certain variations in the shape or arrangement of the crystals making up the cell wall may also be useful for reflecting UV radiation. For instance, it has recently been found that holococcoliths (planktonic microalgae) have crystalline structures in their calcite sheaths that efficiently reflect UV radiation (Quintero-Torres et al. 2006), preventing it from entering the cell.

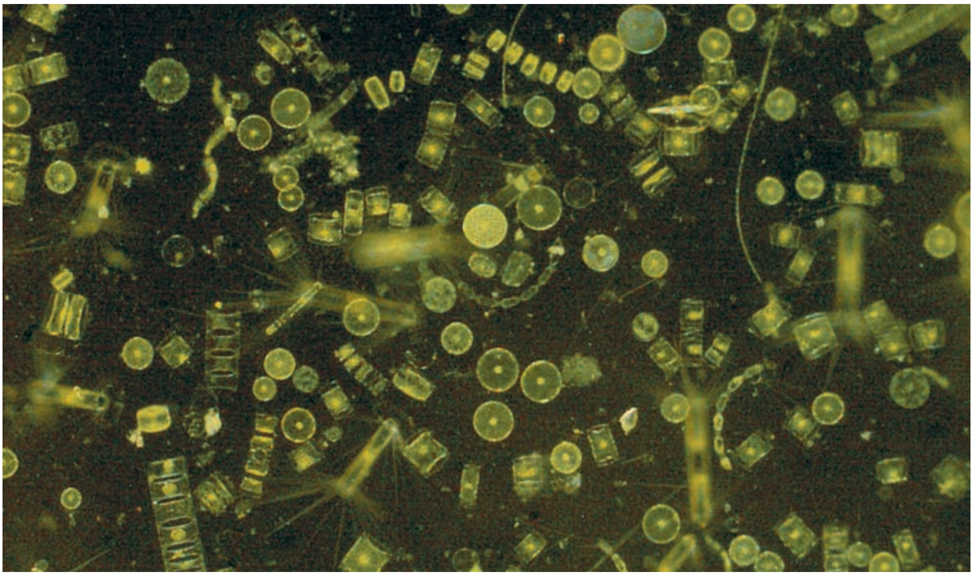


Photo 1.4: A sample of Antarctic phytoplankton dominated by a diversity of diatomea species, viewed under a phase-contrast microscope (x100)

1.4.2.2. "SUN FILTER" PRODUCTION

This is one of the most important protection mechanisms. It is based on the production by phytoplankton cells of chemical substances that absorb ultraviolet radiation to protect the cells from its harmful effects (Roy 2000; Banaszak 2003). Among the most important sun filters is mycosporine, a substance with a strong solar protective function that is secreted by fungi, and the mycosporine-like aminoacids (MAAs), sun filters produced by other organisms. These aminoacids are hydrosoluble and have a maximum absorption capacity at 320 nm, i.e., between the UVA and UVB bands, although different types can be synthesised with the ability to absorb light in the 309-360 nm range. Only bacteria, fungi and algae have the capacity to synthesise these compounds, but they can be passed onto and accumulate within other organisms that feed on planktonic algae. These predators benefit from their function as a solar filter and also transmit them along the food chain.

Other pigments also act as sun filters, including scytonemin, which is secreted by cyanobacteria growing on the polar ice sheet. This substance sticks to the surface of cells, forming a mucus film that acts as a powerful solar filter. Melanin-type pigments too provide protection from UV radiation and, although not synthesised by algae, they are synthesised by other zooplankton organisms, as has been described in the cladocerans of the Arctic Ocean.

Many of these sun-filtering substances have been copied by industry for a range of applications.

1.4.2.3. ANTIOXIDANTS

An indirect effect of ultraviolet radiation is the toxicity of the ROS formed by the action of UV radiation on the molecules of organic substances, or on the oxygen present in the water or the cells themselves. These toxic photoproducts may be more harmful to cells than UV radiation itself. Toxic photoproducts are neutralised by certain antioxidants (Roy 2000; Banaszak 2003), including substances like ascorbate, cleaning enzymes and carotenoids, which act as oxidant traps by combining with and neutralising the free radicals of the ROS. The quantities of antioxidants in a given organism are directly related to its exposure to UV radiation, and their concentration increases with the dose of UV radiation received.

Carotenoids are pigments that can only be synthesised by photosynthetic organisms, such as photosynthetic plankton, but can accumulate in species that feed on phytoplankton. Thus, some copepods (small crustaceans that make up part of the zooplankton) may be transparent or red, in the latter case if they have accumulated carotenoids as part of their diet. And these red copepods are more resistant to UV radiation than their paler fellows. The algae that grow on ice and snow give them a characteristic reddish hue, caused by the large amounts of carotenoid pigments they contain to shield themselves from the strong solar radiation reflected off these surfaces.

1.4.2.4. REPAIR SYSTEMS

Photoprotection systems are not infallible, nor can all the harmful effects of UV radiation be avoided. Living organisms have accordingly evolved systems to repair the cell damage caused by ultraviolet radiation (see, for example, Vincent and Neale 2000; Buma, Boelen and Jeffrey 2003; Banaszak 2003). Protein repair systems are triggered when cells are exposed to ultraviolet light. It is also thought that accelerating protein renewal is a way to replace damaged proteins with new versions. But the main systems in use are those of DNA repair (see, for example, Vincent and Neale 2000; Buma, Boelen and Jeffrey 2003), given this molecule's vital importance for cell function. UV radiation-induced DNA damage consists mainly of the chemical alteration of its bases. One of the most common changes occurs through the dimerization of adjacent pyrimidine bases, producing photoproducts known as cyclobutane pyrimidine dimers (CPDs) which account for between 50% and 80% of all photoproducts induced by the exposure of DNA to UV radiation. CPDs are not mutagenic but they do inhibit replication. Repair systems are of two main kinds: photoreactivation, which involves stimulation by blue light and UVA, and dark repair, which is a light-independent mechanism. Both systems require the organism to synthesise enzymes that can act on the damaged area. Photolyase, for instance, identifies CPDs and uses light energy to repair damaged bases. Dark repair systems require the synthesis of a series of replication enzymes that act on the damaged area to identify them, cut the chain, synthesise the correct sequence and insert it at the appropriate location after excising the damaged sequence. All eukaryote and prokaryote cells are equipped with these repair systems, which have evolved over time to occupy a key place in mammal biology: for example, it has been calculated that the DNA of a human cell experiences about 500,000 lesions a day, almost all of them reparable by these systems.

1.5. IMPACT OF INCREASING UV RADIATION ON THE POLAR OCEANS

The impact of increasing UV radiation on the polar oceans depends on the dose received and the relative effectiveness of protection and repair systems. These are not common to all organisms; rather, distinct species display different sensitivities to UV radiation depending on the efficacy of the systems they employ. Furthermore, the use of these systems exacts an energetic and nutritional cost.

As a consequence, ultraviolet radiation has a considerable impact on the polar oceans, especially the Southern Ocean, which is prone to receive a larger amount of radiation. This impact has been demonstrated in a range of studies.

UV radiation inhibits photosynthesis and, therefore, the production of photosynthetic plankton. In 1992, Smith et al. calculated that increased UV radiation on the Antarctic waters was responsible for a 6-12% reduction in primary production. Given that primary production forms the base of the food chain, a reduction of this magnitude may have consequences for total production in Antarctica. Since the publication of this study, the ozone concentration has continued to decline (by 2006, the ozone hole was 25% larger than in the early 1990s), suggesting that its 1992 estimates need to be urgently revised.

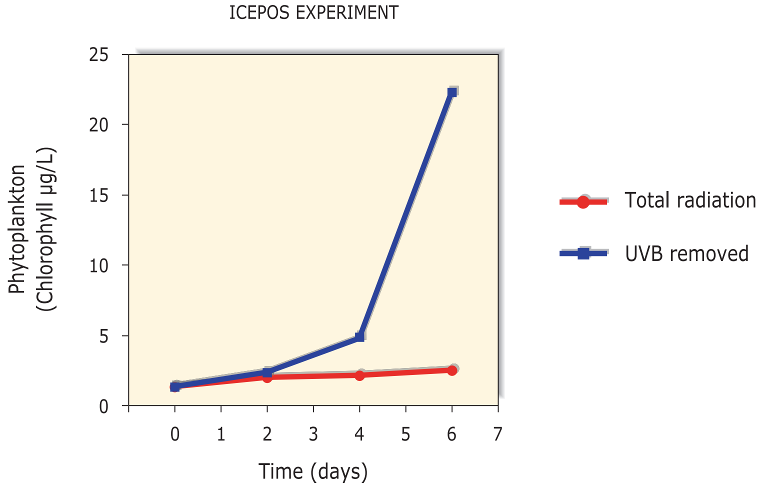
The impact of UV radiation on Antarctic plankton has also been detected from the presence of CPDs in the DNA of natural samples of planktonic compounds even at depths below 20 m. CPD accumulation has been found in certain algae growing under the sea ice (Buma, Boelen and Jeffrey 2003), and it has been confirmed that DNA damage is present throughout the Antarctic summer in both phytoplankton and bacterioplankton (Buma, De Boer and Boelen 2001).

This suggests that UV radiation has a control function for the development of phytoplankton populations. We recently confirmed this in experiments conducted with Antarctic phytoplankton during the Spanish ICEPOS mission at the Spanish Antarctic Base Juan Carlos I on Livingston Island (South Shetland archipelago in the Antarctic Ocean) during the southern summer of 2003-2004. The experiments consisted simply of incubating surface seawater samples taken from South Bay near the Spanish Base. The samples contained natural plankton populations and were incubated in 2-litre bottles hermetically sealed and submerged in large tanks. Water from the bay was circulated through the tanks to maintain a similar water temperature, and the tanks were exposed to natural solar radiation, to keep the plankton exposed to similar natural conditions to those of plankton growing in the surface waters of South Bay. The incubating bottles were made of different materials of varying transparency to solar radiation. Quartz bottles, which are transparent to all visible and ultraviolet light spectra, let in all the solar radiation the plankton naturally receive in their underwater habitat, while polycarbonate plastic bottles are opaque to UVB radiation, thus simulating an environment from which the B band of the UV spectrum has been eliminated. The results show that ultraviolet light strongly controls the abundance of plankton (figure 1.3). Plankton populations incubated in the quartz bottles did not exhibit any significant changes in abundance, but plankton growing in the polycarbonate bottles, which filtered out all the UVB radiation, showed a more than 15-fold increase in abundance in only 6 days (figure 1.3). These experiments demonstrate that UVB radiation exerts a significant control over the abundance of Antarctic photosynthetic plankton, and that this radiation impedes generation of the biomass volume that might otherwise be expected from the high nutrient concentrations in Antarctic waters.

Another important impact of increased UV radiation has to do with species diversity, since a continuing increase will inhibit development of the less vs. more resistant species. This, in turn, could have consequences for the food chain, impairing the efficiency of matter transfer to predators or even altering the make-up of species occupying other trophic strata (Keller et al. 1997).

Ultraviolet light also affects the macroalgae; organisms vital for coastal ecosystems and that dominate primary production on the seabed of the Arctic and Southern Oceans. As with the phytoplankton, a variety of impacts have been detected in

Figure 1.3: Result of experiments to determine the impact of ultraviolet radiation on the phytoplankton populations of South Bay, Livingston Island; an island forming part of the South Shetland archipelago (Antarctica)



The plankton collected and exposed to the natural full spectrum of solar radiation—including visible and ultraviolet light—did not increase in abundance, as measured by changes in chlorophyll concentration, which remained within the usual range of values observed in the Bay. However, when UVB radiation was eliminated with special filters (blue line), the abundance of plankton augmented (in this assay, by over 15 times in just 6 days). These experiments were carried out at the Spanish Antarctic Base Juan Carlos I as part of the work of the ICEPOS Spanish Antarctic Project, led by Carlos M. Duarte.

Source: Data provided by M. Llabrés and S. Agustí.

polar macroalgae populations, including the inhibition of photosynthesis and damage to DNA (see, for example, Bischof, Hanelt and Wiencke 2002). Nevertheless, they are far better equipped than phytoplankton to protect themselves from and adapt to an environment with higher UVB radiation. There is evidence that some macroalgae, despite suffering initial damage, manage to adapt efficiently to the new conditions by, for instance, increasing their production of solar filter substances such as mycosporine-like aminoacids (MAAs) (Bischof, Hanelt and Wiencke 2002). However, we still lack data quantifying the impact of increased UVB radiation on the biomass production of these polar organisms. Laboratory experiments have shown that ultraviolet radiation limits macroalgae growth and their capacity to increase their biomass, but no similar experiments have been conducted on polar populations under natural conditions. For this reason, it remains difficult to assess the impact of UV radiation on the growth and biomass production of this group of primary producers (Bischof, Hanelt and Wiencke 2002).

Non-photosynthetic organisms also experience the effects of ultraviolet light. Marine bacteria, which play an important role in the use and regeneration of

Photo 1.5: Adélie penguins (*Pygoscelis adeliae*). All living organisms inhabiting the polar regions will need to strengthen their defence systems to counter the negative effects of the higher ultraviolet radiation caused by ozone layer depletion.

organic matter processes, have been shown to suffer mortality in Antarctica when subjected to UVB radiation (Helbling et al. 1995). Nor are the deleterious effects of UV radiation confined to microorganisms: higher organisms inhabiting the polar oceans also suffer from UV radiation. Vertebrates and invertebrates like fish and crustaceans that in adulthood are well equipped to avoid and resist the damaging effects of UV light are nevertheless extremely sensitive to it during their egg and larval stages. Several studies have confirmed this sensitivity of fish and crustacean eggs and larvae in both Antarctica and the Arctic Ocean. In the waters north of the Arctic Circle, which are very productive and rich in fish species, the presence of CPDs has been detected in Norwegian and Canadian cod eggs and larvae (Browman and Vetter 2002). Experiments have also shown the capacity of UVB rays to induce significant mortality in Arctic cod eggs and larvae, with all eggs dying after four days' exposure to natural UVB radiation levels in northern Norwegian waters (latitude 70° north), and all larvae dying after six days of exposure. In experiments in which UVB radiation was filtered out from the natural solar radiation, there was no increase in the natural mortality rate of either eggs or larvae (Browman and Vetter 2002). DNA damage measured by CPD detection has also been found in icefish eggs in Antarctica and in the larvae of other organisms such as krill (Malloy et al. 1997). The degree of damage sustained by the eggs of these species is correlated with the incident UVB radiation (Malloy et al. 1997). Although the level of stress induced in krill by this exposure is not known, the increase in UVB radiation has been identified as a possible causal factor in the reduction of the yearly recruitment of new individuals to fish and plankton populations in Antarctica (Malloy et al. 1997). In other words, polar productivity is threatened not only by a reduction in the production of planktonic microalgae, but also by the direct effects of UV radiation on consumers at different trophic levels in the ocean. The impact of increased UV radiation on the polar oceans in the current context of global warming will give it a dominant role in the control of biological production, organism stress and the overall dynamics of polar ecosystems.

ACKNOWLEDGEMENTS

This chapter benefited from discussions to plan the Arctic Tipping Points project, funded by the European Commission.

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2. ARE DECLINING ANTARCTIC KRILL STOCKS A RESULT OF GLOBAL WARMING OR OF THE DECIMATION OF THE WHALES?

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AFTER THE NEAR EXTINCTION of the stocks of great whales around Antarctica by the mid-1960s, krill biomass was expected to increase because of decreasing predation pressure. However, the opposite has apparently happened: krill stocks have declined by about 80% over the past three decades, accompanied by a concomitant increase in salp biomass. One explanation for the decline is that a stretch of sea ice off the tip of the Antarctic Peninsula, believed to be crucial to krill recruitment, has retreated as a result of global warming. If true, then the decline would have happened anyway and, if whale populations had not been exploited, they would now be undergoing severe starvation.

I propose an alternative hypothesis based on evolutionary ecology. In this view the exceptional "food chain of the giants" was maintained thanks to environmental conditioning by the giants, whereby the limiting element iron was recycled in the surface layer for longer by the feeding activity of the whales than in their absence. Since the whales were eating protein but accumulating lipids, they were sequestering energy and could well have been recycling essential elements, specifically iron, back to the ecosystem for phytoplankton to fix more energy. Such a "manuring mechanism" by the giants would have increased the spatial extent of the productive region. In their absence, productivity based on recycled iron has gone down, the productive area has shrunk and salps have moved in. The current trend urgently requires action if we wish to ensure the recovery of Antarctic whale populations from the brink of extinction where they are still hovering.

The iron recycling hypothesis is presented in this essay and can be tested in large-scale, long-term iron fertilisation experiments in the south-western Atlantic where most of the krill population was formerly located. Apart from

◀ **Photo 2.1: Humpback whale (*Megaptera novaeangliae*)**. These cetaceans, avid consumers of krill, migrate thousands of kilometres from their breeding grounds in the tropical seas to the waters of Antarctica where they feed during the southern summer.

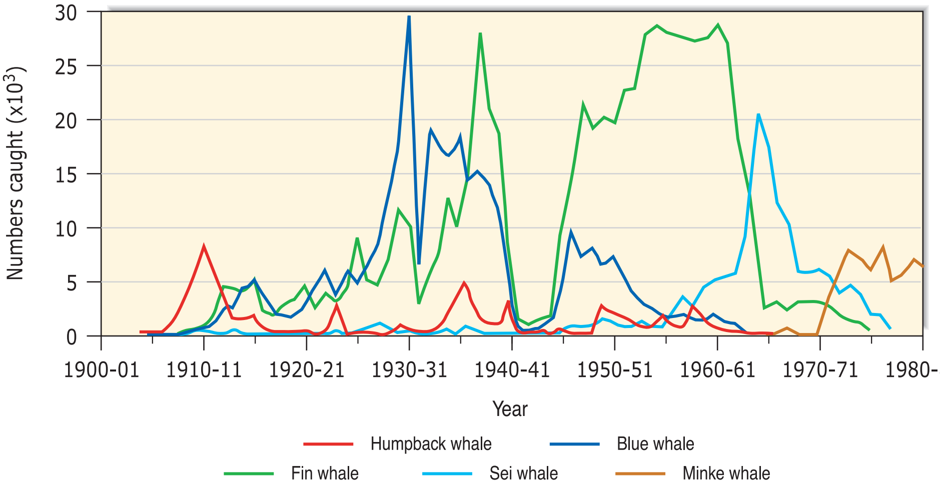
furthering our understanding of pelagic ecosystem functioning, an added benefit of these experiments would be to test the feasibility of larger-scale iron fertilisation to sequester significant quantities of atmospheric CO_2.

2.1. INTRODUCTION

In the 1920s, at the height of the Antarctic "whale rush", when 20,000 great whales were being converted every year into soap, candles and dog food, some far-sighted British scientists and policy makers realised that, without proper management, the bonanza would soon end in disaster (Hardy 1967). History proved them right, and the whale populations were depleted almost to extinction within a few decades. By the end of the 1930s, about 300,000 Antarctic blue whales had been killed (figure 2.1), and the population was further reduced to about 360 individuals by the time the moratorium on whaling was agreed upon in 1964. In 1996, their population size was estimated at 1,700, and it is reported to be increasing (Branch et al. 2004). However, future prospects for the recovery of the Antarctic blue whale—the largest animal that has ever inhabited our planet—are not that bright.

Antarctic blue whales feed on a single species of pelagic crustacean, the Antarctic krill (*Euphausia superba*), and the annual food requirements of the

Figure 2.1: Whale catches in Southern Ocean waters from 1904 to 1981



Including data from land stations, moored factory ships and pelagic catches, though the numbers only represent whales landed.

Source: Laws 1977; Knox 1994.

Photo 2.2: Krill (*Euphasia superba*). This crustacean is among the most abundant marine animals and forms the base of the food chain in the Southern Ocean.

intact whale stock has been estimated at 190 million tonnes (Laws 1977). The magnitude of this figure can only be comprehended by comparing it with others in the same range: the biomass of the blue whale stock prior to whaling was about 40 million tonnes, which is about as much as the biomass of one billion humans, i.e., one-sixth of the current human population. Further, the annual global fish catch since the 1970s is equivalent to less than half the biomass of Antarctic krill that was annually eaten by the whales prior to whaling, and in less than 1% of their distribution area. But while the fish harvest has resulted in serious global depletion of stocks, the krill catch by whales was evidently sustainable. Clearly, the "food chain of the giants" (diatoms-krill-whales) was highly efficient; its resilience demonstrated by survival through past climate cycles. So how was the food supply of the whales maintained?

The greatest advance in understanding of the factors that control ocean productivity in recent decades has been proof of the limiting role of iron. What used to be known as the Antarctic Paradox—low productivity in a sea of nitrate—was later recognised as characteristic for the equatorial and sub-Arctic Pacific as well and termed the high nutrient, low-chlorophyll

(HNLC) condition. Evidence for iron limitation of phytoplankton growth rates in all three regions of the world ocean, otherwise widely differing in their physical, chemical and biological properties, has now resolved the issue. To my mind, incorporating this new knowledge into the current conceptual framework of Southern Ocean pelagic ecosystem structure and functioning is tantamount to a paradigm shift. In the following sections, I briefly outline the history of the concept of iron limitation of productivity in the Southern Ocean before proceeding to the real Antarctic paradox—the presence of remarkably large animal stocks in a moderately productive stretch of ocean.

2.2. IRON LIMITATION OF PRODUCTIVITY

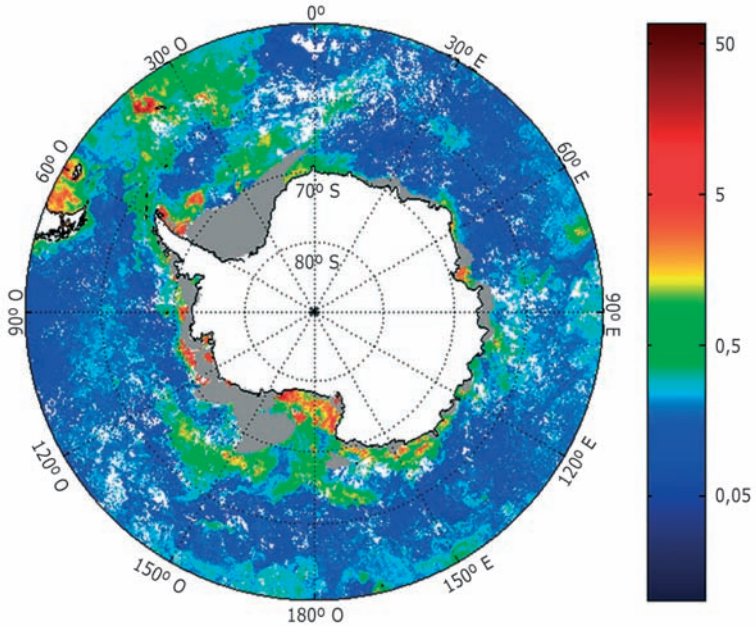
T. J. Hart, one of the scientists who participated in the HMS *Discovery* cruises and worked up the phytoplankton samples, was struck by the high phytoplankton biomass in the waters between South Georgia and the Antarctic Peninsula as compared to other, equally nutrient-rich water masses elsewhere around Antarctica. He observed that productivity was higher in the proximity of land masses when compared to the open ocean and speculated that trace elements such as iron and manganese washed off from the land and sediments could be one of the factors responsible (Hart 1942). At that time, trace metals could not be accurately measured because of contamination problems, so their possible role remained in the realm of speculation. Indeed, it was not until the late 1980s that the first reliable estimates of iron concentrations in sea water were made by the group headed by John Martin. They found over ten times higher iron concentrations in near-shore waters compared to the open ocean (Martin 1990). Also, their low values were much lower than previous estimates.

Martin and his co-workers also added iron to natural sea water in bottles treated with ultra-clean techniques and showed a strong growth response by phytoplankton in comparison to control bottles. Such experiments had been carried out before, but growth had occurred in all bottles and was attributed to a mysterious “bottle effect”. Martin attributed the lack of an effect in earlier experiments to contamination of the control bottles (in the human environment, iron is everywhere), so the real achievement of his group was to demonstrate the lack of an effect in the controls. This was achieved by employing painstakingly decontaminated, ultra-clean sampling gear, as well as bottles and reagents, and was the first real evidence that trace quantities of the essential element iron were needed to stimulate phytoplankton productivity. However, this was insufficient proof that the nutrient-rich waters surrounding Antarctica were poor in phytoplankton because of iron limitation. Light limitation due to deep mixing and heavy grazing pressure by large zooplankton stocks were the alternative explanations for the "Antarctic Paradox" of low productivity despite high nutrient concentrations. The role of these factors, particularly the effect of grazing, could only be tested in situ.

Since the mid-nineties, a total of nine open-ocean iron fertilisation experiments carried out in land-remote north and equatorial Pacific as well as Southern Ocean waters have demonstrated unambiguously that the supply of iron limits phytoplankton growth in these nutrient-rich waters (Boyd et al. 2007). Another of their conclusions was that neither poor light availability due to deep mixed layers nor heavy grazing pressure exerted by small and medium-sized zooplankton hindered the development of diatom blooms. Whereas the biogeochemical significance of these experiments in the framework of climate research is acknowledged, their implications for our understanding of how pelagic ecosystems, particularly their higher trophic levels, deal with iron limitation or its alleviation has not yet been explored. In particular, the higher productivity around the continent and islands evident from satellite images (map 2.1) can now be attributed, with greater confidence than before, to the supply of iron from land masses, including runoff and contact with sediments.

It follows that iron input from upwelling deep water along the Antarctic Divergence is comparatively minor, as can be clearly seen from satellite images of chlorophyll seasonality in the Southern Ocean (map 2.1). Indeed, the southern branch of the Antarctic Circumpolar Current (ACC), which receives the northward moving, upwelling deep water, reflected in its high silicic acid concentrations, is evidently the most barren in the entire Southern Ocean. In striking contrast, productivity along the convergent Antarctic Polar Front (APF), characterised by downwelling and mixing of Antarctic Zone water with warmer water from the northern ACC, tends to be conspicuously higher. However, higher productivity along the APF is not a universal feature, but is restricted to stretches south of the three adjoining continents, which strongly suggests local input of iron, most likely due to settling out of dust mediated by rainfall. As a result of iron limitation, the bulk of the nitrate and phosphate nutrients upwelling along the southern boundary of the ACC and subsequently circulating within it are returned

Map 2.1: Chlorophyll distribution in the Southern Ocean



Composite satellite image of chlorophyll concentrations, a measure of productivity, in the Southern Ocean, recorded by the SEAWifS satellite. Our thanks to the SEAWifS project and the Distributed Archives Centre of the Goddard Space Flight Centre for the production and distribution of these data. Activities sponsored by the Mission to Planet Earth programme of the NASA. Thanks also go to B. Raymond and J. Schwarz for the creation of the map. Colour scale in mg of chlorophyll per m3

Source: Smetacek and Nicol. Reproduced by permission of Macmillan Publishers Ltd: *Nature,* vol. 437/15, September 2005, © 2005.

largely unused to the deep ocean as Antarctic Intermediate Water along the northern boundary of the ACC. In contrast, silicic acid is extracted and retained within the ACC and its underlying sediments. This discrepancy between Si on the one hand and N and P, hence also C, on the other, has been dealt with elsewhere (Smetacek et al. 2004). The point here is that the residence time of iron in the sea must be much shorter than that of all other biogenic elements including Si. However, the factors influencing the eventual fate of iron are still under study, so some educated speculation based on consideration of what is currently known, and can be considered fact, is warranted to guide future research.

The seaward extent of the gradients between the narrow productive margins and the barren open seas are determined by two independent factors: the rate of dilution with iron-limited waters and the efficiency of uptake and retention of iron by the biota in the surface layer. Inorganic iron compounds are highly insoluble in oxygenated, alkaline sea water (saturation values range from around 0.2 to 0.5 nanomoles per litre). However, iron is biochemically highly reactive and is bound by a variety of organic compounds called ligands; in some cases so tightly as to be inaccessible to bacteria. Interestingly, strong iron-binding compounds known as siderophores are deployed by our bodies in saliva and plasma to limit the growth of bacteria in our mouths and blood. The bacteria that do manage to invade are grazed by white blood corpuscles. So it is not only the oceans that are iron- and grazer-limited. Given the trace amounts of iron (around 2 nanomoles per litre) required to achieve phytoplankton growth to bloom status (over 2 mg of chlorophyll per m^3), one can envision highly complex, species-specific interaction between biota and their potential iron supply. We shall return to the ecological impact of iron later following a brief overview of the trophic structure of the ecosystem.

2.3. DIATOMS, EUPHAUSIIDS AND BLUE WHALES

2.3.1. Diatoms

Phytoplankton blooms occur when iron-replete, nutrient-rich waters experience adequate light levels, such as in spring or in upwelling regions of high and low latitudes respectively. These blooms are invariably dominated by diatoms belonging to comparatively few genera of which *Chaetoceros* and *Thalassiosira* are particularly widespread. Colonies of the flagellate genus *Phaeocystis* can also contribute substantially to bloom biomass in some regions. The spring phytoplankton blooms of the land-near Southern Ocean are not exceptional in either composition or behaviour compared to those of other regions. Mass sinking in their aftermath is commonly observed, however, and this is not triggered, as in other regions, by macronutrient exhaustion. It is therefore logical to assume that the decline phase in Antarctic waters is triggered by iron exhaustion, although this has yet to be proven. The diatom species typical of iron-rich coastal regions differ from those of ice-free, land-remote Antarctic Circumpolar Current (ACC) species, which tend to be large, heavily silicified or equipped with long, barbed spines that appear to have evolved as deterrents against grazing by smaller ingestors such as protists and smaller copepods (Smetacek, Assmy and Henjes 2004).

Photo 2.3: Krill feeding on ice algae from the undersurface of sea ice

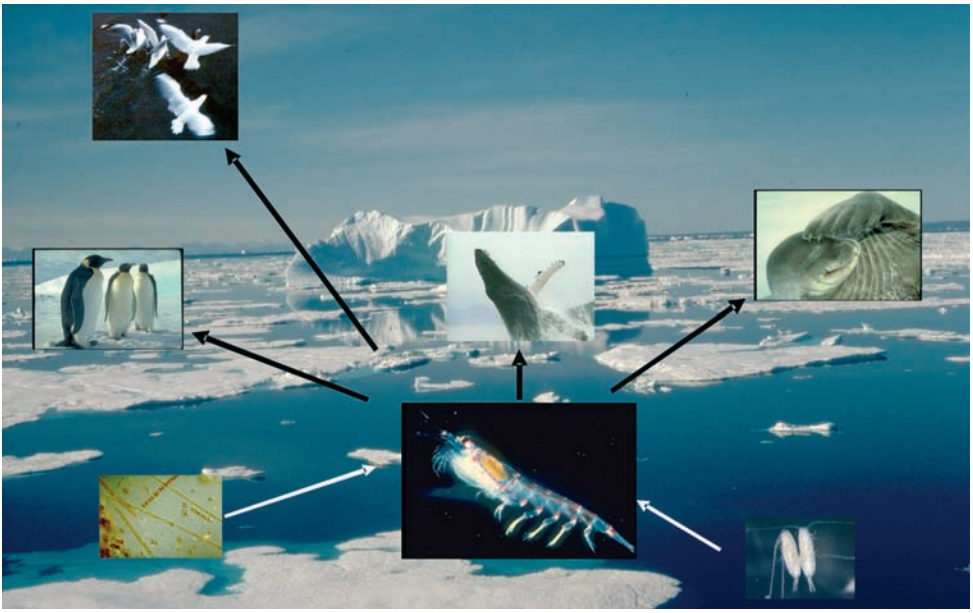
In ice-covered regions, melting of the ice cover is a precondition for bloom development. However, blooms only occur in the presence of sufficient iron, which explains their absence along the retreating ice edge around most of Antarctica. The sea ice itself is also colonised by ice algae, which can reach high concentrations, albeit in narrow layers. Their distribution is highly patchy across scales of tens to hundreds of metres. Hence, although eye-catching, their contribution to water column productivity is relatively minor. Nevertheless, the sea-ice cover provides a source of concentrated food to zooplankton, like copepods, amphipods and krill, that are capable of feeding on them by scraping the ice. In the Antarctic, krill clearly dominates the zooplankton community adapted to life on the underside of sea ice (photo 2.3). However, there are marked regional differences. Thus, although a systematic comparison has not yet been made, it appears that krill stocks in the Weddell Sea, particularly along its northwestern boundary, are much larger than in the Ross Sea. This might be the reason why blooms of *Phaeocystis*, which are easily eaten by euphausiids as compared to copepods, are regular and extensive occurrences along the Ross Sea ice edge, but not that of the Weddell Sea (Smetacek, Assmy and Henjes 2004).

2.3.2. Antarctic krill

Krill belong to the euphausiids, a group of zooplanktonic crustaceans that occupy the size class above the copepods and range in size from 1 to 6 cm. Although not related to them, they resemble the more familiar shrimps in body shape, because their mode of fleeing predators is the same: rapid flips of the strong tail muscles. The diet of the different species varies from filtering the water for the indiscriminate collection of unicellular plankton down to about 10 µm size to capturing motile prey such as copepods. The distribution patterns of the different species mirror oceanographic provinces characterised by temperature. Krill occupy the penultimate temperature range and tend to be concentrated, like euphausiids elsewhere, along the shelf break. The slightly smaller *Euphausia crystallorophias* occupies the coldest strip of water along the deep continental shelves bordered by the Antarctic ice cap.

Krill differ from other euphausiids in their greater size (up to 6 cm), longevity (over 6 years) and flexibility in behaviour: they are equally adept at surviving in the open water column as they are in the rugged undersurface of pack ice. They also feed on the entire range of food accessible to euphausiids in general—from filter-feeding on small-celled plankton to capturing larger copepods (figure 2.2). Another feature of krill feeding behaviour that

Figure 2.2: Krill, its major food (diatoms and copepods) and predators (birds, seals and whales) against the backdrop of its preferred habitat



they share with many other zooplankton taxa, including copepods, is what from our perspective can only be labelled as gluttony: the tendency to ingest far more food than can possibly be digested. This "superfluous feeding" behaviour of krill (Clarke et al. 1988) is illustrated by the individual depicted in photo 2.4. It has collected a large amount of food in its feeding basket which it proceeds to ingest, egesting a continuous faecal string that extends from its tail-end, makes a loop not seen in the photograph and enters the food bolus of the same individual. The adaptive significance of voracity for pelagic copepods has been attributed to environmental "gardening": adults convert a greater proportion of the diatom bloom into faeces that are subsequently recycled by the microbial network and made available to larval stages (Smetacek 1985). In the absence of this retention behaviour (Peinert et al. 1989), a greater proportion of the diatom biomass would sink out, and impoverishment of the surface layer would be more severe, resulting in lower recruitment of the grazers. In the case of krill, an analogous explanation would be the environmental conditioning of the entire habitat, as expanded upon below.

Unlike related species of euphausiids, krill have not been observed to lay down lipid depots in winter in the form of wax esters. Their fat reserves are

Photo 2.4: Two individuals of krill in an aquarium feeding on a dense culture of aggregated ice-algal diatoms. Their voracity is reflected in the size of the food bolus and the continuity of the ingested food and faeces emanating from the tail end of the animal in the foreground.

in the form of readily accessible triglycerides that do not seem to be concentrated in special depots evolved for the purpose (lipid sacs). Nevertheless, these lipids can constitute a significant percentage of body weight (Hagen, Van Vleet and Kattner 1996) in the same proportion as wax esters in species with specialised depots. Krill can also starve for over a year and shrink in body size, presumably after lipid reserves have been used up. The point is that krill are active throughout the year and do not undergo any form of dormancy, which is surprising given the strong seasonality undergone by the winter sea-ice covered environment they occupy.

If krill are starved together in aquaria, they will capture and eat their neighbours. This common observation tends to be downplayed as an artefact of captivity. How widespread cannibalism is in the wild is not known, but it has certainly been observed (Hamner and Hamner 2000). To my mind, it appears unlikely that the complex behaviour necessary for the tasks involved—decision-making, capturing, killing, dismembering and eating one's neighbour—can be learned de novo in the aquarium. That adult krill prey on their larvae is not disputed. Indeed this behaviour is invoked to explain the segregation of adult and juvenile populations. Cannibalism is of interest when considering its ecological and evolutionary implications, as it will enable self-regulation of population size to the food supply, particularly under the ice cover, and select for those individuals practising it. In open water, on the other hand, krill live in tight, fish-like schools that protect individuals against attacking predators (Hamner and Hamner 2000). This safety-in-numbers response implies that individual fitness increases with the size of the population in open water, but not necessarily under the ice, where individual krill seek safety within the recesses of the ice cover (personal observation). Krill aggregations under the ice can form schools and escape in the open water. It is tempting to suggest that environment-switching behaviour patterns evolved by krill enable it to optimally gear population size to the food supply in the sea-ice zone around Antarctica. The properties of krill indicate that it has evolved as a space holder, capable of channelling a substantial proportion of available resources into population biomass.

Unlike salps, which reproduce by budding new individuals on a colony stalk and hence have biomass doubling rates of hours to days, depending on temperature, krill have evolved life cycles in which growth from egg to adult takes well over a year. Krill recruitment is dependent on a combination of adequate food supply and protection from predators in the sea-ice habitat. The gonads of adult krill disappear in winter and only develop when sufficient food is available. Eggs are laid off the continental slope (above 1,000 m depth) where they sink to around 1,000 m depth before hatching. This strategy reduces mortality by predators that live in the surface layer. Larval development occurs on the way up without feeding. First-feeding larvae require high food concentrations and cannot arrest development, i.e., they are reported to starve to death, unlike adults. Larvae are believed to survive best along the melting ice edge, which is rich in ice biota but where they also find shelter from predators under ice floes. However, larvae also occur in open water away from sea ice, so its presence is not obligatory.

In sum, the biology of Antarctic krill (*Euphausia superba*) is unique in many ways: krill exploit an exceptionally broad range of food resources: nano- and microplankton, particularly diatoms, but also zooplankton, particularly copepods. And captive krill, as stated, are even cannibalistic. Krill feed prodigiously when food is plentiful, but can starve for many months. They do not hibernate, but can store substantial lipid reserves and also shrink in size when starved. Krill inhabit sea ice or the open ocean equally well, as dispersed individuals or in tight schools that can swim long distances (up to 30 km/day), enabling them to adequately exploit a patchy food supply. Their population size is much larger than that of any other euphausiid: a century ago, their biomass will have been substantially higher than the current global human biomass (about 250 million tonnes). So krill occupy a broader niche than either zooplankton or planktivorous fish.

2.3.3. Blue whales

Blue whales can weigh as much as 150 tonnes and are the largest animals that ever inhabited the earth. It bears mention that they feed almost exclusively on euphausiids throughout their range. Regional populations occur in all the oceans, but the Antarctic blue whale was the largest, both in terms of individual and population size, prior to the invention of harpoons that exploded inside the animals thus preventing cadavers from sinking. Life cycle stages in blue whales are remarkably short in comparison to their large size—in the same range as cattle and about three times shorter than elephants (and humans). Scientists of the *Discovery* era estimated that adult size and sexual maturity were attained about three years after birth and that life span was about 25 years (Hardy 1967). However, the latter figure is probably a guess,

Photo 2.5: Blue whale (*Balaenoptera musculus*). This cetacean is the largest animals ever to have lived on the planet and a major consumer of krill.

whereas the former was derived from dead whales examined in a whaling station in South Africa (Hardy 1967). Suckling a calf that doubles in size in a single season will require a Herculean effort on the part of the mother, as she must eat more than twice as much as non-suckling whales. Since growing individuals are most susceptible to food shortages, recruitment will depend on adult mortality, which, given the lack of predators, will be in old age. Further indications that recruitment was tightly geared to prey availability, i.e., that population size was located at the upper end of the system carrying capacity, are provided, firstly, by the absence of territorial behaviour, implying that suckling females will be competing with other non-suckling individuals, and, secondly, by the larger size of females compared to males, implying that feeding efficiency increases with size.

Of course, blue whales would have competed with other baleen whales, particularly fin whales, which are significantly smaller, at 50-80 tonnes, but have the same muscular, streamlined body shape. However, they feed on a broader range of prey items, including amphipods and fish. The Antarctic population, which was considerably larger than that of the blue whale, was located further to the north, albeit with considerable overlap. Given the paucity of other food sources, krill must have constituted a significant proportion of their diet. Smaller krill predators such as seals and penguins together constituted less than a tenth of the biomass of the baleen whales, so are not likely to have been serious food competitors.

2.4. DISTRIBUTION OF *EUPHASIA SUPERBA*

The first systematic survey of krill distribution in the Southern Ocean was carried out by the cruises of HMS *Discovery* in the 1920s and 1930s. By that time, large-scale whaling was in full swing and it came as no surprise that the region with the highest densities of krill coincided with that of their main predators, baleen whales. This region, known as the Antarctic Peninsula Plume (APP), is located in the southwest Atlantic and extends from the Antarctic Peninsula (62°S) to South Georgia (53°S) including the South Shetland and Orkney Islands. To the southeast it is bounded by the northern extent of summer sea ice in the Weddell Sea, and to the northeast approximately by the Antarctic Polar Front (APF) up to the latitude of South Georgia. To the east, it extends as far as the South Sandwich Island arc (30°W). The maximum area of the APP is approximately 2 million km^2.

Net catches with fine-meshed nets in this region also collected the highest concentrations of phytoplankton recorded anywhere in Antarctic waters. Clearly, high krill densities were supported by the high productivity of this region, but the reasons for the latter were not clear at the time. This region is a zone where different water masses, and hence the krill populations living in them, mix with one another. Eastward flowing waters from the ACC to the north, and from the northern rim of the Weddell Gyre to the south, mix with water from the Bransfield Strait in the middle along the Weddell-Scotia Confluence. All these water masses are rich in the macronutrients nitrate, phosphate and silicic acid, but the property they have in common, and in which they differ from their source waters outside this zone, is that they have had contact with land masses: the ACC water with the northwestern and the Weddell Sea water with the southeastern coasts, islands and shelves of the convoluted Antarctic Peninsula. Elsewhere around Antarctica, the northern distribution of *E. superba* coincides with the extent of winter sea ice, but the only region where this rule does not hold is the northern half of the APP, where large krill stocks and their accompanying predators extend all the way across a 1,500 km stretch of open ocean to South Georgia and beyond.

Clearly, the Peninsula with its many islands is the richest source of iron in Antarctica, but this does not explain the downstream extent of its effects. One would expect local diatom blooms in coastal waters that would quickly use up the iron and sink it down to the benthos, as usually happens in northern temperate and Arctic seas. Instead, high productivity is maintained across the widening APP from the Weddell-Scotia Confluence to the side of the triangle between South Georgia and the continent. The oceanward extent of this high productive water is remarkable and cannot be explained by physico-chemical processes of iron supply and transport alone. A more efficient recycling of iron needs to be invoked, such that a given atom of iron has a longer lifetime in the surface layer. This can be achieved if predators contribute to retaining iron by deploying larger amounts of iron-complexing compounds (ligands) than elsewhere. Such an iron-recycling ecosystem, in which blooms are grazed down by roving schools of mobile herbivores (krill) that release and maintain the iron inventory in the surface layer, would contrast with the iron-sinking ecosystem dominated by coastal diatoms with a boom-and-bust life cycle (Smetacek et. al. 2004). In the latter case, ungrazed diatom cells and phytodetritus sink out *en masse* in the aftermath of blooms. The iron triggering the bloom is lost with sinking particles weeks after being incorporated into algal biomass. The spatial extent of productive coastal waters is accordingly curtailed. A conceptual framework of the possible fitness advantages accruing to the key players in iron-retaining ecosystems as compared to iron-sinking ones needs to be developed. We will return to the question of self-maintaining control mechanisms amongst the biota after a quantitative assessment of the diatom-krill-whale food chain.

2.5. KRILL STOCK SIZE

Estimating the stock size of krill from direct measurements is a challenge, because it occurs across a broad range of distribution patterns; from tight schools with a very high density of individuals to a few individuals scattered over large areas. Its depth preferences are also not as predictable as those of smaller zooplankton, i.e., a clear diel cycle is not evident. Further, it can hide under ice cover over a significant portion of the year, and krill densities under summer sea ice cover are not known. Hence krill stock size estimated from net catches and acoustic surveys and extrapolated over the known krill areas range between 80 and 1,000 million tonnes (Everson et al. 1990; Nicol et al. 2000).

An alternative means of estimating krill biomass is by assessing that of their various predators, particularly the baleen whales for which reliable numbers exist because of whaling records. Nevertheless, these figures are conservative because they do not include harpooned whales that were not landed but subsequently died. According to industrial whaling records of the past century, about 2.7 million great whales were killed globally, of which the majority were taken in the Southern Ocean. Of these, 300,000 Antarctic blue whales were killed in the Atlantic sector during the 1920s and 30s (figure 2.1). This is too short a time for recruitment to have had a significant effect, so this figure represents a conservative estimate of the actual population size. Some 490,000 fin whales were killed but over a longer period. From figure 2.1, we can derive a minimum size of the krill-dependent whale population prior to whaling of 500,000 individuals. Assuming average weights of 100 and 70 tonnes for blue and fin whales respectively, and including also the krill-feeding humpback whale (of which 130,000 were killed), their combined biomass must have amounted to at least 50 million tonnes. A round figure has been deliberately chosen to emphasise the tentativeness of this number.

So what is the minimum food requirement of this whale biomass? The great whales are reported to have spent about three months in the Southern Ocean feeding and the rest of the year lolling about in warmer waters of lower latitudes. They arrived in their feeding grounds in lean shape and put on enough blubber in three months to tide them over the non-feeding nine months. Employing the textbook transfer efficiency between trophic levels of 10:1, these three whale species will have eaten 500 million tonnes of krill annually. Continuing this line of argument, the size of the krill stock providing this amount of food each year will have been at least three times this figure, i.e., 1.5 billion tonnes. As we shall see below, this stock size is too large to be accommodated by the Southern Ocean ecosystem based on textbook trophic level transfer efficiencies of 10:1. So the whales must have eaten less. But how much less?

Laws (1977) assumed that the great whales ate 3% of their body weight per day during these three months and estimated their food demand at 190 million tonnes of krill annually. This amount came to be known as the “krill surplus”, as it should have been available to other krill predators such as minke whales, seals and penguins after the demise of the whales. However, little evidence for this surplus, manifest in an explosion in numbers of smaller krill predators, has been reported, although it has been searched for. So the whales must have

Photo 2.6: Humpback whale in tropical waters during its breeding season. Like other large whales, the humpback only feeds during its three-month sojourn in Antarctic waters, where it fattens thanks to its huge intake of krill. It then lives off the stored fat as it journeys to its breeding grounds in warmer, more northern waters.

eaten even less, perhaps just 1-2 % of body weight in the three-month feeding season, as suggested by Mori and Butterworth (2006). However, the problem of the missing krill surplus cannot be dismissed by denying the whales their food, as a simple calculation shows.

There are no data to directly assess the food requirements of the great whales. Comparisons with wild land animals are inappropriate, because aquatic animals do not have to work against the gravitational field by carrying their weight around. So their energy demands, even for long migrations, will be much less, although they do have to overcome the viscosity of the medium. Comparison with domestic animals fed with high quality food and kept in confined spaces are more appropriate. Thus, pigs convert about 30% of the ingested food into biomass, the theoretical upper limit being about 50%. Assuming that the difference in weight of whales arriving and departing from the feeding grounds amounted to about 25-30% of body weight, which is a realistic range, their minimum food requirement just to reach this figure will have been 1% of body weight over a 100-day period. Since the blue and fin whales are muscular animals actively seeking and capturing their prey, their food conversion factor over an annual cycle can hardly have been in the same range as that of stall-fed pigs. Besides, pregnant and suckling females will have had to eat twice or more the amount eaten by males. So even 3% of body weight will not have sufficed in their case. The point of this exercise is that Laws (1977) figure of 190 million tonnes of krill annually consumed by predators, of which 150 were due to whales, is actually a conservative number. The biomass of the parent stock recruiting the former figure will have been about 600 million tonnes, given that krill require about two years from egg to egg.

The area covered by winter sea ice around Antarctica is 20 million km^2, so the average biomass of krill in its habitat will have been 30 g per m^2, equivalent to 3 g carbon/m^2. Adult krill weigh about 1 g, so there will have been an average of 30 krill per m^2. Again, employing the standard textbook transfer efficiency of 10:1 between trophic levels, the annual food demand of this krill population will have been 30 g carbon/m^2. If we convert this figure to the amount of nitrate taken up by phytoplankton eaten by krill, we arrive at 10 millimoles nitrate/m^3 in a 50 m deep surface layer. Nitrate concentrations in the Southern Ocean at the beginning of the growth season are 30 millimoles/m^3, so the above figure is feasible but implausible for a number of reasons: the krill population is concentrated in restricted areas; the food demand of other grazers has been ignored; and conservative estimates have been used all along. But we know that the bulk of the krill population (50%) was concentrated in the APP, which has a maximum area of 2 million km^2, including the area north of the winter sea-ice cover. Based on this area and the krill stock size of 600 million tonnes estimated above, the standing stock of krill in the APP will have been 150 g krill/m^2 or 15 g carbon/m^2—about twice the biomass of an average phytoplankton bloom. Clearly the textbook trophic transfer efficiencies of 10:1 cannot apply to the diatom-krill-whale food chain. The "food chain of the giants", in other words, must have been much more efficient.

So why has this problem not received the attention it deserves, given the basic calculations from which it has been derived? The main reason is a drifting apart of the scientific communities concerned with phytoplankton productivity, on the one hand, and population dynamics of fauna and their food base, krill, on the other. Previously, the plankton biology community had justified its research by reference to the need to quantify the food base of top predators, but in the past decades attention shifted to the role of the Southern Ocean in regulating atmospheric CO_2, within the framework of the international Joint Global Ocean Flux Study (JGOFS). Since most of the work was carried out in the open ocean, the role of top predators could be conveniently ignored. Meantime, scientists studying vertebrates are organised in the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) under the umbrella of SCAR (Scientific Committee on Antarctic Research). Since animal populations have shrunk so much, food limitation does not seem to be the problem any longer, except in special cases such as where access to the sea is blocked by icebergs.

An attempt to quantify the contribution of air-breathing predators to the ocean's CO_2 balance (Huntley et al. 1991) was scoffed at by those who used the size of current stocks to downplay the significance of air-breathing krill predators on air-sea exchange of CO_2. The arguments against a significant role of these predators are biased by what Pauly (1995) called the shifting baseline syndrome, according to which each generation of fisheries biologist takes as the baseline the stock size which prevailed at the time when the respective scientist began his or her career. As we have seen in the calculation above, stocks of air-breathing predators were orders of magnitude larger before their decimation by humans. Similarly, a study carried out by Priddle et al. (1998) in

Photo 2.7: Adélie penguins (*Pygoscelis adeliae*). Adélies feed almost exclusively on krill and are among the penguins most exposed to the impact of global warming.

which krill biomass was related to that of their predators, on the one hand, and their phytoplankton food supply on the other, found that the budgets balanced nicely on both sides. However, the predator stock size considered was only a fraction of that prevailing at the time of the great whales. So productivity must also have been much higher, in other words it must have gone down since the demise of the whales.

After the demise of the whales, krill biomass and that of their remaining predators—minke whales, seals and penguins—were expected to increase in the APP. Indeed there is some evidence that the other predators did respond initially, suggesting that they were food-limited. However, the effect lasted only until the 1970s and has since apparently reversed (Mori and Butterworth 2006). Contrary to the expectation that krill biomass would increase following decimation of their major predators, resulting in a "krill surplus", evidence is mounting that krill biomass has undergone a drastic decline over the past few decades.

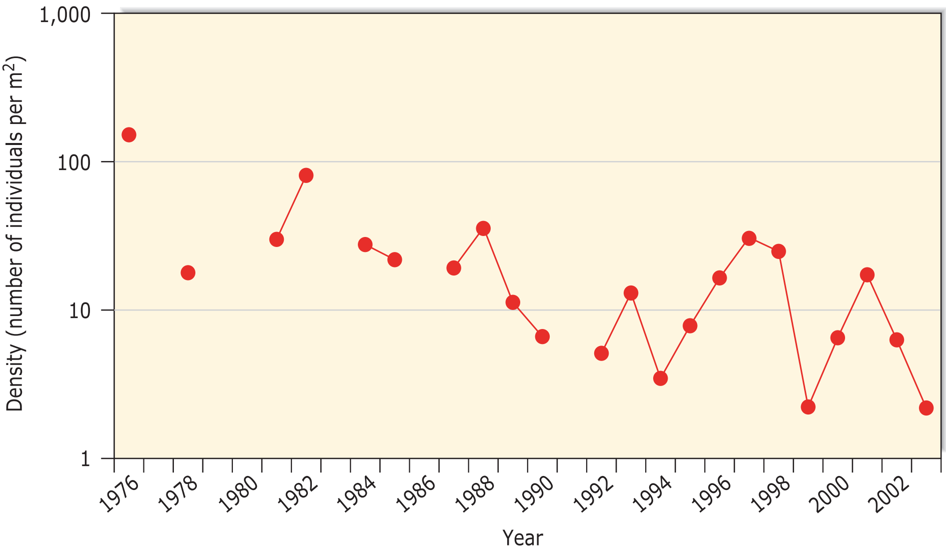
2.6. EVIDENCE FOR THE DECLINE OF KRILL BIOMASS

Evidence for the decline of krill biomass can be gathered from several sources, but the magnitude and reasons are under debate. Comparisons of visual observations of krill swarms from ship decks throughout the Southern Ocean, particularly between pre-World War II and current eras, clearly indicate that krill swarms are no longer sighted as often as they used to be (E. Pakhomov, personal communication). It has been suggested that the decline in sightings of surface krill is due to a change in krill behaviour: schooling krill now stay at greater depths than they used to. The reasons for this change in behaviour and how it could have been modified by natural selection over such a short interval is hard to explain. Decline in total stock size is a more parsimonious explanation.

It has been suggested that a krill surplus did not develop, because the krill continued to be eaten by growing numbers of other predators like minke whales, seals and penguins. This explanation is unlikely because their population biomasses are nowhere near those of the great whales. The biomass of one blue whale is equivalent to 250 crabeater seals or 30,000 Adélie penguins! Given that the food consumption per body mass of whales will be lower than that of seals and penguins, there would still be a huge discrepancy between the food demand of the great whales and that of all other krill predators combined. So it is highly unlikely that predation pressure alone could be responsible for ongoing krill decline. This also applies to the krill taken by current fisheries (Mori and Butterworth 2006).

The most compelling evidence for the decline (figure 2.3) has come from a recent statistical assessment of all scientific krill net catches carried out since the *Discovery* era, which indicates a drastic reduction in krill biomass of around 80% in the APP, above all in the last 30 years (Atkinson et al. 2004). The same study showed that, in contrast, the biomass of salps has increased in the same area. The salp range has been clearly moving southwards in the last 50 years particularly in the Indian and Pacific Sectors. Loeb et al (1997) have argued that salps prefer the permanently open waters of the ACC, whereas krill are more partial to the seasonally sea-ice covered zone further south. Since the sea-ice extent has retreated recently only in the APP region, the circumpolar southward increase in salp occurrence cannot be explained by sea-ice cover. Indeed, as demonstrated by the large krill populations around ice-free South Georgia, productivity expressed in phytoplankton biomass is a more likely determinant of krill vs. salp dominance than the presence or absence of seasonal sea ice. Open-ocean salps are reported to choke at phytoplankton concentrations typical for shelf waters.

Figure 2.3: Decline in krill stocks in the SW Atlantic from 1976 to 2003



Krill density based on data from 4,984 stations.

Source: Atkinson et al. 2004.

Since salps are more abundant in open-ocean, iron-limited areas than in the high-productive regions favoured by krill (Pakhomov et al. 2002), the spreading trend could well be due to a decline in productivity in the SW Atlantic.

A decline in productivity is indicated by a comparison between surface chlorophyll concentrations recorded by the satellite-mounted Coastal Zone Colour Scanner in the seventies and eighties and the SeaWiFS satellites during the past 10 years (Gregg and Conkright 2002). The only larger-scale region of the world ocean where chlorophyll concentrations have dropped 25% over this time period is the marginal ice zone surrounding Antarctica (but not the Arctic) in spring. In contrast, the Patagonian shelf plume has increased productivity by 50% concomitantly, which could be attributed to the ongoing retreat of the Patagonian glaciers and the resultant exposure of vast stretches of glacial flour (finely ground rock) to transport by river runoff or windborne dust.

During the glacials, glaciers were more extensive, sea levels were lower by as much as 100 m and the continents were drier, so the extensive, exposed Patagonian shelf will have contributed much of the iron-bearing dust which fertilised the more productive glacial Southern Ocean (Abelmann et al. 2006). So why Patagonian dust is not reaching the Antarctic Circumpolar Current today is a mystery that might find its explanation in wind patterns or in differences in transport of glacial flour, as compared to dried-out, former coastal sediments. It is worth pointing out that an analogous situation to today's prevailed at the start of the Holocene, when retreating ice-age glaciers exposed large areas covered with glacial flour to the wind and rainfall, and sea level rose reducing the dust supply from the continental shelf region. Dust-borne iron supply to the ocean and accordingly productivity also declined in this period, as indicated by microfossil proxies in sediment layers laid down in the transition from the last glacial maximum to the Holocene (Abelmann et al. 2006).

The glaciers on the Antarctic Peninsula have also retreated dramatically as a result of global warming, but because of the rugged terrain and absence of flatland not much dust is likely to be mobilised from here. Nevertheless, there should be more glacial flour transported by runoff to the coastal waters of the APP. The extent to which iron from this source can be utilised and subsequently recycled and transported out into the open ocean along the APP will need to be investigated. Iron can also be supplied by water coming into contact with sediments in the course of upwelling along the continental slope of the western Peninsula, which explains patches of higher productivity there. However, the mechanisms of iron supply to overlying water, but also replenishment of iron in the source sediments of the slope, the size of the sedimentary source and the rate of iron flux in relation to other nutrients would need to be assessed before the impact of this source can be quantified. In any case, as most of the APP overlies deep ocean, the area impacted by slope-supplied iron is relatively small. Other potential sources of iron that can fluctuate are hydrothermal vents, which need to be considered here because the APP overlies a tectonically active area. There is evidence of hydrothermal activity but currently no information on iron input. Summing up, it does not appear that a decline in productivity of the APP, if such a thing is true, can be attributed to an overall decrease in input of "new" iron to open waters.

An alternative explanation for the krill decline is more frequent recruitment failure during the past decades related to the retreating expanse of winter sea ice (Atkinson et al. 2004). Since years with more ice result in larger krill stocks, there must be a beneficial effect of sea ice on krill recruitment. However, sea ice in the Southern Ocean (in contrast to the Arctic) has only retreated in the region of the APP as a result of global warming, so this particular stretch would have to be crucial to krill recruitment (Smetacek and Nicol 2005). Since the seasonally retreating ice cover crosses the continental slope (the site of krill larval ascent) all around Antarctica, one might wonder why only some stretches are important nursery grounds. Possibly the congruence between iron supply from continental sources and sea-ice cover along the APP is the reason for the beneficial effect. Ice algal growth and subsequently that of blooms developing in iron-fertilised, melt-water stabilised layers at the marginal ice zone enabled the krill larvae to grow faster and hence recruit more biomass into the adult population. It has even been suggested, based on evidence gleaned from whaling records, that the ice edge in the APP has retreated significantly during the last century (De la Mare 1997). If sea-ice retreat is indeed the reason, then the decline in krill stocks would have happened anyway and, if whale populations had not been exploited or had since recovered, they would now be undergoing, or at least facing, severe starvation.

Investigations of krill occurrence and density under sea-ice cover indicate that distribution is highly patchy, as is also that of sea-ice algae. The greatest krill densities are found in association with sea-ice floes coloured brown with algal growth (photo 2.8). Krill are generally absent from barren, white sea ice (personal observations). The provenance of sea ice with differing algal concentrations could be related to the time of formation. Thus, the first layer of sea ice that forms over autumn water will incorporate the largest load of suspended particles, including not only algae and bacteria but also detritus. Since the water column under sea ice is remarkably transparent, the missing particles could only have sunk out or been incorporated into the growing ice matrix. Evidence from sediment trap catches (lack of an autumn peak in flux) and investigations of "first flush" floes support the latter fate. The layer of ice crystals (frazil ice) that forms on the surface layer when cold winds blow over the ocean, and prior to compaction into floes, acts as a "sponge" that "filters" particles out of the water column. As ice forms, brine is discharged which homogenises the water column vertically and replenishes the pore water within the surface ice matrix, which eventually compacts into floes. These first-flush floes subsequently get pushed on top of each other in pressure ridges, so that new floes form in the temporary stretches of open water formed as a result. Brine discharged during the freezing of these later floes will mix the water column deeper than the previous mixed layer, bringing up particle impoverished, sub-surface water. So the later in winter the floes form, the less particles, but also iron, they contain. Since first-flush floes are mixed with younger, hence barren ones forming over clear water,

Photo 2.8: An ice floe raised by surface waves shows the ice-algae layer on its undersurface, the ideal habitat for krill

the distribution of productive and barren floes in the ice cover will be highly patchy but accessible to exploitation by the swimming abilities of krill. So the size and mobility of krill enable it to make optimum use of the patchiness inherent to the sea-ice habitat.

One of the questions discussed at the time of the *Discovery* surveys was whether krill was an animal of the pack ice or the open, ice-free ocean. Marr's (1962) detailed monograph on the biology of krill, which was widely accepted, came down strongly against any role for sea ice. He ridiculed the accounts of whaling captains of krill observed on the underside of overturned ice floes. Marr's view was based on the results of a cruise which had entered the pack ice but failed to catch any krill in vertical net hauls. We now know from direct observations by divers and cameras that the krill assemble on the ice undersurface, so cannot be caught by nets pulled through the water column. Now that the importance of ice as a winter habitat for krill seems to be widely accepted, one needs to remember that half the krill habitat in the APP is permanently open water. Satellites indicate a great deal of meso-scale patchiness, due probably to hydrographical features in the APP. However, the density of krill stocks prevalent in the APP prior to whaling is difficult to imagine today. We only know that it must have been there since so many whales were dependent on it. So is the decline of krill in the aftermath of whaling pure coincidence, and would it now be causing the starvation of the whales had they not already been depleted? In the following section, I argue that the simple "food chain of the giants" (diatoms-krill-whales) was maintained precisely by the giants. The formerly massive krill stocks declined with the whales, leaving no krill surplus behind. And now the APP seems to be reverting to the status of a "normal" stretch of salp-dominated HNLC ocean.

2.7. ECOSYSTEM CONDITIONING BY THE "FOOD CHAIN OF THE GIANTS"

So how could the top predators enhance the population size of their prey? The answer would be by disrupting the "normal" course of events, i.e., the mechanisms and pathways along which pelagic ecosystems run in the absence of large whale densities. But first of all one needs to acquire a quantitative picture of the animal densities prevalent in this area prior to whaling. This can be achieved by reading the reports written by Hardy (1967) on board the *Discovery* cruises at the height of the whaling. According to his diaries, great whales, generally in groups, were encountered more or less daily in the Antarctic Circumpolar Current south of Africa. In striking contrast, I have seen only 10-20 minke whales in this region, but less than a handful of great whales, in the course of six two-month research cruises at different seasons over the past 15 years on board RV *Polarstern*.

One of these cruises was spent in the ice edge zone of the Scotia Sea (APP), where we saw no large whales but instead observed a krill swarm move into and graze down, in the course of several hours, a diatom bloom we were studying during a long-term station. The krill densities were so large that they interfered with light measurements and left behind ammonia concentrations never before recorded from the surface ACC (Treguer and Jacques 1992). The diatom species grazed down by the krill, a typical ice-edge flora, were replaced by cryptophytes. Although difficult to quantify, the impact of the krill swarm on the entire pelagic biota was immense. The analogy with a locust swarm or a herd of elephants arose when the data became available, shortly after the krill swarm left. Surely such a swarm must also influence the iron budget, whether by exporting it out of the system in sinking faeces or by stepping up the rate of recycling. The krill swarm mentioned above left behind plenty of faecal matter in the water column, but their patterns of vertical distribution did not suggest export as the main fate (González 1992). The impression gained was that the bulk was recycled in the surface layer.

It would be interesting to follow the fate of iron in phytoplankton communities grazed by krill. The point is that such krill swarms must have been much more plentiful in the past. Indeed, their densities would have resulted in regular "conditioning" of the environment. Thus, the krill grazing pressure we observed led to transfer of essential nutrients from the classic, ice-edge diatom bloom (dominated by small pennates) to a flagellate bloom which most likely developed because the krill had removed their protistan grazers such as ciliates together with the diatoms. The effect would enhance recycling and prolong the lifetime of individual iron atoms in the surface layer.

The krill swarm was followed by petrels, but mammals were conspicuous by their absence. Such krill swarms will have been the target of the abundant great whales prior to whaling. Since the whales were eating protein but accumulating lipids, they were sequestering energy and could well have been recycling essential elements, in particular iron, back to the ecosystem for phytoplankton to fix more energy. The faeces of marine birds and mammals tend to be fluid (photo 2.9) and, being warm, rise to the surface before being dispersed (I have seen this happening). Taking the terrestrial analogy of savannahs and steppes, where the growth of grasses favoured by herbivorous ungulates as food is also promoted by them, I have come to speculate that whale feeding behaviour and their waste products conditioned the surface layer in a way that promoted the abundance of krill. Dung beetles and earthworms mediate between ungulate faeces and grasses in the soil, so it is possible that some zooplankton such as *Oithona* or the harpacticoid *Microsetella* play a similar role in the pelagial. Such a "manuring mechanism" by the giants would have increased the spatial extent of the productive region. In their absence, recycled productivity has gone down, the productive area has shrunk and salps have moved in.

An additional mechanism by which swimming animals, including zooplankton larger than a centimetre, can influence their environment is by turbulent mixing of the deep water column below the depth of wind mixing. This surprising effect, first broached on the basis of theoretical considerations by

Photo 2.9: A minke whale that had been feeding on krill, photographed in the Antarctic Peninsula Plume while defecating in surface water. Note the fluid nature of the faeces.

Source: Smetacek and Nicol 2005. Our thanks to Captain J. Borkowski III of RV *Nathaniel Palmer* for his kind permission to reprint this photo.

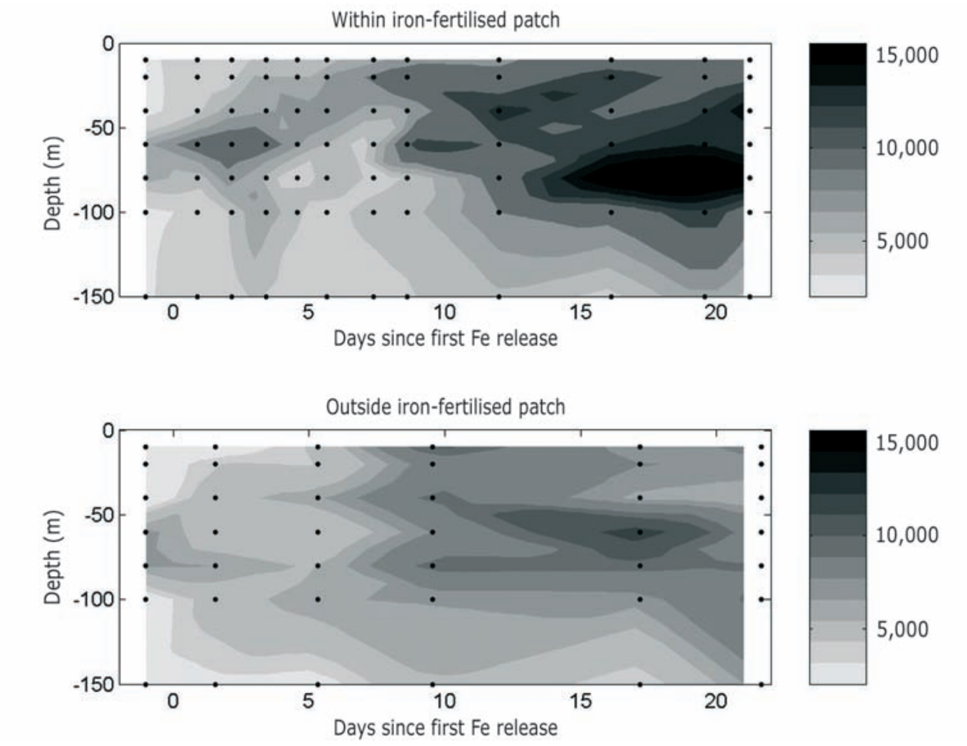
Huntley and Zhou (2004) and now confirmed by field measurements of vertically migrating North Pacific krill (*Euphausia pacifica*), has the potential to enhance nutrient input through the pycnocline to the surface layer (Kunze et al. 2006). Given the high densities of krill and whales that prevailed in the APP 100 years ago, the effect must have been quite significant. It has even been suggested that the global depletion of fish and whale stocks could have a measurable impact on the intensity of the ocean's conveyor belt and hence climate, because of declining turbulent mixing in the deep ocean (Kerr 2006). The impact of this "stirring" effect needs to be investigated in different regions, but it is a good example of how large animals can modify their environment by conditioning it.

It should be noted that the beneficial effects of environmental conditioning, whether by manuring or stirring or both, increase with the increasing density of the whale population. A limit is imposed by the carrying capacity of the system, i.e., when competition for resources within the population constrains recruitment. However, in the context of environmental conditioning, carrying capacity is linked with population size in a dynamic way. It is likely that whale populations in the past glacials were larger and their connections to diatoms and krill tighter, because the seasonal sea-ice zone was more extensive and also more productive due to enhanced dust input (Abelmann et al. 2006). Further, the total area of the habitat will have been larger, due to equatorward displacement of the sea ice edge. It is possible that the absence in the ACC of planktivorous swarm-building small fish like sardines is due to the past predation pressure of baleen whales. The low temperatures apparently render fish more vulnerable to attack by warm-blooded predators, unlike invertebrates such as cephalopods and krill that seem to retain their agility over a broader temperature range.

The question arising in this connection is: which type or stage of pelagic system would sequester more CO_2 per iron atom from the atmosphere? The boom-and-bust system of a diatom bloom which exports large amounts of new biomass including iron to depth early in the growth season (Smetacek et al. 2004), or the recycling system where the bloom is grazed down and prevented from sinking out? The waste products of recycling would subsequently be returned to a system altered by the feeding activity of the herbivores. The latter system would also suffer losses to sinking particles albeit over a longer period, during which energy in the form of lipids, channelled off the spinning wheel of iron-based regenerated production, could accumulate in herbivores and predators over annual cycles.

It should be pointed out that copepod stock sizes in the ACC may be in the same range as the biomasses of phytoplankton blooms (Henjes et al. 2007). Such a large zooplankton population would need to eat three times the biomass in the surrounding water to double its own, assuming a 30% ecological efficiency. So the grazing impact, even just of copepods, is large and could have been even larger when the krill were still around (figure 2.4). So the above question boils down to: does the Fe:C ratio of sinking particles rise or fall along the gradient from fresh diatom cells to reworked faeces? Indeed, does iron sink out as insoluble rust particles in the course of regenerated production or is it always bound to some organic molecule whether in dissolved or particulate form? The fertilisation experiments indicate otherwise, because the colloidal ferric hydroxide precipitate that must have formed as the acidified ferrous sulphate solution released from the ship mixed with alkaline sea water, was more or less quantitatively utilised by

Figure 2.4: Accumulation of broken and empty diatom siliceous shells (frustules per litre) as an indicator of copepod grazing within and outside an iron-fertilised patch, recorded during the EisenEx experiment



Source: Assmy et al. 2004. Data from P. Assmy, AWI.

diatoms. So, little iron was lost, although this form of input is definitely the most likely to result in sinking out before utilisation: precisely the fate predicted before the first experiments. Either diatoms can take up insoluble ferric hydroxide or it is made accessible in another form by some mechanisms involving ligands (iron-binding organic molecules) present in the water.

2.8. TESTING THE HYPOTHESIS

The hypothetical relationships dealt with above cannot be observed in field investigations carried out along transects and grids, and nor can they be studied in enclosure experiments. In situ iron fertilisation experiments have emerged in the last 10 years as a reliable method for testing biogeochemical and ecological hypotheses not accessible by other means. Larger-scale experiments than those above, carried out in the APP itself, would enable us to determine the current extent of food limitation of krill. Thus if an extensive bloom was induced by fertilisation, and a krill swarm present in the area responded to it by increasing grazing rates, individual weights and egg production rates, a case would be made for food limitation. Such a response was recently demonstrated for a copepod species (*Rhincalanus gigas*), which developed its gonads and laid unusually high numbers of eggs after stimulation by an iron-fertilised bloom (Jansen et al. 2006). The impact on salps could be derived as well: if their numbers declined in the bloom, then they would indeed be creatures of low-productive waters. If they grew in the bloom, then they would be competitors of the krill as some suggest. In either case, we would advance our knowledge and understanding of pelagic food webs.

An iron-fertilisation experiment carried out in the APP to extend the growth season by supplementing the iron supply to the regenerating, summer system would not only test the recycling hypothesis, with its prospects for boosting today's declining krill stocks, but also the iron hypothesis of John Martin (1990), with its CO_2 sequestering intention. Both hypotheses address fundamental questions of integrated Earth system science that are relevant to our understanding of the role of the marine biosphere in past and ongoing climate change. They would not only provide basic information on the structure and functioning of pelagic ecosystems, but would also help validate various proxies for palaeoproductivity and glacial CO_2 drawdown. Measuring the composition and magnitude of vertical flux (ungrazed phytoplankton vs. zooplankton faeces) would help us learn how to optimise the fertilisation technique so as to sequester as much carbon per unit iron as possible. It should be pointed out that if all the unused macronutrients in the HNLC ACC were taken up by phytoplankton and converted to biomass in the 60 m mixed surface layer, the amount of carbon dioxide drawn down from the atmosphere to compensate the resultant deficit would be approximately equivalent to the annual rate of accumulation of anthropogenic CO_2 in the atmosphere (approximately 3 gigatonnes). The frequency with which this amount could be taken up is not clear, but it is too much for humankind not to consider this option seriously. If krill and whales can profit from this fertilisation, so much the better. It would be the marine equivalent of ecosystem restoration and maintenance.

2.9. CONCLUSIONS

As pointed out above, the real paradox of the Antarctic seasonal sea-ice zone is, or rather, was, the concentration of large animal stocks, specifically krill and its air-breathing vertebrate predators, in a relatively small region, the Antarctic Peninsula Plume, characterised today by moderate productivity. Unfortunately, the "food chain of the giants" no longer exists, so it cannot be investigated and its structure and primary productivity patterns compared with regions like the Ross Sea to ascertain the mechanisms maintaining high animal biomass concentrations. The "rule of thumb" ecological transfer efficiencies of 10:1 between trophic levels very evidently did not apply here, implying that this "food chain of the giants" must have functioned differently, channelling energy to higher trophic levels with greater efficiency than food chains quantified elsewhere. However, as shown by Jackson et al. (2001) in an assessment of lower latitude coastal ecosystems, stocks of large marine animals prior to human exploitation must have been much larger than they have been since historical times. So perhaps the Antarctic paradox is merely due to the fact that, because of its inaccessibility, this ocean was the last marine ecosystem to be fully exploited by humans and in a period when the decimation could be documented systematically (Smetacek and Nicol 2005).

The reconstructed krill densities of the first third of the twentieth century are hard to believe in comparison to today. Clearly, krill stocks must have declined significantly. The sea-ice retreat along the Peninsula, due to global warming, is believed to have affected krill recruitment, because the sea ice in this region provides protection and food in the form of ice algae to ascending krill larvae. I have argued that the ongoing decline of krill stocks is a result of the collapse of the diatom-krill-whale food chain following the removal of the whales. Although the effect of sea-ice retreat due to global warming cannot be ignored as a cause of krill decline, the role of whales in maintaining high phytoplankton productivity and hence high krill biomass by virtue of iron recycling is likely to have been more significant. I base this conclusion on the following considerations:

1. The decline in whale stocks was not accompanied by a significant increase in the stock sizes of other smaller krill predators, implying that a krill surplus did not accumulate after the whales were removed.
2. The productivity of the area occupied by the "food chain of the giants" has apparently gone down, as indicated by a comparison with satellite images made in the 1970s (CZCS) with those of the 2000s (SeaWiFS).
3. The spread of salps in the same region is also an indicator of declining productivity.
4. The decline in productivity is unlikely to be due to a decline in input of "new" iron, but is more likely the result of a decline in recycled iron released by the feeding of the whales and krill.

The "iron recycling hypothesis" to explain declining krill stocks can be tested via a large-scale iron fertilisation experiment in the Scotia Sea. Apart from furthering our understanding of pelagic ecosystem functioning, an added benefit of such experiments would be to test the feasibility of larger-scale iron fertilisation to sequester significant quantities of atmospheric CO_2 and hence mitigate the effects of climate change, not only on polar but also global ecosystems. Antarctic sea ice is not threatened by a rapid retreat in the course of this century, as is happening with the Arctic ice pack. However, if atmospheric CO_2 concentrations are allowed to rise over the next century, there can be little doubt that the southern sea ice and its ice-dependent ecosystem will also be seriously affected.

ACKNOWLEDGEMENTS

This paper was completed during my stay as an Adjunct Scientist at the National Institute of Oceanography, Goa, India.

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3. THE IMPACT OF CLIMATE CHANGE ON ANTARCTIC MEGAFAUNA

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THE ANTARCTIC MEGAFAUNA takes in most of the air-breathing predator species: marine birds and mammals. These species are all long-lived and slow to reproduce and are therefore vulnerable to climate changes that increase the variability of their population growth rate. Most of them rank high in the marine food chains and feed on Antarctic krill, their staple food. Except for the cetaceans, which are fully aquatic, all other Antarctic megafaunal species depend on the terrestrial environment to reproduce. The impact of climate change on the megafauna is especially severe in some Antarctic regions and is expressed at several levels. It arises as a consequence of climatic and meteorological changes operating on different temporal scales—from years to decades—and is generally related to global phenomena such as the El Niño Southern Oscillation (ENSO). A number of Southern Ocean marine bird and mammal populations have shown cyclic alterations in their reproductive success, productivity and survival that are consistent with the environmental alterations associated with the ENSO. These take the form of a reduced sea-ice extent and higher air and water temperatures and cause a temporary modification in the structure of marine ecosystems. Their impacts on krill and other prey, together with the transformation they effect on the ice environment of Antarctica, have significant knock-on effects for marine birds and mammals. The reduction in available food and habitat during the crucial breeding and rearing season alters the distribution and abundance of pinniped species, along with that of penguins and other seabirds. Climate change will increase ecosystem fluctuation and only those species capable of adapting to a more variable environment can successfully survive climate change. For the remaining species, these environmental alterations bring changes in their distribution, abundance and certain aspects of their biology.

◀ **Photo 3.1: A group of king penguins (*Aptenodytes patagonicus*).** Penguins, the quintessential Antarctic birds, are severely affected by global warming and its effects on populations of krill, their main food source.

3.1. INTRODUCTION

The Antarctic megafauna consists of aquatic organisms, such as marine mammals and penguins, and other animals, like flying seabirds, that have adapted to life at sea. Most of them depend on terrestrial ecosystems to complete their life cycles. Some complete part of their life cycle on the ice, but others need ice-free surfaces to survive. Antarctica is a frozen desert of which only 4% approximately is free of ice during the summer months, when the coastal ice-free areas essential for their reproduction become available. However, all Antarctic megafauna depend on the ice to at least some extent, in order to rest, rear their young and find food. Ice shelves and sea ice not only provide a critical habitat, but ensure the food supply of most of these species, due to their dynamics and their influence on the oceanographic processes favouring primary production.

The Antarctic continent is covered in ice, extending over the terrestrial medium, including the frozen seabed, and the pelagic system, where it forms shelves. These shelves are dynamic, changing throughout the year in length, breadth, thickness and cohesion. Occasionally chunks break off and drift out to sea as icebergs (photo 3.2). Sea ice forms beyond the ice shelves when the

Photo 3.2: A drifting iceberg, showing the different types of ice formed at successive stages. Ice compression and mineral composition generate the diversity of ice colouration.

surface of the sea freezes due to the low temperatures of the Antarctic winter. Ice shelves and sea ice are both sensitive to small temperature changes, which is why the most important effects of global warming on Antarctic megafauna, mediated by higher atmospheric and ocean temperatures, have to do with the disruption of terrestrial and sea-ice dynamics and their thickness and expanse over time and space. Furthermore, greater freshwater influx into the ocean due to the accelerated melt of glaciers, icebergs and ice shelves is modifying the biodiversity and structure of marine ecosystems, of which megafaunal species are an essential component.

The effects of warming on the megafauna are multiple, but we can single out two main types: those relative to the loss or gain of critical habitat without which the megafauna cannot exist (e.g., the physical environment required for some marine birds and mammals to breed and rear their young); and those that modify food webs with direct repercussions on the food the megafauna consume. The diminishing extent and seasonal duration of the sea ice affects those species that most depend upon it to complete their reproductive cycle. Other, less ice-dependent species probably benefit from this reduction, so it is reasonable to expect alterations in food webs and species communities, as well as in their distribution and abundance. In many instances, the consequences of global warming stem from the interaction of many different factors, giving rise to distinct population responses among different species, which bring about changes in communities and ecosystems. These changes are expressed regionally and on differing time scales as a function of the local impact of warming, the climate cycles related thereto and the repercussions on each megafaunal species.

The impact of global warming on the megafauna coincides with other anthropogenic impacts, such as the expansion of marine fisheries and, to a lesser extent, the increase of tourism in certain areas of the Antarctic continent. While the impact of tourism is probably low for the moment, more intense fisheries in the Southern Ocean may disrupt the equilibrium of some marine ecosystems, with direct and indirect effects on the megafauna. To understand the full repercussions of man's actions, we must study their ecosystems impacts on a combined basis, starting with the regions most affected by global warming, i.e., where its effects are most readily detectable. It is these regions that are suffering the most far-reaching ecosystem changes, and the most severe impacts on their megafauna, above all those species sensitive to ice loss.

The impact of global warming on Antarctic megafauna is not as readily apparent as it is in the Arctic, where the accelerated loss of sea ice, especially during the summer, is jeopardising the reproductive success and survival of species like the polar bear (*Ursus maritimus*) (Derocher 2005). Other species affected, though to a lesser extent, are harp seals (*Pagophilus groenlandicus*) and hooded seals (*Cystophora cristata*) (Johnston et al. 2005), since both species are heavily reliant on ice shelves and sea ice for rearing their young. Nevertheless, one southern region where similar changes are now being detected is the Antarctic Peninsula.

The western Antarctic Peninsula is among the world regions that is warming up the fastest. The average annual temperature rises recorded at scientific bases during the last 50 years are up to 10 times greater than the equivalent figures for the planet as a whole (Vaughan et al. 2003). And in the last few decades, the ocean's surface temperature has risen by approximately 1°C, with increases sharpest in the winter months (Meredith and King 2005). Since the 1960s, the changes in atmospheric circulation known as the Southern Annular Mode (SAM) have contributed to increase the force of the westerly winds over this area (Marshall, Van Lipzig and King 2006). These impacts are irrefutable evidence of the connection between human activity and the destruction of large areas of ice shelf, among the best known being the Larsen Ice Shelf.

3.2. THE ANTARCTIC MARINE ECOSYSTEM AND THE IMPORTANCE OF KRILL FOR THE MEGAFAUNA

Antarctic ecosystems are conditioned by their strongly seasonal climate and the extreme temperatures of the long winter. Large changes in solar irradiation and the extent of the sea ice create very different conditions from winter to summer that are of direct importance to Antarctic organisms. The way species respond may depend on their levels of tolerance and adaptation to extreme temperatures (Peck, Webb and Bailey 2004). However, their distribution and abundance are mainly determined by the availability of food sources, and here the outcome is decided over the brief summer months, when conditions favour their development. This is the case of the marine plankton, the organisms at the base of the food chain, and for the rest of the organisms that depend on them to complete their reproductive cycles and survive the winter months with their scarce resources. For the plankton, the most productive areas of the Antarctic Ocean are the continental margins, where the terrestrial minerals carried and deposited by the seasonal ice melt favour the blooming of phytoplankton near the shoreline. Also, the ice melt helps to stabilise surface sea layers by facilitating the accumulation of seaweed biomass. This highly productive medium is home to an abundance of crustaceans and salps

Photo 3.3: Krill (*Euphasia superba*). The decrease of krill populations caused by global warming is having a negative cascade effect on many of the predator species that make up the large marine bird and mammal community of the Antarctic.

(gelatinous plankton). These are the predominant components of zooplankton and the main food of predators, most of them megafaunal species. The brevity of summer means that food chains are relatively short (Clarke 1985) and hinge upon a few key species, such as Antarctic krill (*Euphasia superba*).

The high density of crustaceans in the Southern Ocean assures them a fundamental role in the structure and function of marine food webs (Smetacek and Nicol 2005; Murphy et al. 2007). This is especially true for euphausiids (krill), an order whose main species have life cycles linked to seasonal changes in the sea ice. Antarctic krill is found in great abundance from the sea ice to the open ocean waters, and is the most important food for fish, squid, seabirds and marine mammals. Sea ice provides seaweed for the krill to feed on and refuge from predators, especially during the larval stage (Smetacek and Nicol 2005). This dependence on ice means that the krill is probably among the groups of species most exposed to the effects of global warming, with indirect consequences for their main predators, which have difficulties finding a similarly copious source of nourishment. These impacts are gravest where krill is abundant and the ice retreat is more advanced.

One of the most productive areas of the Southern Ocean is the southwest Atlantic sector running from the Antarctic Peninsula to the Antarctic Convergence and the Scotia Arch, including South Georgia and the South Sandwich Islands. This is the area with the greatest density of krill in the entire Southern Ocean (Atkinson et al. 2004) and consequently with the greatest diversity and abundance of its main predators, including true seals, fur seals, whales, penguins and other seabirds, especially albatrosses and petrels (Laws 1984). A number of oceanographic phenomena in the Scotia Sea, including the swift flowing Antarctic Circumpolar Current, its bathymetric features and the climate and its interaction with the Pacific Ocean through the Antarctic Circumpolar Current, together with the ice dynamics of the Weddell Sea, alter the pattern of krill transport from the west of the Antarctic Peninsula towards the Scotia Arch and Islands. Because of these interactions, the effects of warming on the climate and oceans in this and other regions remotely connected to it alter the availability and abundance of krill. These connections between the physical environment of planetary regions separated by large distances, such as the Scotia Sea and the tropical Pacific Ocean (Trathan and Murphy 2002), occur as a result of the transfer of climate anomalies in the atmosphere, the ocean's circulation and the physical processes derived from ocean-atmosphere interactions (Turner 2004). Such interactions affect the entire food chain and, ultimately, the population dynamics of marine predators (Forcada et al. 2005; Forcada et al. 2006; Trathan et al. 2006).

In the last 50 years, the expanse of sea ice in this sector of the Southern Ocean has diminished as a consequence of global warming, and glaciers have receded considerably (Cook et al. 2005), increasing freshwater runoff into the ocean. This has directly affected food webs by altering ice dynamics with a negative impact on Antarctic krill (Murphy et al. 2007). The reduction of sea ice in winter modifies the regional variety and composition of phytoplankton, favouring the proliferation of salps to the detriment of krill, whose density and availability to predators drop significantly (Loeb et al. 1997; Atkinson et al. 2004). The increased influx of freshwater from melting glaciers has contributed to the seasonal modification of phytoplankton species diversity, and consequently of the marine zooplankton (Moline et al. 2004). Considering the oceanography and ice dynamics in the Weddell Sea, south of the Scotia Sea, as well as the effect of global climate and the oceanographic conditions of the Pacific Ocean, the impact of warming on the Antarctic Peninsula affects not only the boundaries of the ice and the predators that depend on it, but also the sub-Antarctic islands.

In other Antarctic regions, the ice dynamics differ (Zwally et al. 2002; Parkinson 2004), and the effects of global warming on marine ecosystems are less detectable. For instance, in the Ross Sea, in the Pacific sector of the Southern Ocean, the expanse of sea ice has apparently enlarged in recent years, and the effects of warming are perhaps less perceptible than in the Antarctic Peninsula; however, the temperatures of the troposphere and high atmospheric strata also seem to have risen considerably in these regions (Turner et al. 2006), and their dynamics have decoupled from those of the lower layers that are in contact with the ice. For this reason, we have no accurate picture of the long-term consequences of this rapid warming phenomenon, and it is important to assess its effects on a regional scale. To reach general conclusions about the impacts of warming, we need to make comparative studies of its effects on the marine ecosystems of distinct Antarctic regions.

3.3. ANTARCTIC MEGAFAUNA: LIFE HISTORY, ICE ADAPTATION AND CRITICAL HABITATS

Some groups of megafaunal species, like the pinnipeds (seals and sea lions), and seabirds (mainly penguins, albatrosses and petrels), depend on terrestrial ecosystems to complete their life cycles, while others, like the cetaceans, are exclusive-

Photo 3.4: Emperor penguins (*Aptenodytes forsteri*) diving. Emperor penguins are amongst the vertebrates best adapted to the inhospitable Antarctic conditions. They are the only penguins capable of withstanding the winter season in these latitudes, where temperatures can reach –50 °C.

ly aquatic. Not all the species in these groups evolved and adapted to Antarctic environments in the same manner or during the same geological period, so their development has occurred in different ecological contexts. The variation in the values of life history characteristics (age of sexual maturity, fecundity, growth and survival rate) as a response to extreme environments is specific to each species, and it is this variation that determines their demographics and population dynamics, which in turn determine their distribution and abundance. Furthermore, the ecophysiological adaptations of each species (such as tolerance to extreme temperatures or aquatic or semiaquatic life habits) limit or favour their adaptation to ice and other extreme living conditions. Thus, we need to identify species-specific life history strategies and adaptation mechanisms in order to understand the consequences of global warming on different species.

The marked seasonality of the Antarctic ecosystems forced megafaunal species to adapt their life cycles to the extreme climatological and physical changes that differentiate winter from summer. Almost all megafaunal species reproduce during the southern summer, when the expanse of sea ice recedes, leaving the terrestrial environment more accessible. Nevertheless, this ice-free space is still small, and there is considerable local competition for it. After completing their reproductive activity, most species migrate or disperse because they cannot survive the Antarctic winter. Some species drift at sea looking for food, others disperse towards winter grounds further north, and others remain on the ice, near areas where food is accessible, such as polynyas, the open areas in the ice formed by strong oceanic currents that allow safe access to the sea waters where food may be found.

Given the high seasonality of their life cycles, all species depend on stimuli or environmental signs that tell them the right time to start their migratory movements or to engage in a given life stage. The disruption of these stimuli by global warming (for instance, changes in the onset of the spring melt or ice formation in the autumn, or temperature oscillations) can have serious consequences for populations and communities of living organisms (Barbraud and Weimerskirch 2006). During years when climatic anomalies cause the ice retreat to be particularly extreme, birds and pinnipeds do not return to nest or breed in greater number even though there is more space available, because there is usually an accompanying reduction in the availability of food.

The scarcity of ice-free land and the influence of climate and physical changes in the Antarctic continent make the Antarctic and sub-Antarctic islands an important refuge for the megafauna. Not only do they tend to have more available land and easier access to food, they are also optimum reproductive sites for seabirds and pinnipeds. Many of these islands are a long way from the continent, such as those of the Scotia Arch or the Indian Ocean sector of the Southern Ocean, including the Kerguelen and Crozet archipelagos. The predators inhabiting these archipelagos depend almost exclusively, in most cases, on the food they can find in the pelagic environment, yet the availability of this food, mainly krill or krill predators, may be a lot more variable and unpredictable than in other areas due to interactions between the climate and various oceanographic phenomena.

3.3.1. Life history variability and ice adaptation

During the short breeding season, restricted to the summer months, sea mammals and birds congregate in colonies on land or on ice. However, the two groups have adapted to the seasonal cycles in different ways conditioned mainly by their energy budgets.

3.3.1.1. SEABIRDS

Seabirds invest the greatest part of their reproductive energy in feeding their young. The chicks must be fed until they become independent of their parents. Penguin chicks fledge a month after hatching. During this time the parents make multiple foraging trips to sea to provide a constant flow of nourishment to ensure their reproductive success, i.e., the survival of their offspring. They accordingly depend on the marine environment to supply them with prey, but are limited by the distance they can travel from the breeding colony and the maximum time they can spend away from the chicks without jeopardising their development. The chicks of other seabirds, particularly the albatross, take longer to become self-sufficient. Those of the wandering albatross (*Diomedea exulans*) may need up to eight months of parental care, making the parents' energy investment in rearing much greater, leading to two-year breeding cycles.

The effects of warming on seabirds have been detected mainly in species, like penguins, that depend on an abundant, constant and nearby source of food, and whose chicks fledge quickly. For these species, ecosystem warming translates as a decline in available food, which directly affects their reproductive success (Fraser and Hofmann 2003; Forcada et al. 2006; Trathan et al. 2006). In years when the expanse of sea ice is small, due to higher temperatures, there is a reduced availability of krill, the main prey for many penguins and some petrels, so they must spend more time at sea looking for food.

Other seabirds that are less dependent on the physical and biological environment near their breeding colonies can forage over distances of hundreds or even thousands of kilometres. For instance, many albatrosses that nest in the sub-Antarctic islands travel for days looking for food, covering hundreds of kilometres before returning to their nests to feed their chicks. This is the case of the black-browed albatross (*Thalassarche melanophrys*) and the grey-headed albatross (*Thalassarche chrysostoma*) (photo 3.5), which nest in South Georgia but travel regularly to the Patagonian continental shelf or the Antarctic Peninsula in search of prey like squid and krill, respectively. Their ability to cover large distances in a short time allows them to look for more distant prey, spreading out the effort of searching for food, thereby maximising the amount transferred to the chicks when they return to the colony. Global warming-driven environmental anomalies have less effect on species like these, which do not depend directly on the sea ice.

For some petrel species, such as the snow petrel (*Pagodroma nivea*) (photo 3.6), ice dependence limits access to food. This species nests exclusively in ice- or snow-covered zones, sometimes hundreds of kilometres away from krill, their main source of food. To feed their young, the parents must regularly cover these

Photo 3.5: A grey-headed albatross (*Thalassarche chrysostoma*) feeding its chick on South Georgia Island after returning from a long foraging journey

long distances, expending a considerable amount of their energy in flight. Given the krill's relationship with the sea ice, the snow petrel faces shortages when the ice recedes, significantly reducing the availability of krill and other ice-dependent resources (Jenouvrier, Barbraud and Weimerskirch 2005). Like most petrels and albatrosses, the snow petrel is a long-lived species that takes a long time to reach sexual maturity and reproduces slowly. This means they must marshal their available energy effectively, allocating more to reproduction than to survival. Reproduction is energetically costly, so the snow petrel survives at the expense of curtailing reproduction in those years when climate conditions and the dynamics of sea ice adversely affect its coverage and the availability of food.

Amongst the Antarctic penguins, the Adélie (*Pygoscelis adeliae*) and emperor (*Aptenodytes forsteri*) have the greatest affinity for ice. The emperor penguin is one of the best ice-adapted Antarctic vertebrates. It can survive in temperatures of less than -50°C during winter gales in one of the most hostile and extreme environments on the planet. Emperor penguins have one of the longest reproductive cycles, starting in March, during the winter, and ending in December, during the summer. They breed on quick-forming sea ice, the kind that solidifies in winter on the ocean surface and breaks up during the

Photo 3.6: Snow petrel (*Pagodroma nivea*). These seabirds breed in permanently frozen areas far from the sea, so must travel hundreds of kilometres to find the krill with which they feed their chicks.

summer. While they incubate and hatch their single egg, and during the first weeks of the chick's life, the male can go for more than three months without food while exposed to extreme temperatures, losing up to 45% of its body weight. Meanwhile, the female feeds at sea, eating mostly fish. Studies of this species in the Indian Ocean sector of the Southern Ocean indicate that males survive less well than females due precisely to this greater investment of energy in reproduction, but that rising temperatures during both summer and winter may decrease the survival rates of both sexes. An extreme reduction of sea-ice cover could push up male mortality in particular (Jenouvrier, Barbraud and Weimerskirch 2005), as a result of lower food availability.

The biological strategies of the emperor penguin and the snow petrel—some of the seabirds most adapted to Antarctic ice—differ in several aspects (Jenouvrier, Barbraud and Weimerskirch 2005). The emperor penguin reproduces almost every year, despite the extreme environmental conditions and what they signify for male adult survival, while the snow petrel may delay reproduction to avoid this cost, as well as having a much shorter reproductive cycle. The emperor also reaches sexual maturity quite young, while the snow petrel may take up to seven years and is possibly longer-lived. However a reduction of sea ice could entail significant long-term population changes for both species.

3.3.1.2. MARINE MAMMALS

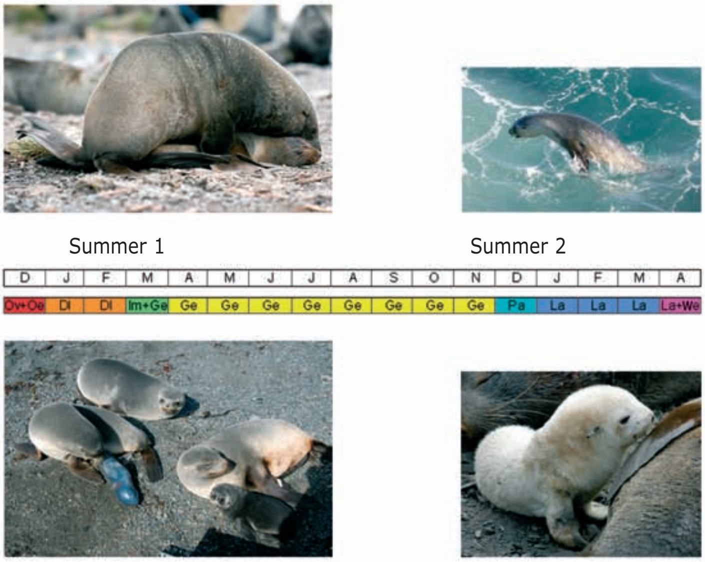
Unlike seabirds, whose reproductive energy investment is limited to egg laying and incubation, sea mammals have a long gestation period whose final stage requires high energy expenditure from the mothers. The gestation period of Antarctic pinnipeds normally lasts from the end of one summer to the start of the next. Then during lactation, the females must transfer even more energy to their offspring. The lactation period for seals (phocids) lasts a maximum of one month, while for the otarids, specifically the Antarctic fur seal (*Arctocephalus gazella*), it lasts approximately four months. As a rule otarids (sea lions and fur seals) lactate for a period of around one year, but shortening this to four months may be a necessary adaptation to survive Antarctic seasonality. Most pinniped species are able to reproduce during consecutive summers, meaning that the new gestation starts while the previous offspring is still lactating. This makes females more dependent on terrestrial conditions when giving birth, besides environmental conditions and food availability. For the Antarctic fur seal, whose reproductive success is based on shorter lactation periods and earlier offspring emancipation than those of similar species, food scarcity is an even greater challenge than for other pinnipeds.

Figure 3.1: Reproductive strategies of Antarctic pinnipeds

A: Southern elephant seal

O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F
	Ov+Oe	Di	Im+Ge	Ge	Ge	Ge	Ge	Ge	Ge	Ge	Ge	Pa+La	La+We			

B: Antarctic fur seal



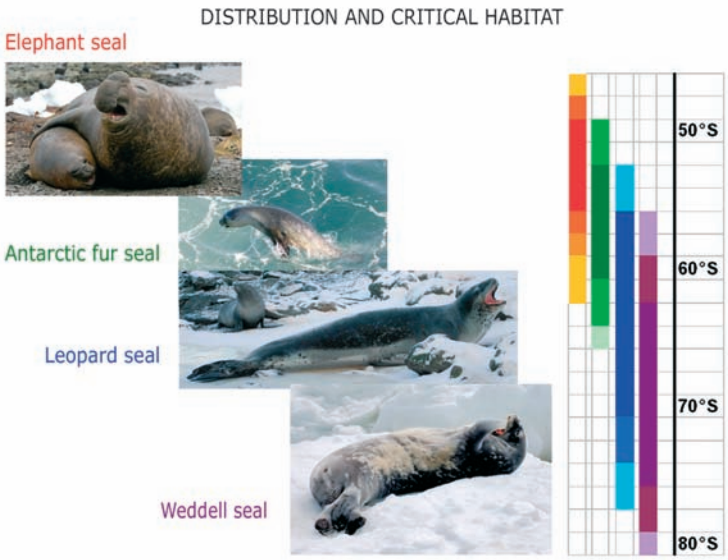
D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
Ov+Oe	Di	Di	Im+Ge	Ge	Ge	Ge	Ge	Ge	Ge	Ge	Ge	Pa	La	La	La	La+We

A: For southern elephant seals the length of the lactation period depends on the fat reserves accumulated by nursing mothers far from their breeding grounds. **B:** Antarctic fur seal mothers rear and suckle their pups while simultaneously feeding near the breeding colony. This, and their long lactation period, make the species more vulnerable to resource shortages driven by global warming.

Reproductive cycle: Ov: ovulation; Oe: oestrus; Di: diapause; Im: embryo implantation; Ge: gestation; Pa: partum; La: lactation; We: weaning.

In order to complete their reproductive cycle and transfer the necessary energy to their young during lactation, pinnipeds have developed two different feeding and energy-storing strategies (figure 3.1). One of these, called capital breeding, entails the accumulation of energy reserves as fatty tissue that can be mobilised and put to use during the breeding and rearing period. Adults usually stop feeding at this time, and they require sufficient energy reserves to maintain their bodily functions and metabolism. This is the strategy used by all Antarctic seals, from the southern elephant seal (*Mirounga leonina*) to leopard seals (*Hydrurga leptonyx*), crabeater seals (*Lobodon carcinophagus*), Weddell seals (*Leptonychotes weddelli*) and Ross seals (*Ommatophoca rossi*) (figure 3.2). The other strategy, called income breeding, requires a food source near the breeding colony sufficient to satisfy the energy demands of mother and pup. Like penguins, fur seal mothers make frequent foraging trips to sea before returning to land to suckle their young. This limits the time they can spend feeding at sea—usually no longer than a week—during which female fur seals convert most of the energy ingested into milk. This strategy increases the fur seal's dependence on the environmental conditions determining food availability near breeding colonies.

Figure 3.2: Latitudinal variation of Antarctic seals and fur seals



Each colour in the figure represents a species. The tonal variation in the latitudinal scale on the right shows the variability in their south-north distribution. The most intense colours indicate the mid-point of the distribution and the least intense colours its limits. The Weddell seal is the pinniped most adapted to life on ice and therefore the most resistant to extreme conditions. The Antarctic fur seal is the least adapted to icy conditions and needs ice-free surfaces for breeding.

Photo 3.7: Antarctic fur seal (*Arctocephalus gazella*). The reproductive success of this otarid is conditioned by changes in climate and the abundance of krill.

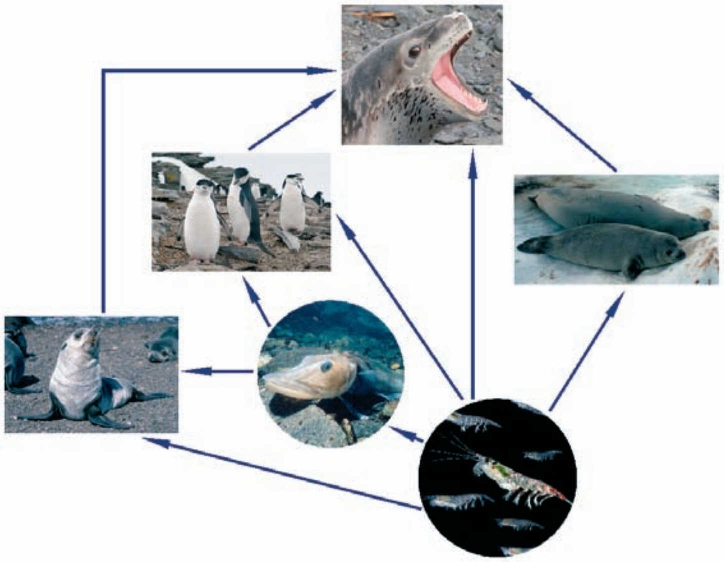
The effects of global warming on the life of pinnipeds are observed mainly during the breeding season or the preceding months, when adults need to accumulate sufficient reserves. The most obvious repercussions are related to climatic disturbances that modify the ecosystems and the main food source of breeding individuals. For instance, the productivity, reproductive success and other vital parameters of Antarctic fur seals breeding on South Georgia have been found to be impaired by the environmental changes arising from the El Niño phenomenon in the tropical Pacific (Forcada et al. 2005). This climate disturbance is transferred to the southwest Atlantic sector of the Southern Ocean, manifesting itself as high sea temperatures and a reduction of sea ice in winter. In this region, the disappearance of the ice cover is associated with decreased food availability for the Antarctic fur seal, affecting both Antarctic krill—their main food—and the fish species that form part of their diet.

El Niño has also been shown to affect the survival of offspring in the case of the southern elephant seal, a species with a completely different strategy from that of the Antarctic fur seal and a broader latitudinal distribution. Elephant seal mothers accumulate lipid reserves by ingesting more food during the final stage of gestation. This generally occurs above the boundary of the Antarctic Convergence, the area that separates the Southern Ocean from the temperate and subtropical ocean waters. After the pups are born, they are suckled for nearly a month, over which time their mothers transfer large amounts of energy. When they are weaned and become self-sufficient, the young have to survive using their own energy reserves and other resources. In some El Niño years, food is more abundant for both mother and offspring, because the oscillation boosts the abundance of squid, one of the seal's main prey species. Greater energy investment during years of climatic anomalies seems to favour the survival of the first-year young on Macquarie Island (McMahon and Burton 2005). For this species and region, El Niño exercises the opposite effects to those observed for the Antarctic fur seal in South Georgia.

The effects of warming on true Antarctic seals are not so evident, due to their capacity to survive on the food reserves they build up outside their breeding season. For these species, in contrast to their Arctic relatives like the ringed seal, receding sea ice does not bar them from access to their primary food source, or leave their offspring more exposed to predators. One of the most ice-adapted Antarctic seals is the Weddell seal (figure 3.2). It feeds mainly on large benthic fish, which do not seem to have become less available with the disappearance of sea ice. Weddell seals are also adapted to extreme temperatures, and their reproductive success depends on environmental conditions. The young may die during extreme temperature conditions and fierce storms, but the mothers are sufficiently well adapted to survive such conditions. The stability of the population is thus ensured, because the mothers survive even though their pups are occasionally lost. The opposite is true for the Antarctic fur seal. Both mother and young are affected by hostile environmental conditions, and consequently their demographic trends and net population growth are affected, potentially causing significant long-term population declines.

Other Antarctic seals have adapted differently to the ice. For example, the leopard seal (figure 3.3), one of the main Antarctic top predators, is associated with ice, particularly quick-forming ice, as well as floating brash ice and drifting icebergs, where it can often be seen resting after hunting forays. Their young are usually born on ice floes and fast ice but, unlike Weddell seals, they do not live permanently on the ice. During the breeding season, leopard seals feed on other ice-associated species like Antarctic krill, some benthic fish species, penguins and, especially, the young of other pinnipeds, mostly crabeater seal pups. In many Antarctic regions, crabeater seal pups are their main source of food. Indeed some speculate that this reproductive cycle, more flexible and adaptable to Antarctic seasonality than those of other seals (like the Weddell and crabeater seals), is precisely to allow the leopard seal to have its pups later than other species, like the crabeater seal, ensuring a ready source of food for pre-breed-

Figure 3.3: The leopard seal and its main prey



The leopard seal is one of the largest Antarctic predators. It is not a specialist and can feed equally on krill or on the pups of other pinnipeds. Yet the cascade effects on food webs produced by climate change may affect the availability of many of its prey species, making it harder to obtain food.

Photo 3.8: Leopard seal (*Hydrurga leptonyx*). This seal is among the largest and most efficient predators in the Antarctic waters, giving it the top place in the food chain. Leopard seals prey on the pups of other seals and on penguin chicks. The photo shows a leopard seal capturing an Adélie penguin underwater.

ing leopard seals. Also, because they are not selective predators, leopard seals can change prey according to availability, which theoretically would make them less vulnerable to climate changes affecting food abundance. Even so, during periods when climate abnormalities reduce the extension of sea ice, the leopard seal too faces a decline in the abundance of Antarctic krill and their many predators, because food webs are substantially altered. In addition, leopard seals go through a period of post-reproductive dispersal associated with climate change-driven sea-ice changes (Jessopp et al. 2004). In years of high sea temperatures and less ice cover, this dispersal phase is altered, and the number of leopard seals travelling to the penguin and fur seal breeding colonies in the Antarctic and sub-Antarctic islands reduces sharply. These conditions are associated with a lower abundance of krill for penguins in the breeding colonies (Fraser and Hofmann 2003), and also seem to suggest that there is less food available for leopard seals.

We have less information about the effects of warming on the remaining Antarctic seal species, especially the Ross seal, whose biology is largely unknown. In the meantime, speculation continues about whether the increase in crabeater seal populations ensues from the demise or decline of the whale in many Antarctic regions. Reduced whale predation pressure on krill may have benefited the effective population size of the crabeater seal by producing the so-called “krill surplus”. For many years, this seal species has been thought to represent 70% of the world pinniped biomass, precisely as a result of this surplus, but because it is fundamentally a krill-dependent species, it can also be regarded as one of the worst affected, albeit indirectly, by the impact on krill of global warming. However, it is not known for certain whether this is the case, since abundance estimates are poorly reliable and the species’ real population numbers are unknown.

The krill surplus theory, which is now open to question given the evidence of their reduced numbers (Atkinson et al. 2004; see chapter 2), has also been used as a possible explanation for the changes observed in Antarctic penguins (Fraser et al. 1992). However, as discussed in the next section, the combined effects of global warming on the transformation of critical habitats and the increase in marine ecosystem fluctuations with the subsequent alteration of food availability conditions seem a more convincing explanation (Fraser and Hofmann 2003; Forcada et al. 2006).

The impacts of climate change on cetaceans, mainly whales, have yet to be ascertained, because their large dispersal range throughout the Southern Ocean, their extensive migratory movements and their low population density hinder detailed studies of their ecology in relation to the dynamics of ice and climate. Nevertheless, several scenarios and hypotheses have been advanced about the adverse effects of global warming on certain species. The most plausible involve the effects of global climate change on the environment as mediated by cyclical phenomena like El Niño. This is the case for the southern right whale (*Eubalaena australis*), whose productivity and reproductive success seem to have diminished with the increase in global temperature (Leaper et al. 2006). Even so, the exact distribution and abundance of most Antarctic whale species remains unknown, as a result of the overexploitation of many populations for commercial purposes. Some populations are showing signs of recovery, including the most damaged species such as the blue whale (*Balaenoptera musculus*), but their large winter dispersal and low density throughout their range continue to make further studies difficult. At regional scales, it is possible that the diminishing numbers of their main prey caused by an increase in the frequency of climatic disturbances, especially those that have extreme effects on the physical environment and particularly on sea ice, determine the mothers’ nutritional status and cause variability in some of their reproductive biological parameters.

3.3.2. Ice adaptation and critical habitats

One of the clearest examples of the effect of global warming on the megafauna is the change in population and distribution observed in congeneric penguin species that live and breed in the same regions. Under these conditions, the transformation or loss of critical breeding habitat is compounded by the fluctuations of the marine ecosystem and the resulting alterations in the availability of food. The most obvious effects have been detected in the Antarctic Peninsula and adjacent islands.

The Adélie, chinstrap (*Pygoscelis antarctica*) and gentoo (*Pygoscelis papua*) penguins, pygoscelids of similar morphology and life history, are the species most affected by the consequences of warming, seen mostly in the Antarctic Peninsula and in the adjacent Antarctic and sub-Antarctic islands (Fraser and Hofmann 2003; Forcada et al. 2006). The gentoo penguin is an essentially sub-Antarctic species with a subspecies in the Antarctic Peninsula. The Adélie penguin has a circum-Antarctic distribution, particularly on the continent, that is closely associated with ice, and is mainly found during winter in its marginal area. The chinstrap penguin is restricted to the maritime area of the north of the continent and during the breeding season inhabits mostly the Antarctic and sub-Antarctic Islands. All three species sometimes co-occur in the same geographical areas and are considered sympatric. However, there is some ecological segregation amongst them due especially to their adaptation to their preferred habitats—largely characterised by the dominance or absence of sea ice—but also to differences in their feeding habits, migratory patterns, reproductive biology and phenology (the timing of different events). The consequences of global warming for these species depend on their affinity for habitats initially dominated by ice, the degree of transformation of these habitats, their ability to exploit alternative ecological niches and the alterations arising in the timing of their reproductive cycle.

The Adélie penguin (photo 3.9) is perhaps the most severely affected by global warming via the loss of critical sea ice habitat, particularly during the breeding season, and the decreased abundance of their main prey, krill, due to the variability of the marine ecosystem and the modification of food webs. This species needs sea ice to survive, and its increased instability reduces their chances of completing their reproductive cycle in years of extreme climatic conditions. This gives rise to significant population fluctuations that make them more vulnerable to warming than their congeneric species. Of these, the chinstrap penguin (photo 3.9) benefits from the enlargement of ice-free territory during the breeding season, but is likewise harmed by the food pressures caused by the recession of sea

Photo 3.9: Adélie (right) and chinstrap (left) penguins. Both species breed on the Antarctic islands, sometimes in colonies where the gentoo penguin, a congeneric species, is also present. The reduction in the expanse and cover of sea ice alters their reproductive habitat and the availability of food during the breeding season.

Photo 3.10: Gentoo penguins, a species potentially benefiting from the effects of warming in certain regions. Although the breeding habitat of the gentoo penguin increases as the sea ice retreats, warming also modifies the marine ecosystem and reduces the availability of its prey.

ice. This species feeds almost exclusively on krill in habitats dominated by this crustacean and does not appear to switch to other prey in years when krill is locally scarce. This causes their populations to fluctuate with extreme climatic conditions, although to a lesser extent than Adélie penguin populations. For the gentoo penguin (photo 3.10), which is adapted to ice-free habitats, receding ice cover caused by warming increases the availability of habitat for breeding, but the consequences of warming on its main prey affect its reproductive success and possibly other population parameters. The gentoos have a lower density than the other species, so their competition with them for food and other resources is less intense. Also the gentoo penguin, unlike its cousins, does not feed predominantly on krill, but also catches fish and other marine species, enabling it to exploit a different ecological niche. Given these congeneric differences, the gentoo penguin might benefit from the effects of warming in some regions.

3.4. THE CONSEQUENCES OF INTERACTING ANTHROPOGENIC EFFECTS FOR ANTARCTIC MEGAFAUNA

For several groups of Antarctic species, the effects of global warming are compounded by adverse anthropogenic effects, such as pollution of their habitats caused by oil spills and the introduction of non-native species (rats and cats, for example), which have proliferated and eliminated whole populations of nesting birds in some sub-Antarctic islands. Most of the invasive species come from temperate climates and benefit from the region's increased summer temperatures, making eradication more difficult—if attempted at all—on the islands where they have become established. Nevertheless, the worst anthropogenic impacts on the megafauna are incidental capture by fisheries and the food loss caused by their intensification.

The groups of species most affected by incidental capture are albatrosses and petrels nesting on sub-Antarctic islands. Many of these species travel long distances from their nesting ground to forage for food at sea, where they also have juvenile dispersal phases that can last for years. Pelagic and demersal longlining are the most damaging types of fishing. Pelagic longlining, which uses nets of more than 130 km fitted with thousands of hooks, is used to catch commercially valuable fish species like tuna and swordfish. Albatrosses have learned to feed on the bait used in these operations, but the fishing lines cause the death by drowning of tens or even hundreds of thousands of seabirds. Demersal longline fishing, usually for Chilean hake, takes place mostly in the waters of the continental shelf and also results in numerous incidental captures.

Photo 3.11: Wandering albatross (*Diomedea exulans*). The seabird with the largest wing span and one of the longest reproductive cycles, breeding only once every two years. During the breeding season, an albatross may travel hundreds of kilometres over several days in search of food before returning to the nest to feed its single chick.

It is estimated that 17 of the 24 extant albatross species are severely threatened by these commercial practices, and the populations of some spending most of the year in Southern Ocean waters are at risk of extinction. Special working groups coordinated by the United Nations have developed surveillance programmes to evaluate the damage caused by these fisheries and are promoting the use of exclusion devices and mechanisms to reduce the rate of incidental capture. Despite these efforts and those of other international groups, the FAO considers that many countries have failed to seriously address this problem. Furthermore, Chilean hake is a species much sought after by illegal fishery operations, many of which are run by vessels under flags of convenience. For them, incidental capture is merely a momentary disruption of business rather than a grave conservation problem that needs to be tackled. The albatrosses nesting in South Georgia are especially sensitive to these commercial fisheries, and their populations are listed as among the most threatened in the world. For some of these species, particularly the grey-headed albatross and the black-browed albatross, decreased availability of food due to global warming is another serious obstacle to their reproductive success.

3.5. IS GLOBAL WARMING A REAL PROBLEM FOR THE ANTARCTIC MEGAFAUNA?

Most of the megafaunal populations studied in regions of the Southern Ocean show changes or fluctuations that are ultimately related to the effect of global warming on the physical environment; in other words, significantly higher temperatures and recession of the sea ice. In some regions, these populations are showing a periodicity in parameters like reproductive success coinciding with the ENSO cycles. Where in-depth studies have been conducted, population processes at the middle and upper trophic levels, such as those affecting krill and their predators respectively, have been shown to be connected to the ENSO-related local environmental variability observed in some regions of the Southern Ocean and tropical Pacific waters. These short-term correlations detected during ENSO oscillations have potential long-term consequences for the structure and function of Antarctic ecosystems that are difficult to explain by any cause other than global change. The cascade effect on food webs and, ultimately, on megafaunal species can now be measured. Although it is yet to be conclusively shown that the ENSO cycles have been altered by global warming, it is accepted that El Niño has appeared with greater frequency in the last 20 years, and there has been a simultaneous progressive retreat of sea-ice cover in the winter, the result of a rise in temperature of anthropogenic origin.

3.6. IS IT POSSIBLE TO PREDICT THE FUTURE?

To predict how increasing greenhouse gas emissions are going to affect Antarctic ecosystems, we can use climate models to study the Antarctic climate and its interactions with the physical environment. Current models predict a several-degree increase in the prevailing temperature over most of the Antarctic continental area during the present century. However, average temperatures over most of the continent are not expected to rise above melting point, so it is possible that warming over the next 100 years will not cause a significant loss of most continental ice. On the other hand, the model also predicts a rise in the temperature of the Southern Ocean that could wipe out 25% of the existing sea ice, although there is great uncertainty surrounding this prediction. Likewise, warmer ocean waters may have a negative effect on ice shelves and accelerate their fragmentation and melting. It seems clear that the retreat of sea ice will continue to affect Antarctic megafaunal species to varying degrees. The consequences will be directly related to each species' dependence on sea ice as its critical habitat and its ability to adapt to the disturbances caused by the seasonal nature of food availability. Alterations in the food chain and variation in prey availability will also modify the environmental carrying capacity of many species, whose populations will increase or decrease in line with changes in this capacity.

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4. IMPACTS OF GLOBAL WARMING ON ARCTIC PELAGIC ECOSYSTEMS AND PROCESSES

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THE ARCTIC has an important, but so far inadequately known role on the climate of the globe. Recent observational studies have revealed significant reductions in Arctic sea-ice cover and thickness and increased air and ocean temperatures, indicating that we may already be seeing the early warning signs of an ecosystem on the verge of dramatic changes. Warming in the north is several times greater than in central Europe and the pronounced changes in the Arctic can be used as bellwethers for the general state of the northern hemisphere. The current changes in the Arctic Ocean have consequences for fisheries, animal abundance and diversity, the formation of deep water (which influences atmospheric CO_2 concentration), storm patterns and the living conditions of northern people. The Arctic is an integrated part of our lives, and we cannot ignore it just because it is far away and few people live there. By the middle of the century, most of the ice cover may have disappeared from the pan-Arctic shelves in late summer, leaving just a core of ice over the pole. The basin-wide band of the marginal ice zone and flaw polynyas, which in today's Arctic is situated on the shelves but will shortly move from there into the deep Arctic Ocean, is the most visible indication of our era of climate change.

In this chapter, we describe some of the variability, dynamics and reduction of sea ice and how the production of biogenic matter in open Arctic waters and the marginal ice zone varies as a function of ice cover and the physical structure of the water column. We show that a warmer climate with less ice cover will result in greater primary production, a reduction of the stratified water masses in the south, changes in the relationship between biological water column processes and sediments, a reduction in niches for higher trophic levels and a displacement of Arctic by boreal species. In addition, increased runoff from the large Siberian rivers and the reduction of permafrost will result in

◀ Photo 4.1: Frozen landscape typical of the Arctic Ocean near the island of Spitsbergen (Svalbard Archipelago, Norway)

higher turbidity, decreased primary production and an increased supply of old biogenic matter to the Arctic Ocean. The changes ahead of us stand to radically change the productivity, functional relationships and biodiversity of the Arctic Ocean.

4.1. INTRODUCTION

The sub-Arctic has played an important role for the development of Europe, as stockfish and whale oil (lamps) were essential for European living conditions in earlier times. While the sub-Arctic still represents the most important fishing ground in Europe, sea-based extraction of gas and mineral oil is moving steadily northwards due to climate warming and ice reduction. Soon vital economic activities will enter the Eurasian Arctic with the development of the largest ever marine gas field, the Shtokman Field in the central-eastern Barents Sea. And similar plans exist for other regions, given that 25% of the world's gas and oil reserves are assumed to be located in the Arctic. The Arctic is thus no longer the remote, ice-covered, inhospitable place of past eras, but a well-integrated part of our contemporary global economy, playing a significant role for the Northern Hemisphere population.

Climate defines the prime forcing of Arctic ecosystems, and both observations and models suggest that climate is changing (see Sorteberg et al. 2005). Arctic shelf ecosystems are likely to be more sensitive to climatic perturbations than those of temperate shelf areas, firstly because disproportionate warming is expected (see Hassol 2004), and, secondly, because these ecosystems are characterised by comparatively few trophic links and low biodiversity (see Sakshaug et al. 1994). Indeed, recent studies have revealed significant reductions in Arctic ice cover at both pan-Arctic (Johannessen et al. 2004) and regional (Shimada et al. 2006) scales, and we may already be witnessing the early stages of ecosystems on the verge of dramatic change (see Grebmeier et al. 2006). Reductions in ice cover thickness, extent and duration, and changes in current patterns and fronts will likely have both gradual (predictable) and catastrophic (surprise) consequences. Hence bottom-up controls (e.g., stratification, mixing, upwelling) will certainly change; keystone predators within a given region may be recruited, relocated or made extinct; and ecosystems may shift from tight to weak pelagic-benthic coupling. Changes in the cryosphere will have cascading effects throughout the ecosystem, from altered patterns of primary production (Wassmann et al. 2006a) to changes in trophic structure and elemental cycling pathways (see Grebmeier et al. 2006), the introduction of boreal and the displacement of Arctic species (see Berge et al. 2005) and modifications in oceanic and atmospheric transport mechanisms (see Olsen, Johannessen and Rey, 2003). System perturbations brought on by climate change will interact with human activities such as fishing, mineral extraction, oil and gas exploitation and shipping, which will grow significantly in the near future. Because change may be rapid and sweeping, extraordinary and novel measures of conservation will be required to ensure marine animals have the resilience to relocate as existing biomes are altered by climate forcing, be it natural, anthropogenic or both.

In contrast to the poorly productive deep Arctic Ocean basin, the surrounding marginal seas of the European Arctic contain some of the most dynamic and productive ecosystems in the world, supporting food webs that culminate in large populations of seabirds, mammals and species targeted by regional fisheries whose harvesting has important consequences for system sustainability and northern populations (see Wassmann et al. 2006b). The structure and functioning of these ecosystems are intimately linked with ocean and sea ice dynamics and biogeochemical exchange processes. These highly productive regions appear to be more sensitive to climatic perturbations than temperate areas, due to expected disproportionate warming of these areas and ecosystems characterised by comparatively few trophic links (Carrol and Carroll 2003; Hassol 2004).

Recent observational studies have revealed significant reductions in Arctic sea-ice cover and thickness as well as increased air and ocean temperatures (Lindsay and Zhang 2005). What is now needed is to develop a predictive understanding of the effects and long-term ecosystem responses of the Arctic and its marginal seas to changes in climate and human activities. However, the state of our environmental knowledge of the Arctic Ocean is fairly limited, and time series are particularly scarce. We are faced with a number of questions that we cannot yet answer and have an immense amount of work in front of us to investigate and understand the basic function of the Arctic Ocean. And matters are further complicated by the fact that rapid environmental change is already taking place.

In the first part of this article, we explain something of the geographical setting and basic physical and marine ecological dynamics of the pelagic zone of the Arctic Ocean for the less familiar reader. We describe annual ecosystems dynamics, with particular regard to primary production, in general terms and with a more detailed example from one of the best known Arctic shelves, the Barents Sea. We also discuss the role of pelagic-benthic coupling in the Arctic Ocean and speculate how global warming might alter biogeochemical cycling in decades to come. In the next section, we examine these changes in the light of ecosystem variability over geological time scales, before concluding with a call for international cooperation to address the scientific challenges involved in studying a remote and ice-covered region.

4.2. A FEW FACTS ABOUT THE WORLDS LAST *TERRA INCOGNITA:* THE ARCTIC OCEAN

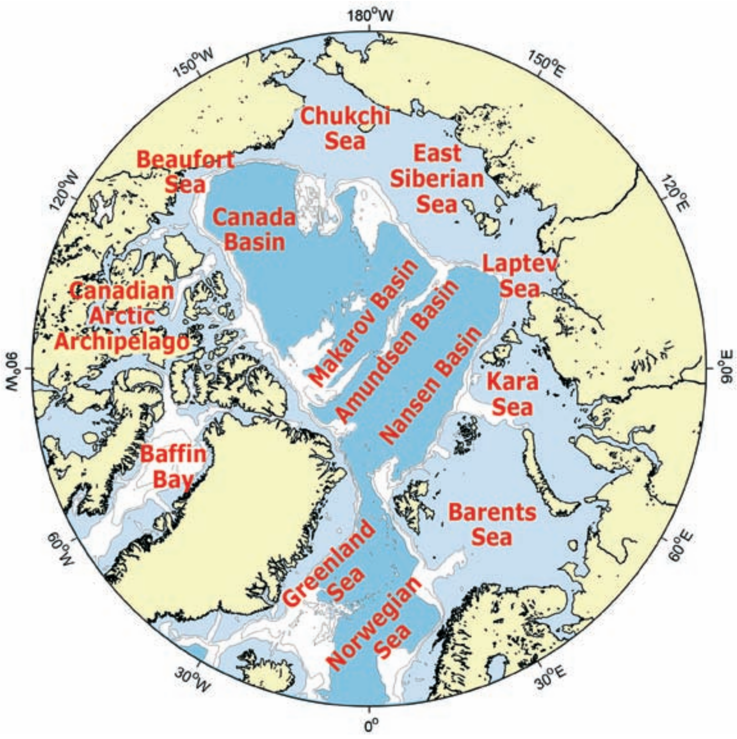
After the early exploration of the Arctic Ocean (see Nansen 1906) and scientific expeditions into the marginal ice zone (MIZ) of the Greenland Sea (see Gran 1902), a few local marine biological investigations were conducted before World War I off Spitsbergen, Franz Josef Land and in the Barents and White seas (see Zenkievich 1963; Vetrov and Romankevich 2004). Russian scientists were active in the inter-war years in the Barents Sea and along the Siberian shelves (see Zenkievich 1963), as well as in the central Arctic Ocean (see Ugryumov and Koronin 2005). The Soviet Union's closure of the North-East Passage after World War II ruled out international and pan-Arctic research activities in the Arctic Ocean. On the Siberian shelf, the Soviet Union gave precedence to studies of ice dynamics and physical oceanography, lending scant attention to the benthos, let alone plankton or ecosystem dynamics (but see Codispoti and Richards 1968, for an investigation carried out by intruding US naval vessels). The geopolitical climate of the Cold War awakened greater interest for the southern polar oceans, and International Geophysical Year 1958 was devoted to Antarctica. This has been a dominant trend in polar research until recently.

Thanks to a recent suite of research programmes (SHEBA, PRO MARE, SBI, CASES and CABANERA, to mention just a few), we have gained a basic understanding of certain sections of the pan-Arctic shelf expanse (for two recent summaries, see Stein and Macdonald 2004; Wassman 2006). However, some shelf regions have never been investigated and the majority only for limited periods of time (mainly summer to early autumn). Beyond the pan-Arctic shelf and the shelf break, information on the deep Arctic Ocean is decidedly scarce, save for the likes of the SBI and CASES projects. The regions of the shelf edge and slopes are among the main targets of International Polar Year 2007-2008, and significant advances can be expected in the near future.

The shelves of the Arctic Ocean are strikingly different from those of the world's other oceans. Approximately 50% of its surface is made up of shelves (map 4.1), engirdling four basins, more then 3,000 metres deep and separated by deep ridges such as the Lomonosov and Gakkel ridges. The Nansen and Amundsen basins are closely connected to the Atlantic, while the Canadian Basin, the most isolated of all, is fairly weakly connected to the Pacific. The Makarov Basin occupies an intermediate position. There are also significant differences among the pan-Arctic shelves. The shelves off North America are typically narrow, while those of Eurasia are wide with very steep slopes. The shallowest shelves are those of the Chukchi, East Siberian and Laptev seas (often only a few tens of metres deep), while those of the Barents Sea and the Canadian Archipelago are relatively deep.

The Arctic Ocean is a Mediterranean ocean in the strict sense of the Latin term *media terra.* Its shelves are connected to the hinterland by some of the

Map 4.1: Topography of the Arctic Ocean and pan-Arctic shelves



The image evidences the width of the shelves, shown in light blue, the circular structure of the Arctic Ocean and the separation of the deep basins, shown in darker blue, by a series of ridges.

world's major rivers (e.g. the Lena, Ob and Mackenzie rivers), which drain enormous territories as far south as central Asia and North America. Around 10% of the world's freshwater discharge enters the Arctic Ocean. This highly seasonal freshwater supply supports the formation of sea ice, as stratified waters freeze quickly. Most of the Arctic Ocean is ice covered during winter and spring with a reduction during summer and early autumn (photo 4.2). Ice cover is one of the prime factors driving ecological processes such as primary production in the Arctic Ocean, and this in and out "breathing" determines the seasonal and interannual pace of productivity. The Arctic shelves are also characterised by polynyas; open areas in ice-covered regions that are important sites for the production of new ice and biogenic matter. They can be persistent or transient, and the most prominent of all are the flaw polynyas that, later in the season, unite with the permanent MIZs in the Barents and Greenland seas. Together they form a continuous MIZ rim that moves northwards towards the permanently ice-covered region over the North Pole.

The oceanographic dynamics of the Arctic Ocean are heavily influenced by the import and export of water. Most imported water is brought in by the

Photo 4.2: A view of the seasonal ice zone with around 10% of open water

Norwegian Atlantic Current either through the Barents Sea or along western Spitsbergen (Wassmann et al. 2006b). Pacific water enters the Arctic Ocean through the Bering Strait (Woodgate and Aagaard 2005). The Atlantic inflow is more then six times greater than that of the Pacific, and much of the fauna in the Arctic Ocean suggest an Atlantic origin (Zenkievic 1964; Wassmann et al. 2006b). Arctic water and ice flows out over the export shelves (see Carmack et al. 2006) of the western Fram Strait and through the Canadian Archipelago.

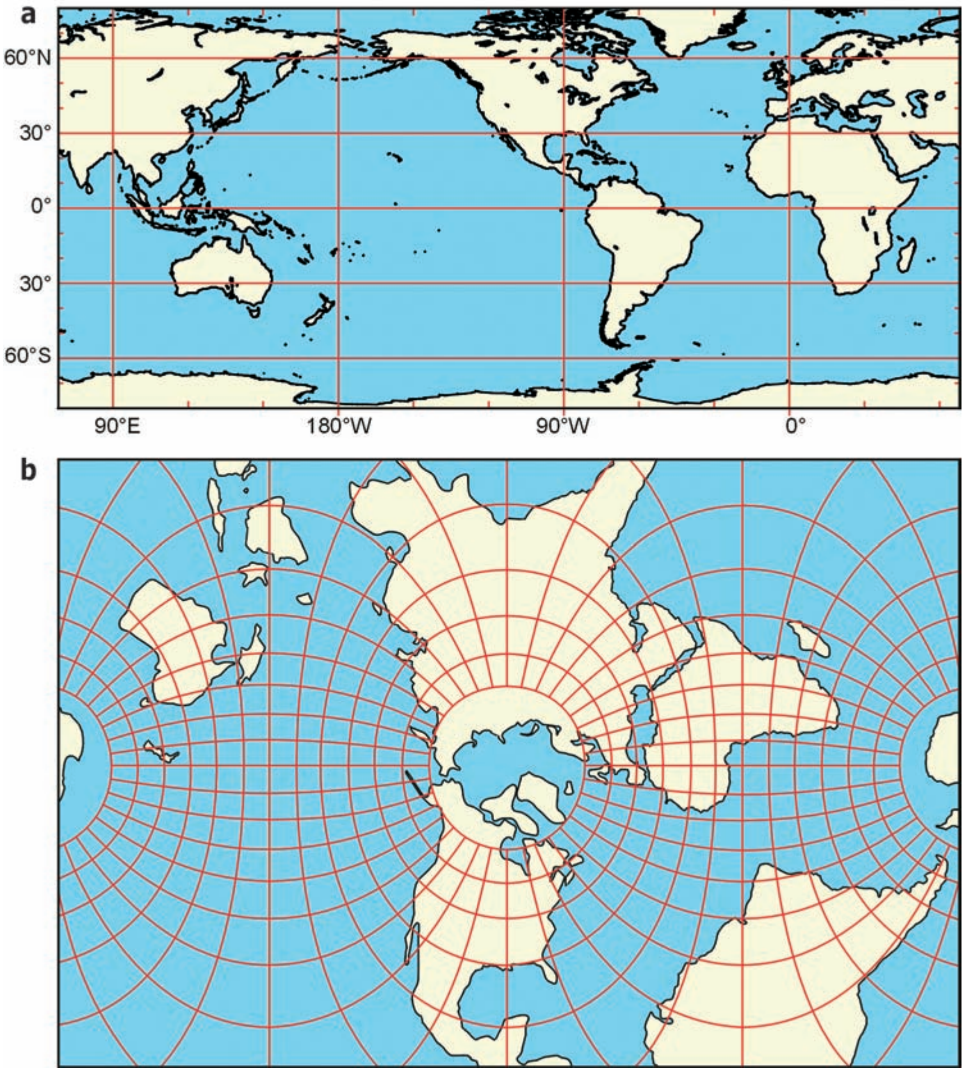
People's general perception of the Arctic has been strongly influenced by the projection chosen for maps. The most widely used is the Mercator projection (map 4.2a), which presents the distance and proportions of regions between 60° south latitude and 60° north latitude to considerable advantage, but simultaneously depicts high-latitude regions like the Arctic as remote, vast and "linear", and the Atlantic and Pacific oceans as separate and far apart. In reality, the Arctic Ocean is small and circular, the distance between the Atlantic and Pacific is relatively short and the two are directly connected (map 4.2b). This kind of projection allows us to get a true grasp of Northern Hemisphere oceanography. And the comparison shows us that progress can be made by determining the most appropriate perspective, even before any science is carried out.

4.3. PRIMARY PRODUCTION AND CARBON BUDGETS IN THE ARCTIC OCEAN

Over the last 30 years, our view of the Arctic Ocean has changed considerably: from the early days when it was considered an ocean with little variability to the more recent conclusion that it is the most variable of all, both in space and over time (Wassmann et al. 2004). Simultaneously, primary production estimates for the Arctic Ocean proper have increased from about 10 to 30 g of carbon per m^2 ($g\ C\ m^{-2}$) (Sakshaug 2004). Primary production estimates on the shelves and from polynyas range from about 10 – 20 $g\ C\ m^{-2}$ in the Laptev Sea to > 300 $g\ C\ m^{-2}$ in the North Water Polynya (Deming et al. 2002). The general increase in primary production estimates is primarily the result of an increased number of measurements, and not of a lesser extension of thinner ice due to global warming.

A complete overview on primary production in the Arctic Ocean is not possible for the moment (but see Sakshaug 2004). We accordingly start our account with a summary of the general principles of primary production in

Map 4.2: Two differing geographical projections of the terrestrial globe; that of Mercator (a) and a Northern Hemisphere perspective with the North Pole at its centre (b)

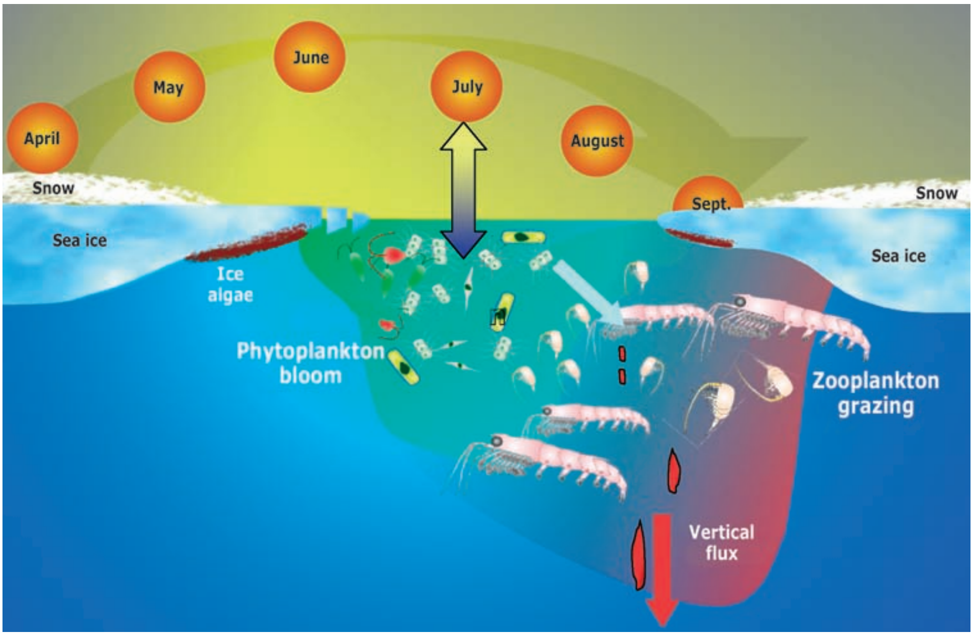


These two maps illustrate how geographic perspectives determine our vision of the Arctic.

Source: Maps redrawn from Carmack and Wassmann 2006.

ice-covered Arctic waters (figure 4.1), followed by a more detailed description of the primary production in the Barents Sea (map 4.3). Primary production in the Arctic Ocean is primarily determined by light availability, which is a function of light penetration (ice thickness, ice cover, snow cover, light attenuation), the abundance of both ice algae and phytoplankton, nutrient availability and surface water stratification. In winter and early spring, the sun is either under or low over the horizon (figure 4.1), and this, along with the snow and ice cover, prevents algae growth. The first signs of spring are already apparent in March (Reigstad et al. 2002), but it is not until the ice thins out and the snow has disappeared that the algae begin to proliferate on the underside of the ice (figure 4.1). Nutrients are abundant. The break-up of the ice and formation of an MIZ are followed by a major bloom of a few weeks duration made up basically of phytoplankton (Sakshaug and Skjoldal 1989) (figure 4.1). Larger mesozooplankton in the Arctic Ocean, having adapted their life cycle to unpredictable food supply by means of overwintering strategies, move from their hibernation to their potential feeding grounds before the spring bloom (Falk-Petersen et al. 1999; Kosobokova 1999; Arashkevich et al. 2002). Grazing thus occupies the entire length of the productive season (figure 4.1) and is only partly phased as in boreal and temperate waters. The bloom is able to take place despite heavy zooplankton grazing pressure (reducing the bio-

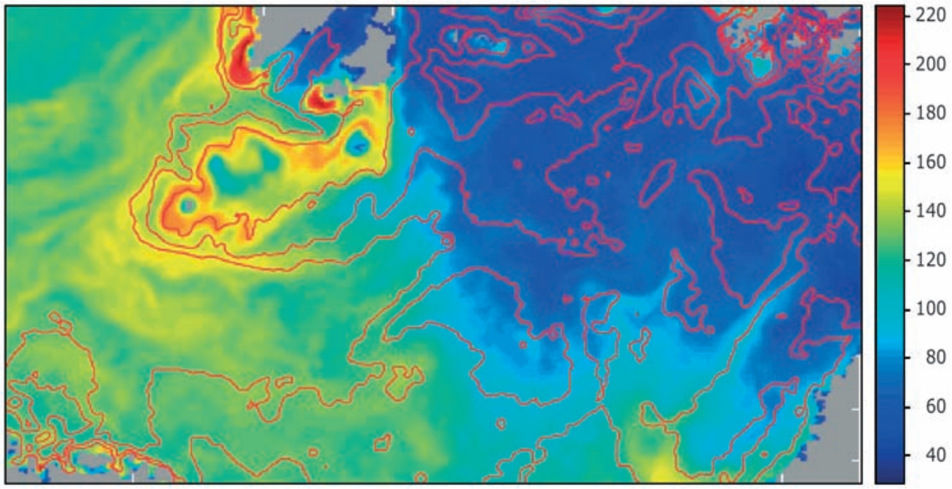
Figure 4.1 The annual cycle of physical forcing and biological response in the Arctic



The figure shows the variation in depth of the euphotic zone, the predominance of autotrophy and the shift with time into heterotrophy (green to red). The vertical arrow symbolises the exchange of CO_2 from and to the atmosphere, illustrating the important role played by the Arctic Ocean in atmospheric CO_2 dynamics.

Source: Wassmann et al. 2004.

Map 4.3: Average annual primary production in the Barents Sea, based on a physically-biologically coupled 3D model driven by a meteorological, hind-cast database



Average annual primary production, expressed as g of carbon per m^2 (see scale), is based on results from four different years. Also shown is the 100-300 metre bathymetry (isobaths in red). On the lower left is the northern part of Norway; centre top, the island of Spitsbergen; in the top right corner, Franz Josef Land; and on the lower right, the archipelago of Novaja Zemlja.

Source: Wassmann et al. 2006.

genic matter that can sink while producing faecal pellets with a high sinking rate), because phytoplankton growth outstrips feeding activities in biological spring (Wassmann et al. 1999). Under Arctic conditions the ecosystem spring bloom is net-autotrophic, but turns into a net-heterotrophic system over time (signalled by the change from green to red in figure 4.1) as the euphotic zone deepens. Ice formation resumes with the pronounced decline of sunlight in early autumn, accompanied by ice algae growth and a drastic reduction in water column light availability. The overwintering zooplankton then descend to depths. The winter in the Arctic Ocean remains largely an enigma.

Among the best known Arctic shelves is the highly productive Barents Sea, which supports one of the largest fisheries in the world (see Falk-Petersen et al. 2000; Wassmann et al. 2006b). Some of the typical dynamics of Arctic primary production can be exemplified by modelling results from this shelf (map 4.3) (for more details, see Slagstad and McClimans 2005; Wassmann et al. 2006a). What we find are compelling annual differences in primary production between the southwestern and northeastern Barents Sea, ranging from below 30 to over 200 g C m^{-2} a year. This is basically a result of ice cover. The regions where annual primary production fails to reach 80 g C m^{-2} are all ice covered in spring, and a highly stratified surface layer is left behind in the wake of the receding ice, limiting phytoplankton growth. In the ice-free, Atlantic-water-influenced regions to the southwest, annual primary production is approximately in the range of 120-160 g C m^{-2}, but certain high-production structures are clearly visible (map 4.3). This is especially true of the area around the Svalbard Bank and Bear Island. This region is characterised by a band of very high production, caused firstly by the shear currents of the Polar Front (between Atlantic and Arctic waters) at around 100 m depth, and, secondly, by extensive tidal currents sweeping over the Bank. This generates high productivity along the rim of the Bank throughout the productive season and nutrient depletion in the centre, resulting in a crosswise gradient of about 100 g C m^{-2} a year. The model also points to upwelling close to the Spitsbergen coast, but that has so far not been verified. On average, annual primary production is 93, 130, 68 and 132 g C m^{-2} for the entire Barents Sea, its Atlantic and Arctic sectors and the Svalbard Bank respectively (Wassmann et al. 2006a). However, interannual variability is on a significant scale, due mainly to climate-induced changes in ice cover, particularly in the Arctic sector where it is estimated at ± 26 %.

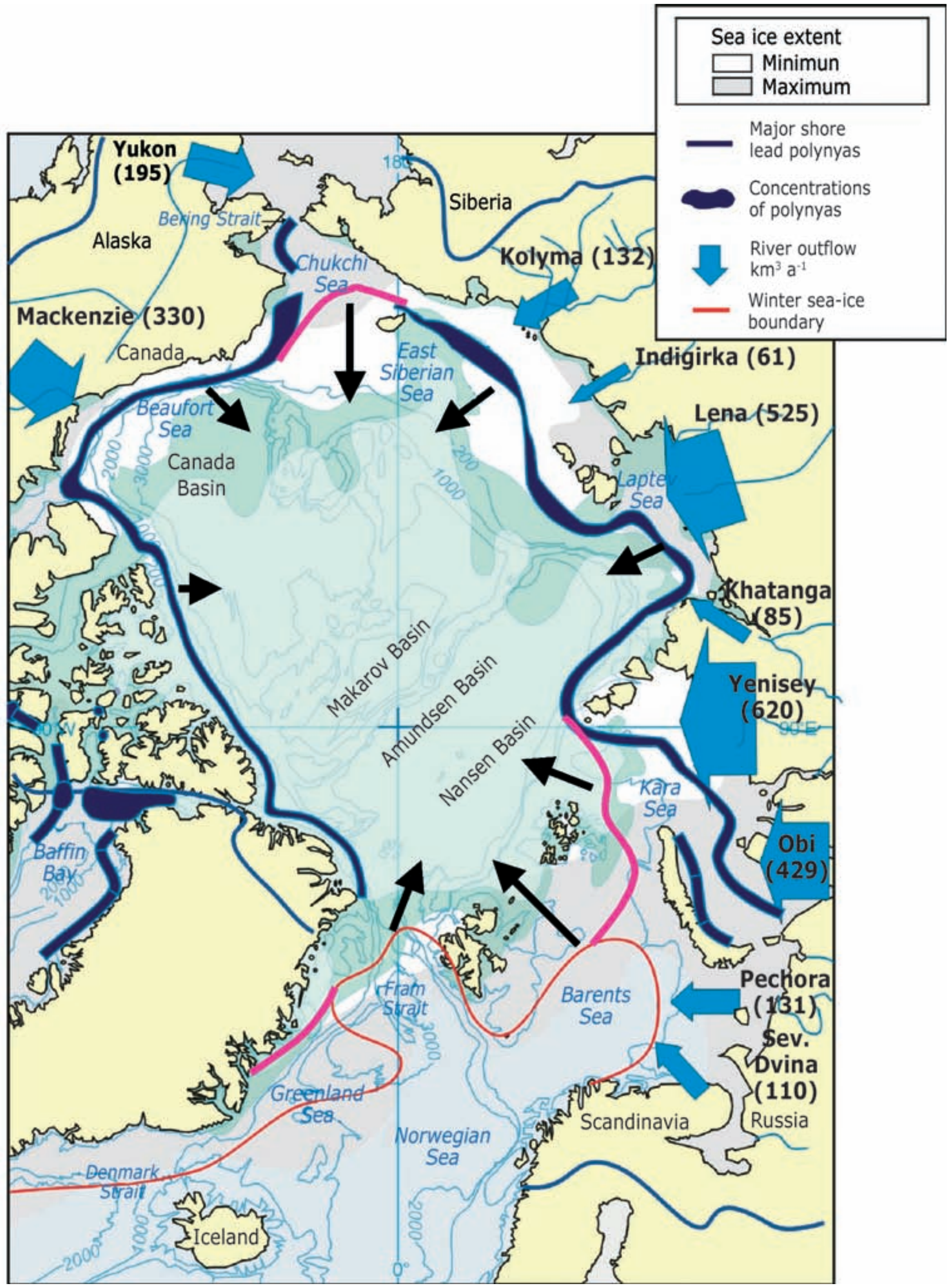
The Barents Sea/European Arctic Ocean corridor is an area of bi-directional horizontal exchange and a critical zone for the physical transition of freshwater—in the form of low-salinity water and ice—and carbon from the Arctic to the North Atlantic (Aagaard and Carmack 1998). Changes in the volume of freshwater input to the North Atlantic influence the properties of the world's oceans via impacts on thermohaline circulation and deep water formation. Water exiting the Arctic basin is also characterised by significantly higher dissolved organic carbon (DOC) levels than the receiving North Atlantic, due to inputs from Siberian rivers entering the Arctic Ocean (Anderson et al. 1998). In the other direction, highly productive Atlantic water flows around and through the Barents Sea as a boundary current into the Arctic basin, carrying large amounts of newly fixed organic carbon in the form of living plankton and organic detritus (Wassmann 2001)

A warmer climate will result in reduced ice cover, increased primary production and a wide band of highly stratified surface water that stretches from the shallow southern rim of the seasonal ice zone (SIZ) to the, for the moment, permanently ice-covered regions of the deep Arctic basins. Another likely consequence will be a change in the horizontal exchange of freshwater, dissolved and particulate organic material (increased river run-off, precipitation and loss of permafrost) and living organisms across the Barents Sea/European Arctic Ocean corridor. The implications for system processes such as geochemical cycling, trophic interactions and shelf-basin exchange may prove to be significant. The supply of organic matter to the benthos will increase significantly, boreal species will spread northwards, and Arctic shelf species may "run out of shelf". The advent of boreal Atlantic and Pacific species (see Berge et al. 2005) will profoundly change the ecological and biogeochemical function of the currently ice-covered regions, causing what we might call an "Atlantification" or "Pacification" of the inflow shelves and adjacent internal shelves (see Carmack et al. 2006).

4.4. ENGIRDLING THE ARCTIC OCEAN: MARGINAL ICE ZONES AND FLAW LEAD POLYNYAS

Before turning to the pelagic-benthic coupling in the Arctic Ocean, we will look more closely at its rim: the SIZs (photo 4.2), MIZs and flaw lead polynyas (map 4.4). It is inside this rim of sea ice that most of the primary production of the Arctic Ocean takes place and where global change is revealed in its fullest impact. The SIZ is the ice-covered region that melts annually; that is, the region between the maximum (April-May) and minimum (September-October) ice extent. The boundary between the ice-covered region and the open water is what we call the MIZ, a physically complicated region that may be 100 or more km wide. Beyond the SIZ we find the multi-year ice (MYI), several metres thick, that covers the central Arctic Ocean. On the Atlantic side, the SIZ is represented by a permanent MIZ, while on the Siberian and Pacific side last fast ice (LFI) connects the SIZ to dry land (map 4.4). It is in the interface between the LFI and the SIZ that flaw lead polynyas are found; permanently or periodically open leads that, together with other polynyas, form specific regions especially important for Arctic Ocean productivity and biogeochemical cycling. In the Laptev Sea, for example, flaw leads are important sites for ice formation. This new ice crosses the entire Arctic Ocean as the Transpolar Drift in the direction of the Fram Strait, where it melts releasing sediments and terrestrial matter (Bauch and Kassens 2005). The North Water Polynya is a highly productive open water site between northwestern Canada and western Greenland (Deming, Fortier and Fukuchi, 2002) that is home to the world's northernmost human settlement, the Inuit village of Thule. Intermittent polynyas around Franz Josef Land and St. Lawrence Island support rich benthos and walrus communities (see Grebmeier et al. 2006).

Map 4.4: Flaw polynyas and marginal ice zones of the Arctic Ocean



A seasonal flaw polynya-marginal ice zone continuum engirdles the pan-Arctic shelves and the deep Arctic Ocean proper. In light green: minimum ice cover during summer.

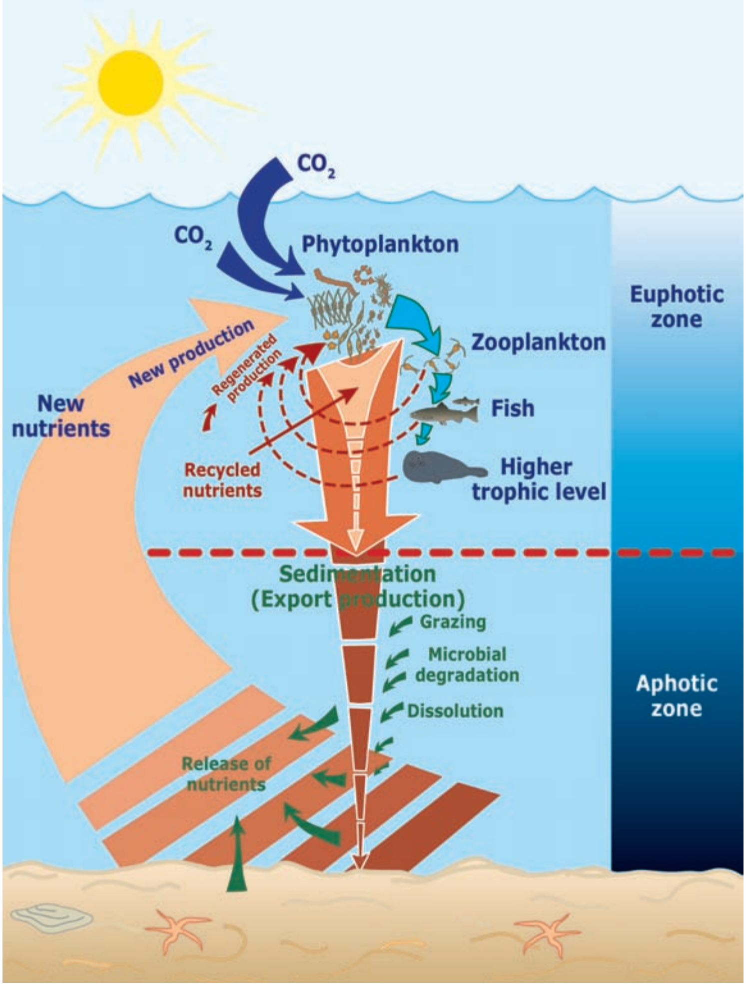
With time, the MIZs and flaw lead polynyas unite, forming a single ecosystem that engirdles the Arctic Ocean, and the central ice cap shrinks towards its minimum, dominated by MYI. In decades to come, most of the changes in the Arctic Ocean with a bearing on pelagic ecosystems and processes will take place in the SIZ-MIZ-polynya complex. As the winter ice advances less, the edge of the presently stratified outer SIZ will be modified and torn by storms, diminishing its stratification. Regions with a strong vertical mix in the water column—like, for instance, the southwestern Barents Sea—will gain in extent, adding to the general increase of primary production in the Arctic Ocean. The SIZs will also widen, supporting increases in primary production in regions still presently covered by MYI. However, stratification and thin ice cover will limit primary production to a relatively low rate.

4.5. PELAGIC-BENTHIC COUPLING AND PHASING IN THE OPEN WATER-SIZ-MYI COMPLEX: SOME BASIC CONSIDERATIONS

CO_2 is transferred via the atmosphere-ocean interface and taken up by phytoplankton with the aid of light and nutrients (figure 4.2). A part of primary production is defined as new production because it is based on winter-accumulated or lately supplied, i.e., new nutrients. The phytoplankton biomass is at the base of the connection between the pelagic and benthic realm (Wassmann 1998) (figure 4.2). Phytoplankton or ice algae (photo 4.3) can sink direct to the bottom or be grazed by organisms such as copepods (photo 4.4). The copepods are, in turn, grazed by fish and mammals (Wassmann et al. 2006b) (figure 4.2). Collectively they recycle some of the resulting biogenic matter back to nutrients, the so-called recycled nutrients, which can again be taken up by phytoplankton, supporting regenerated production. These upper layer retention processes together determine the flux of biogenic matter to the benthic boundary layer and sea floor. To investigate the connection between the pelagic and benthic realm, we have to analyse the production and retention processes taking place in the upper layers. A close connection between the pelagic and benthos realm may be caused by a high biomass accumulation in the upper layers, low vertical flux attenuation efficiency, i.e. low retention, or else a combination of the two (figure 4.2). If the connection is tight and immediate, we talk about "pelagic-benthic coupling". If retention is significant, and delays between primary production and biogenic matter deposition are considerable, we talk about "pelagic-benthic phasing". The nutrients generated by the benthos are released into the water column. These are the new nutrients that ultimately become the winter-accumulated nutrients fuelling the MIZ vernal bloom (figure 4.2).

Pelagic-benthic coupling and phasing are regulated by physical forcing and by the composition, function and efficiency of the pelagic food web (figure 4.2). It was previously assumed that the grazing food chain running from large phytoplankton such as diatoms (photo 4.3) to copepods (photo 4.4) was dominant in the Arctic Ocean and adjacent shelves, justifying the strong emphasis given to these organisms. Larger copepods, rich in lipids, are key organisms for many pelagic fish and birds in the region (see Falk-Petersen et

Figure 4.2: Carbon flux, nutrient cycle and pelagic-benthic coupling



al. 1998). However, many of these copepods, specialised herbivores that grow well during phytoplankton blooms, can also adopt an omnivorous feeding strategy. In periods with low phytoplankton abundance—for example after the spring bloom—they may depend for food on microzooplankton and faecal pellets. It would therefore be necessary to revise the traditional planktonic food web with results also including the microbial loop (figure 4.3). In effect, a whole range of autotrophic organisms supply energy to a wide variety of heterotrophic organisms that ultimately support the growth of fish larvae and larger organisms (Buch 2002). The Arctic Ocean is not that different from other oceans, except that it is characterised by an extreme seasonality and some specific adaptations to a demanding and unpredictable environment.

Specific studies on the vertical export of biogenic matter suggest features that may also be true for other Arctic Ocean areas (see Wassmann et al. 2003; Olli et al. 2006; Wexels Riser et al. 2006). Based on 24-hour measurements of 6-10 drifting sediment traps in the upper 200 m, we can identify some characteristic vertical flux profiles (figure 4.4). Vertical flux attenuation is basically a function of new production, suspended biomass accumulation, zooplankton grazing and microbial degradation. While the first two determine export production, i.e., the amount of biogenic matter that enters the aphotic zone, the last two determine the relative efficiency of vertical flux attenuation. The southern region of the SIZ, characterised by prominent ice-edge blooms and a plethora of zooplankton organisms, stands out for its high export production and vertical flux attenuation. Consequently, vertical export exhibits a marked curvature, especially above 60 m depth (figure 4.4-*A*). In the northern SIZ, ice-edge blooms and zooplankton abundance are lower, while vertical flux attenuation is on a smaller scale and occurs mainly in the uppermost part of the aphotic zone (figure 4.4-*B*). Close to the North Pole (Olli et al. 2006), there is extensive grazing and also extensive retention of the low quantities of freshly produced biogenic matter, presumably taking place above the uppermost sediment trap (30 m), which is why no vertical flux attenuation is observed (figure 4.4-*C*). In the open waters of the Barents Sea with its high primary production and weak vertical stratification, vertical mixing is considerable. The rich amounts of vertical export are not only grazed, but also mixed deeper into the water column. As a consequence, vertical export from the upper layers is lower compared to the southern SIZ, but higher at depth (figure 4.1-*D*). Pelagic-benthic coupling and phasing is thus likely to be fairly dynamic in time and space, albeit with its variability in the Arctic Ocean only rudimentarily understood.

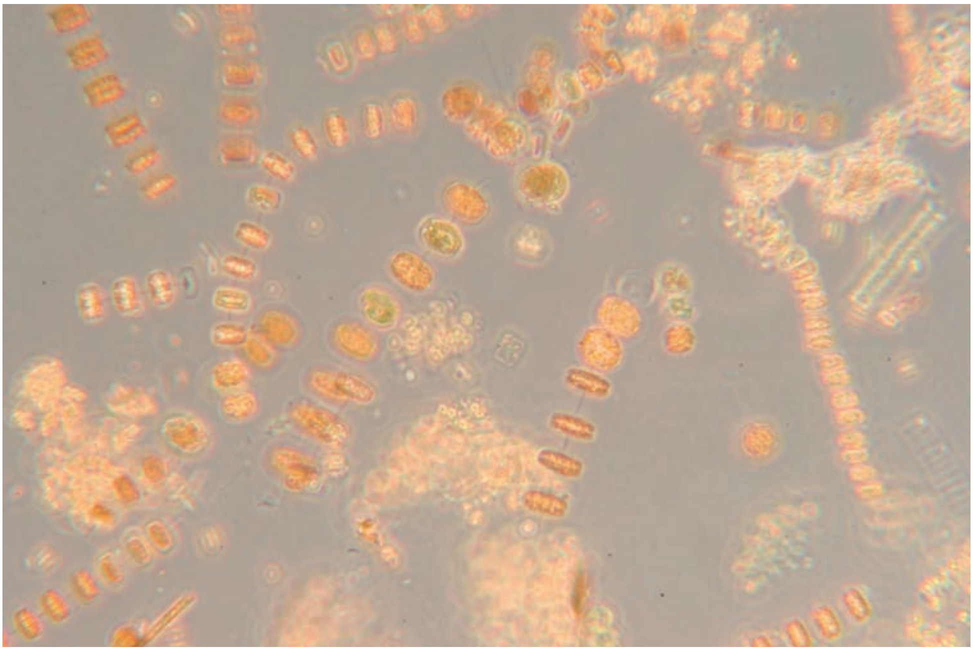
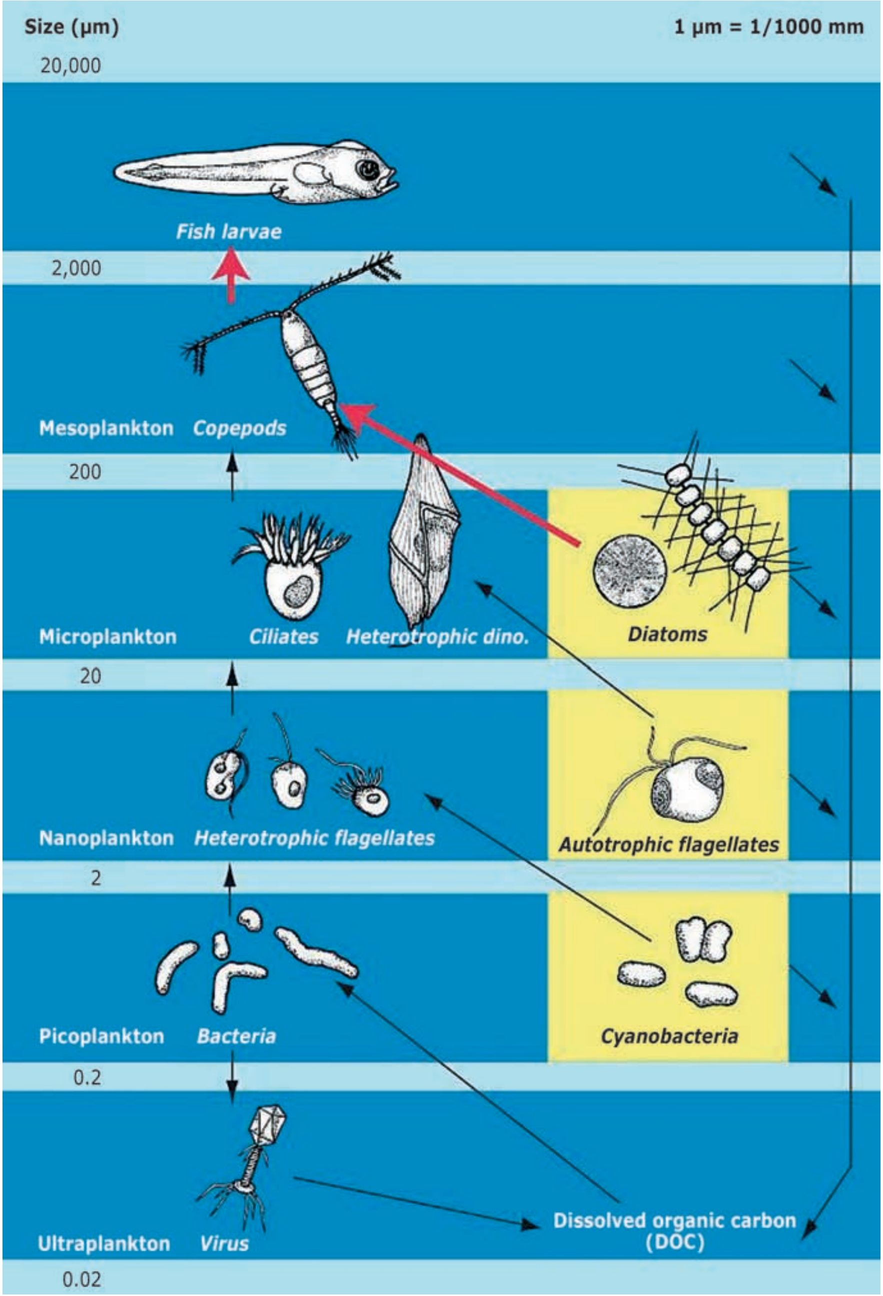


Photo 4.3: Microscopic view of Arctic marine diatom *Thalassiosira nordenskioeldii*

Photo 4.4: The calanoid copepod *Calanus hyperboreus*, one of the most important grazers in the Greenland Sea and Arctic Ocean

Figure 4.3: The Arctic food web ordered by size and characterised by key organisms (autotrophs on the right and heterotrophs on the left)



In addition to the classical food web (large phytoplankton, copepods, fish larvae), the microbial food web also plays an important role in the Arctic Ocean, according to recent research.

Source: Buch 2002.

Vertical flux measurements and tracer studies on the Arctic Ocean shelves indicate tight linkages between pelagic and benthic ecosystem components. Climate change may influence the processes governing geochemical cycling pathways, like the migration and overwintering capabilities of zooplankton and the dynamics of the microbial food web, with cascading effects on benthic communities, including species targeted by fisheries. In this section, we speculate as to what a region currently dominated by MYI might experience in terms of pelagic-benthic coupling during global warming and ice reduction. Of the scenarios reflected in figure 4.4, we would start with scenario *C*, followed by *B* and *A*. Finally, when the ice has withdrawn for good and remaining freshwater stratification has broken down, we might even have to confront scenario *D*. Global warming and ice reduction will not only change primary production and vertical flux attenuation, they will also strongly affect pelagic-benthic coupling and phasing in the Arctic Ocean, in particular on the shallow shelves. When the vertical export of biogenic matter moves from situation *A* to *C* at depths greater than 50 m, the increase in biogenic matter supply to the benthic boundary layer and sediments is more than an order of magnitude (figure 4.4). Thus, global warming and its accompanying ice thinning and reduction will most probably entail dramatic changes for the benthic communities on the northernmost shelves. These changes, however, are hard to predict and evaluate, because we start from too little data and too limited an

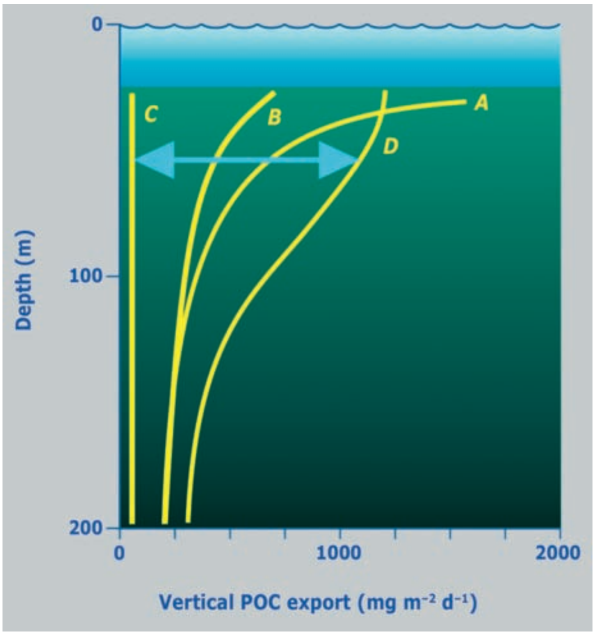


Figure 4.4: Representative and schematic vertical export profiles of particulate organic carbon (POC) in the upper 200 metres of the open Barents Sea (*D*), its marginal ice zone (*A*, *B*) and the permanently ice-covered central Arctic Ocean (*C*). The horizontal arrow suggests the potential increase in vertical export at about 50 metres depth assuming a change from permanent ice cover (*C*) to marginal ice (*D*), due to Arctic Ocean warming. The figure shows how vertical sediment flux would react to the loss of the ice cover, from curve *C* to curve *D*.

Source: Figure redrawn and changed from Carmack and Wassmann 2006.

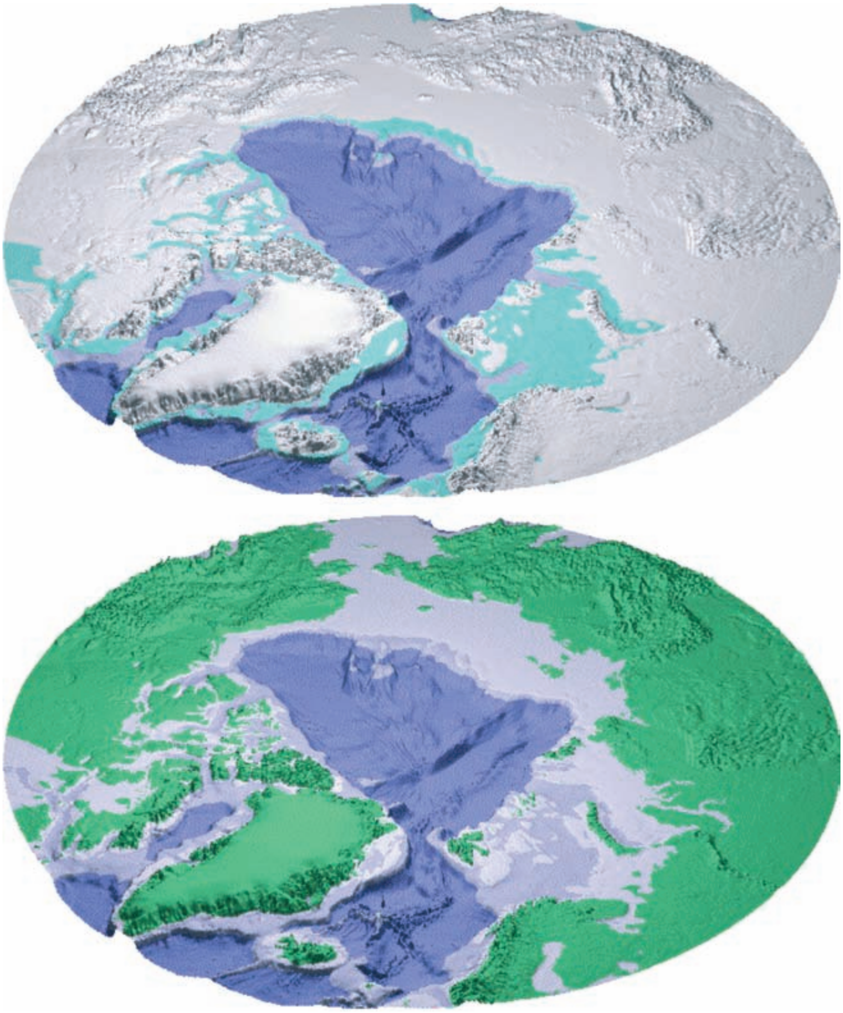
understanding. Only through a combination of focused, long-term experiments and synthetic efforts in the region will it be possible to evaluate these critical vertical exchange processes and their sensitivity to climate change.

4.6. PHYSICAL-BIOLOGICAL FORCING OF ARCTIC SHELVES: PAST, PRESENT, FUTURE

CO_2 levels are already double what they were at the peaks of glacial-interglacial fluctuations, and rising fast. With continued loading of greenhouse gasses into the atmosphere, the future Arctic Ocean is likely to have far less multi-year ice than it does at present and perhaps, eventually, none (see Johannessen et al. 2002). It is therefore worth considering how the Arctic Ocean may have functioned at various times in the past. For example, how does the present Arctic Ocean differ in structure and function compared to the end of the last glacial period? Did it have completely different environmental conditions or has it evolved gradually to its present state? To answer these questions, it is useful to start with the freshwater budget and stratification. In the modern Arctic Ocean, the freshwater budget is dominated by river inflows, Pacific inflows through the Bering Strait and water mass transformations on the broad pan-Arctic shelves (map 4.5). However, only 10,000 years ago, sea level was more than 100 metres lower, massive glaciers may have blocked many of the north-draining rivers, the Bering Strait was closed and shelves were practically non existent (map 4.5). The rivers drained directly over the shelf break into the Arctic Ocean, and the water column of the outer shelves was subject to no tidal modifications (Carmack et al. 2006). There was almost no shelf, the permafrost extended to what is currently the shelf edge, and the Arctic Ocean was basically a set of basins. Going back further in time, to the early Pliocene (~5-3 million years in the past), sea level was higher than at present (~25 m), surface temperatures were considerably hotter, and the belief is that there were no glaciers in the Northern Hemisphere.

These “paleoscenarios” provide us with a spectrum of possible futures within which to consider the impact of change on northern food chains. For example, the projected 1-2 m increase in sea level over coming decades and planetary warming will result in large-scale erosion of coastal regions, and an increase in river discharge is to be expected. The combined effects will be a higher discharge of terrestrial organic matter into the Arctic Ocean, decreased primary production on the shallow shelves (induced by increased turbidity) and possible food web expansion on the interior shelves. Further,

Map 4.5: The Arctic Ocean region 12,000 years ago (above) and at present (below)



The image shows the low water level at the end of the last glacial age, when the Bering Strait was closed.

Source: Carmack and Wassmann (2006).

Aagaard and Carmack (1994) proposed a simple conceptual model of convective renewal occurring at various sites in the Arctic Ocean and adjacent seas under varying scenarios of increased and decreased freshwater supply. If these physical systems were to undergo catastrophic (abrupt) change, so too would their ecological functions. A logical consequence is that gyres and fronts would shift along with physical habitats, triggering changes in the structure and function of the food web.

The pan-Arctic shelves have gone through radically different phases in the geologically recent past, punctuated by abrupt changes in state. Whether or not we see the Arctic Ocean as moving to a new state outside the known paleo-record is thus a question of the time interval we choose to consider. The immense changes in Arctic Ocean climate forcing over relatively short evolutionary time scales suggest that its ecosystems are capable of coping with additional fluctuations, however abrupt, but the survival of individual species is a lot less certain. Points of no return, where climate forcing irreversibly alters the state of an ecosystem, are extremely hard to assess and may simply not exist in the case of the Arctic.

In sum, we can conclude that global warming, now and even more so in the future, will cause the recession and thinning of the ice cover, an increase in primary production, and the advent of boreal and subsequent reduction of Arctic species. The supply of organic matter to the benthic boundary layer and sediment will increase, particularly in the northernmost pan-Arctic shelf regions. Collectively, this will profoundly change the biogeochemistry of the Arctic Ocean with global ramifications that are inadequately known. In addition, these changes will impact on higher trophic levels in the northern

Photo 4.5: Walruses *(Odobenus rosmarus)*. These corpulent marine mammals dive to the bottom of the shallow Arctic shelves in search of the bivalves they feed on. The retreat of the ice cover on Arctic continental shelves is causing a decline in their ideal habitat.

regions, including human beings. Marine bird colonies may suffer the loss of feeding grounds, seals may lose their resting sites, and polar bears may be deprived of their feeding habitat while facing human encroachment on their overwintering and hunting sites. These changes will also interfere with settled hunter communities, who may have problems reaching their northward-moving hunting grounds or may even lose them altogether. In both cases, this will have severe implication for their livelihoods.

4.7. ARCTIC MARINE RESEARCH: A PRESSING NEED FOR INTERNATIONAL COOPERATION

The lack of a consistent perception of the Arctic Ocean means the first challenge is to acquire a more balanced view of pan-Arctic shelves and their adjacent, deep-ocean basins. The reduction in sea ice and the establishment of commercial and industrial activities in what is commonly assumed to be among the most pristine of ecosystems obliges us to reflect on the ecological consequences of both climate change and regional human activities. Whatever scientists and policy-makers do, they must do it together. The first step should be a collaborative effort to recognise and fully understand the characteristics of the Arctic Ocean, including the social domain and its responses to changes. This will enable the development of more effective adaptation and mitigation strategies to address global warming and other anthropogenic activities affecting the Arctic.

Changes in the Arctic Ocean ecosystem and their effects on ecosystem functioning and human conditions are a significant challenge that deserves the attention of all Northern Hemisphere nations. Improved research on the Arctic is also indispensable for the strategic interests of Europe. The management of marine systems must demonstrably be based on scientific knowledge, environmentally safe resource exploitation and precautionary principles. An efficient European marine ecological research programme in the pan-Arctic region calls for actions and structures that advance and enlarge on the current strategy with the support of general scientific principles opportunely applied.

ACKNOWLEDGEMENTS

I wish to thank Fundación BBVA for the invitation to participate in the scientific debate on “Impacts of Global Warming on Polar Ecosystems”. This publication was supported by the Research Council of Norway (Nordklima) projects “Carbon flux and ecosystem feedback in the northern Barents Sea in an era

of climate change" (CABANERA) and "Marine climate and ecosystems in the seasonal ice zone" (MACESIZ). This chapter benefited from discussions to plan the Arctic Tipping Points project, funded by the European Commission.

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5. EFFECTS OF GLOBAL WARMING ON ARCTIC SEA-FLOOR COMMUNITIES AND ITS CONSEQUENCES FOR HIGHER TROPHIC LEVELS

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5.1. INTRODUCTION

A CONSPICUOUS FEATURE OF THE ARCTIC OCEAN is the vast extent of continental shelf beneath the marginal seas. While the ecology of bottom communities (benthos) of the deep Arctic Ocean remains largely unexplored, research efforts over the past 25 years have expanded our understanding of the structure and function of the biological communities of the Arctic shelf seas. One emerging result is that shelf benthos may play a more important role in carbon cycling in the Arctic than at lower latitudes. Climate change, which has been predicted to be disproportionately greater in the Arctic than at lower latitudes, will likely alter benthic biodiversity, community structure and trophic interactions. This will take place through direct pathways such as temperature change and via indirect effects on ice and water mass distributions, primary production, and sedimentation. We draw evidence from long-term data sets, case studies, and experimental results to predict potential changes to Arctic shelf benthic communities and their functional role in Arctic marine ecosystems under climate warming scenarios. As benthic communities are important for regional fisheries, seabirds and marine mammals, and indigenous peoples, the effects of climate change are more than just academic, and will likely be felt across the biological, economic, and social landscape of the Arctic and the world.

5.2. WHY STUDY BENTHOS?

Over 70% of the Earth's surface is inhabited by marine benthic communities. The majority of the sea floor is located in the deep sea; an area with no light, low density and biomass of organisms, and about which we know very little. In contrast, many seafloor habitats of continental shelves are ecological

◀ **Photo 5.1: The coastal zone of Spitsbergen Island is home to some of the Arctic's most widely studied benthic communities** hotspots (e.g., coral reefs, kelp forests, seagrass beds) and among the most productive and diverse in the world. From a global perspective, benthic communities support rich commercial fisheries and provide important "ecosystem goods and services" (Costanza et al. 1997).

Many species of commercially harvested fin fish (e.g., cod, plaice, turbot) and invertebrates (e.g., shrimp, crabs, lobsters) rely on infaunal and epifaunal invertebrates as food during at least part of their life. They are also dependent on benthic habitats for shelter, particularly as juveniles (Watling and Norse 1998; Turner et al. 1999), and vegetated soft sediments are critical habitat for a wide variety of vertebrates and invertebrates (Heck, Nadeau and Thomas 1997). Arctic soft-sediment communities are important sources of food for bottom-feeding mammals (walrus, bearded seal and grey whale) and birds (eider) (Oliver et al. 1983, Dayton 1990). Beyond providing food and habitat, however, other ecological functions provided by the benthos are less appreciated but equally significant.

Bottom communities are the repository of much of the material that reaches the ocean by river runoff and precipitation or that is produced in the overlying water. Organic matter from primary production in the water column and contaminants scavenged by sinking particles accumulate in sediments where their fate is determined by physical, biological, and chemical processes occurring at the sediment-water interface and within the sediment. A large portion of organic matter reaching the benthos may be remineralised (broken down), and the nutrients bound in this material mixed upward into the overlying waters. A smaller fraction accumulates in coastal and shelf sediments and may be removed from the carbon cycle for millions of years. Organisms such as corals and molluscs incorporate dissolved carbon dioxide (CO_2) into their skeletons, buffering ocean chemistry and helping to slow the rise in atmospheric CO_2 levels. Contaminants reaching the bottom are either buried or degraded, reducing their movement through the ecosystem. Benthic processes, therefore, can have large effects on carbon and nutrient cycling, and the availability of pollutants in marine ecosystems.

The long life and low mobility of many benthic organisms make them ideal monitors of environmental variability (Kröncke et al. 1998; Schöne et al. 2003). The hard parts of benthic organisms are well preserved after death and often contain a record of environmental conditions such as temperature (Klein, Lohmann and Thayer 1996; Ambrose et al. 2006), upwelling events (Jones and Allmon 1995), productivity (Eberwein and MacKensen 2006) and salinity and/or hydrology (Khim et al. 2003; Müeller-Lupp, Erlenkeuser and

Bauch 2003) during the animal's life (photo 5.2). Water column and benthic processes are particularly tightly coupled in the Arctic (Grebmeier, Feder and McRoy 1989; Ambrose and Renaud 1995; Piepenburg et al. 1997; Wollenburg and Kuhnt 2000). This is due to several factors, including strong seasonality, a mismatch between abundances of water column (pelagic) algae and grazing zooplankton, and perhaps a less efficient pelagic microbial community. Tight benthic-pelagic coupling is responsible for the benthos being particularly useful for storing a long-term, integrated picture of water column conditions in the Arctic.

Many benthic communities support a rich diversity of invertebrates with important ecosystem functions (photo 5.3). The deep sea is the least well known of all benthic communities, and has been estimated to contain up to 10 million species; far more than the 250,000 described (Grassle and Maciolek 1992). So few deep-sea taxa have been described that their roles in the structure and function of the deep-sea ecosystem or their potential commercial value as medicinal drugs are largely unknown. High latitude benthic communities have been even less studied. Due to the under-sampling of benthic habitats within the Arctic, it is difficult to make generalisations about their diversity or community structure. There is no evidence that Arctic shelves are any less diverse than those at lower latitudes (photo 5.3; Kendall 1996), and the pattern of decreasing diversity with increasing latitude common for many ter-

Photo 5.2: Growth bands in the shell of a large ocean quahog (*Arctica islandica*) collected in 1906 from the north Norwegian coast. The distances between the 56 annual growth lines provide a partial record of environmental conditions between 1850 and 1906.

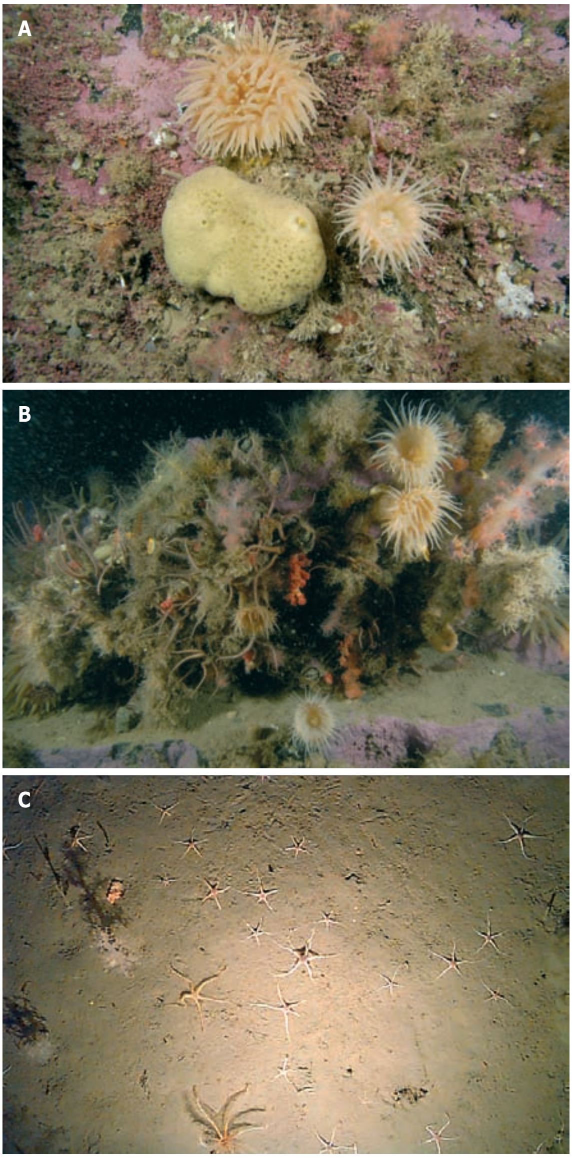


Photo 5.3: High-latitude benthic communities boast a rich diversity of species with important functions in the Arctic ecosystem

A and B: Two high-diversity benthic communities from around 20 m depth in northeastern Svalbard, in the Arctic Ocean. The photos feature coralline algae, filter-feeding invertebrates and small mobile animals. The horizontal dimension of the objects is approximately 50 cm.
C: Soft-bottom benthos from 180 m depth in the Beaufort Sea, in the Canadian Arctic. Brittle stars, crinoids (feather stars), and soft corals are clearly visible, but the majority of the biodiversity in soft-bottom habitats resides beneath the surface. The area of the frame is approximately 0.6 m^2.

restrial taxa does not hold for marine soft-sediment organisms (Kendall and Aschan 1993; Kröncke 1998).

Arctic benthos play key roles in the functioning of regional ecosystems. Soft sediments dominate high-latitude shelves and support some of the highest infaunal and epifaunal biomass in the world's ocean (see Piepenburg 2000). Several Arctic shelf communities rank among the ocean's most productive (Highsmith and Coyle 1990). The response of these communities to climate change will have a ripple effect throughout the Arctic ecosystem. Predicting the impact of climate change on Arctic shelf ecosystems, therefore, is dependent to a large extent on anticipating the response of Arctic benthos.

5.3. THE SCOPE OF THIS CHAPTER

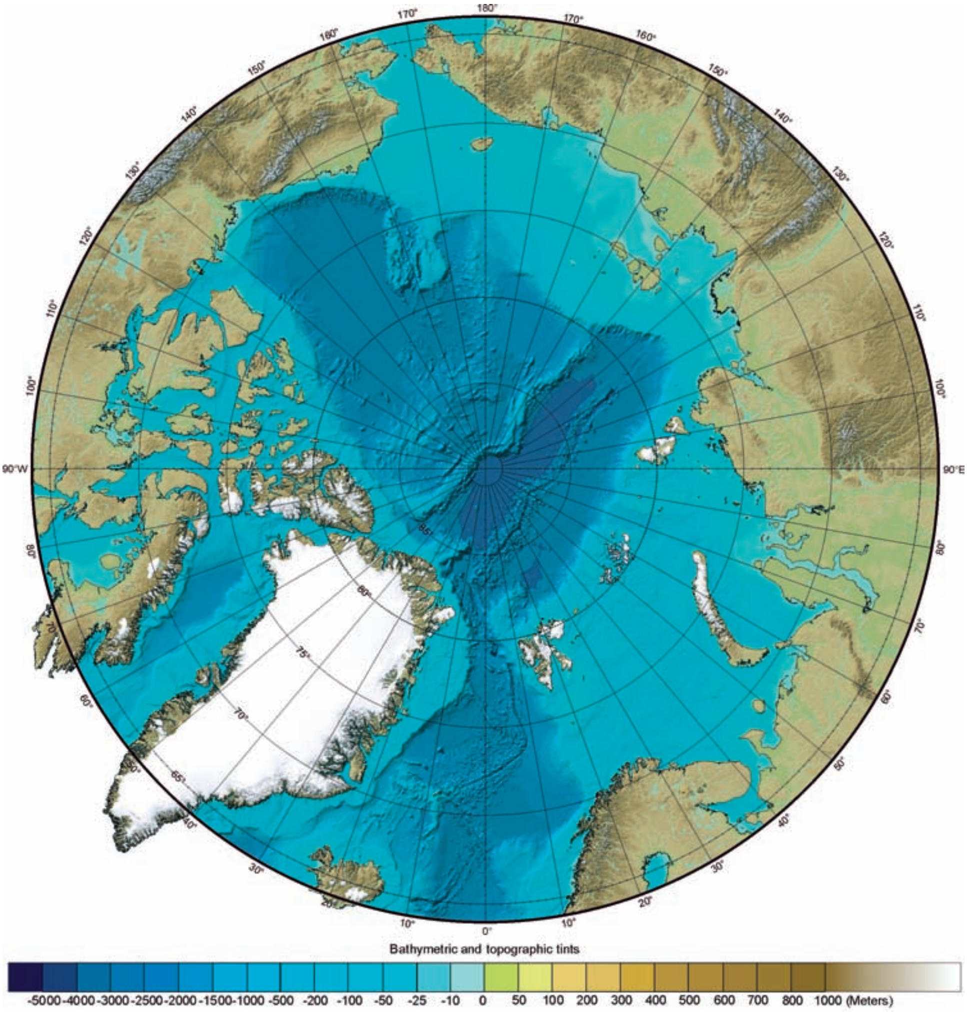
Arctic benthic ecology has been the subject of recent reviews (see Piepenburg 2005), and it is not our purpose here to duplicate these efforts. Instead, our goal is to predict potential effects of climate change on benthic communities and their consequences for Arctic marine ecosystems in general. Not surprisingly, we know far more about the benthic ecology of the seasonally ice-free Arctic shelves than the perpetually ice-covered slope and deep sea. Few studies of macrofaunal community structure have been conducted in the Arctic deep sea (Kröncke 1994, 1998; Bluhm et al. 2005; Renaud et al. 2006a) and even fewer studies of foraminifera (Wollenburg and Kuhnt 2000), meiofauna (Vanreusel et al. 2000), and benthic processes (Clough et al. 1997, 2005) have been performed there. The shelves of the Arctic Ocean represent 25% of all the ocean shelves (map 5.1), and the processes occurring on them impact deeper areas in the Arctic (Davis and Benner 2005), as well as biogeochemical cycles on a global scale (Carroll and Carroll 2003). The marginal seas of the Arctic Ocean (the Barents, Bering and Laptev seas for example) are reasonably well studied, and processes occurring there are known to impact much larger areas. Our focus, therefore, will be on the shelves and marginal seas of the Arctic Ocean, though we will also consider the impact of the likely northern retreat of the permanent ice in response to climate change on slope and deep-sea communities.

5.4. CLIMATE CHANGE AND CLIMATE VARIABILITY IN THE ARCTIC

5.4.1. A period of climate change

The Earth's climate, while always in flux, is presently experiencing a period of rapid change. The average surface air temperature rose by 0.6ºC during the 20th century, an increase likely to have been the largest of any century during the past 1,000 years (IPCC 2001). This period of climatic change has coincided with unprecedented and well-documented increases in concentrations of greenhouse gases (CO_2, CH_4, CO, NO_x). The complexity of the Earth's Atmosphere-Ocean-Biosphere system, however, has made it difficult to definitively attribute the cause of climatic fluctuations to human activities. Nevertheless, the latest consensus of an expert panel comprised of hundreds of scientists around the world is that "most of the observed increase in global average temperatures since the mid-20th century is very likely due to the increase in anthropogenic greenhouse gas concentrations" (IPCC 2001).

Map 5.1: International bathymetric chart of the Arctic Ocean and its marginal seas



The blue colour scale indicates depth. Note the large areas of the Arctic that are coloured light blue, indicating continental shelves (< 400 m depth).

Source: Based on the work of Jakobsson et al. (2000) and published with permission of the IBCAO project (International Bathymetric Chart of the Arctic Ocean).

Global warming trends have been amplified in the Arctic region relative to the global mean, with dramatic changes observed in the last several decades (see Overpeck et al. 1997; Johannessen et al. 2004; Hassol 2004). The average annual air temperature has increased by 1-4°C in the last half century, and water temperatures have warmed by 0.6°C since the beginning of the 20th century (Hassol 2004). This has been accompanied by changes in the Arctic hydrological cycle, weather patterns, and in the dynamics of sea ice. The trend of a warmer world seen in the last century is predicted not only to continue, but to accelerate. The results of large-scale simulations of future climate by several global climate models predict an additional 3°C rise in global average temperature by the end of this century (IPCC 2007), leading to further reduction in ice cover, changes in weather patterns and higher sea levels (Overpeck et al. 1997; IPCC 2007; Moritz, Bitz and Steij 2002). The polar regions are predicted to incur some of the most pronounced of these effects (Manabe and Stouffer 1994; Weller and Lange 1999; IPCC 2007). As these regions play important roles in climate regulation, we need to understand the potential response of Arctic marine ecosystems to environmental variation.

5.4.2. Temporal patterns of environmental variability

Environmental variability in the Arctic exists on multiple time scales, ranging from seasonal and interannual differences to decadal, centennial and millennial periods due to climatic oscillations (Dickson et al. 1988; Ebbesmeyer et al. 1990). Seasonal variability in the Arctic is greater than in most places on the planet: short, productive seasons contrast with months of ice cover and complete darkness. Organisms living here must tolerate changes in temperature, salinity, light regime and food supply, and do so through biochemical, behavioural, and ecological adaptations.

The existence of inter-annual variation is well documented in the meteorological (Dement'ev 1991) and oceanographic (Treshnikov and Baranov 1976; Nikiforov, Romanov and Romantsov 1989; Parkinson 1991) literature. In the European Arctic, annual primary production may be 30% higher during a "warm" year compared to a "cold" year (Slagstad and Wassmann 1997). While some ecosystem components may have little response to this interannual variability, it clearly drives other aspects of the ecosystem, both in the water column and on the sea floor.

Multi-annual to decadal time scales are under the primary influence of hemispheric-scale oscillatory climatic forcing. Those of primary influence in the

Arctic are the Arctic Oscillation (AO) (Thompson and Wallace 1998), North Atlantic Oscillation (NAO) (Hurrell 1995) and the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997). Climate oscillation indices are generally defined by atmospheric air pressure differences between fixed locations within their regions, and influence regional climate through the wind and weather patterns they generate and the resulting shifts in ocean currents. They occur in cycles with one phase lasting for several years to a decade or more before oscillating to a different state. Decadal-scale oscillations are important for studying ecosystem structure and function because they remain in a climate state long enough to allow the ecosystem to adjust to those conditions. Thus, identifying ecosystem function during different climate cycles can provide a foundation for understanding the likely oceanographic and ecological responses to a more sustained climatic shift.

While dramatic trends have taken place in the Arctic in the past several decades that have been attributed to "climate change", it is important to emphasise that climate change in the Arctic, as elsewhere, is a time-averaged shift in the relative proportion of warm vs. cold years, rather than a unidirectional change in physical variables. Any patterns associated with climate change will be superimposed over fluctuations taking place at other time scales. Despite such a variable baseline, long-term climatic trends have been detected across broad regions of the globe. But just as climate warming is not reflected by each year being slightly warmer than the previous one, all areas of the Arctic do not respond to climatic forcing in the same manner.

5.4.3. Spatial patterns of environmental variability

Since the Arctic takes in a large area of the planet, numerous factors influence both climate and ecosystems on a variety of sub-regional scales. General climate warming documented across the Arctic region masks large variations in temperature trends in different locations. Areas such as Alaska and western Russia have warmed by more than 1°C per decade over the past 30 years, while others, such as northeastern Canada, southwest Greenland and the Labrador Sea have exhibited cooling trends (Chapman and Walsh 1993; Serreze et al. 2000). In the Siberian and North American sectors of the Arctic, global warming is predicted to result in increased sea-surface temperatures, freshwater inflow and nutrient fluxes onto the shelf, and decreased sea-ice extent (Hassol 2004). Models for the European Arctic show that the inflow of warm, salty water via the North Atlantic and its subsequent sinking in the Greenland and Labrador seas (called thermohaline circulation) are extremely sensitive to changes in salinity and temperature (Broecker 1990, 1994; Manabe and Stouffer 1995; Clark et al. 2002). A surprisingly small change in Arctic surface water temperature or salinity in response to global warming has the potential to significantly weaken or stop the large-scale currents driven by thermohaline circulation (Broecker 1994, 1997).

Sea ice has also been definitively shown to be decreasing in both extent (Parkinson and Cavalieri 1989; Maslanik, Serreze and Barry 1996; Cavalieri et al. 1997) and thickness (see Wadhams 1990; Johannesen et al. 1995a, 1995b; Rothrock, Yu and Maykut 1999) over the past two decades. Yet there are regional differences in sea-ice trends as well. In fact, sea ice at any specific location in the Arctic is under the influence of both local factors controlling the growth and break-up of locally-produced sea ice, combined with basin-wide wind patterns that will shift the existing Arctic ice pack from one location to another (Cavalieri et al. 1997, Barber and Hanesiak 2004). Thus, one location's loss of sea ice may be another location's gain.

Regional oceanographic features also vary within the Arctic and predetermine to a large extent the impacts of climatic forcing, both locally and across the region. The Barents Sea and, to a lesser extent, the Bering and Chukchi seas are the gateways to the Arctic from the Atlantic and Pacific oceans respectively. Since the Arctic Ocean has a strong influence on global ocean circulation (Aagaard and Carmack 1989), climate effects on heat, salt, and water exchange at these gateways will have considerable and cascading effects. Biological processes taking place in these areas, including CO_2 uptake, geochemical transformations and biological production, may also be expected to change due to climate change, with potential impacts on global elemental cycles.

5.5. INSIGHTS FROM PALEOCEANOGRAPHY AND HISTORICAL CASE STUDIES

Studies of past changes in ecosystem structure can suggest potential responses of biotic communities to climate change and provide evidence as to the sensitivity of ecosystem drivers (e.g., ocean currents, nutrient distribution) to climate variability. We describe several case studies that illustrate possible ecosystem consequences of climate change. Many of these studies are correlative, so caution should be taken when interpreting or extrapolating results. Nevertheless, these studies are unusually integrative in their approach, synthesising data from studies of climate, oceanography, paleoproxies (see below), and pelagic and benthic biology. While they differ in their scope and comprehensiveness, these four studies illustrate how climate change dramatically affects ecosystems and confirm that human impacts on ecosystems may be far-reaching. In addition, they suggest which ecosystem components may provide evidence of this change and some likely ecological consequences of global warming.

5.5.1. Case Study 1: proxy studies of climate change over the past 3 million years

The field of paleoceanography is largely based on the quantification of biological, chemical, or geological indicators (proxies) that can be linked with specific oceanographic conditions. For example, stable (non-radioactive) isotopes of oxygen in the skeletons of marine plankton indicate the seawater temperature when the organisms were alive. The use of a combination of such proxies can help to describe environmental conditions at discrete periods in the geological past. Recently, paleoceanographers have used oxygen isotopes, radiocarbon and volcanic ash-layer dating, elemental ratios, and pelagic and benthic microfossil community structure to study climatic change at three levels of resolution in time: the past 11-12,000 years, the past 200,000 years, and the past 3 million years. Proxy data indicate good correspondence of large-scale oceanographic features and processes with warming and cooling cycles in the Earth's climate. A 1-2°C change in water temperature has had significant effects on thermohaline circulation (Bartoli et al. 2005), the position of oceanographic frontal zones (Fronval et al. 1998), global heat, salt, and freshwater budgets (Hald et al. 2004; Bartoli et al. 2005; Jennings et al. 2006) and glacial-interglacial cycles (Cronin et al. 1999). Many of these impacts on global ocean circulation and consequences for ecosystem processes are expressed in microfossils on the sea floor. Additionally, cyclical changes in climate over the past 11,000 years identified from fjord environments show good correspondence with large-scale ocean circulation (Sejrup et al. 2001; Hald et al. 2004), suggesting that these areas may be suitable for studying effects of climate change. Proxy studies, then, have shown the ocean to be sensitive to modest changes in climate, with benthic systems in high latitude environments being particularly responsive.

5.5.2. Case Study 2: human impacts and the structure of ecosystems

Human activities are increasing in the Arctic, and many may have direct or indirect impacts on benthic communities and general ecosystem structure. The best long-term data for human impacts on high latitude ecosystems come from direct impacts of fisheries. Atlantic cod (*Gadus morhua*) has attracted fishing fleets in the North Atlantic for centuries and has provided a valuable food supply and income source for many nations. The cod sits high in boreal and sub-Arctic food webs and, consequently, exerts some force on how the food web below it is structured. Cod, along with other target species of fisheries such as halibut, haddock and pollock, is a demersal predator; one that lives and feeds near the sea floor. Benthic prey comprise a large proportion of its diet at some stages in its life. Until recently, historical levels of fishing pressure have had an unquantified impact on cod population size. But using fishing log books from 19th century fleets, Rosenberg et al. (2005) calculated the biomass of the cod population on the Canadian Scotia Shelf at 1.26 x 10^6 megatonnes (mt) in 1852, compared with the current biomass of less than 5 x 10^4 megatonnes (mt)—a reduction of 96%.

Photo 5.4: Atlantic cod (*Gadus morhua*). This fish is a key piece in the Arctic food chain and among the most important fisheries in the North Atlantic.

While it is impossible to accurately predict the impact that such a reduction in top-predator biomass has had on the entire ecosystem, it is likely that the populations of pelagic fish and benthic organisms look very different today than they did 150 years ago.

One study has attempted to address the ecosystem effects of hunting of marine mammals in the western Barents Sea. Weslawski et al. (2000) used population estimates of the walrus and Greenland whale from 1600 to 1900, along with modern understanding of feeding energetics, to show that the virtually complete exploitation of these predatory species had major impacts on the regional food web. Greenland whales filter zooplankton from the water and would thus have the greatest impact on plankton populations, while walrus feed largely on benthic molluscs. Removal of these predators was suggested to result in significant increases in pelagic fish and piscivorous seabirds (gulls, auks), as well as bearded seals and diving ducks (eiders), since more of their prey would now be available. The Barents Sea today is characterised by generally high pelagic fish stocks and large breeding colonies of seabirds.

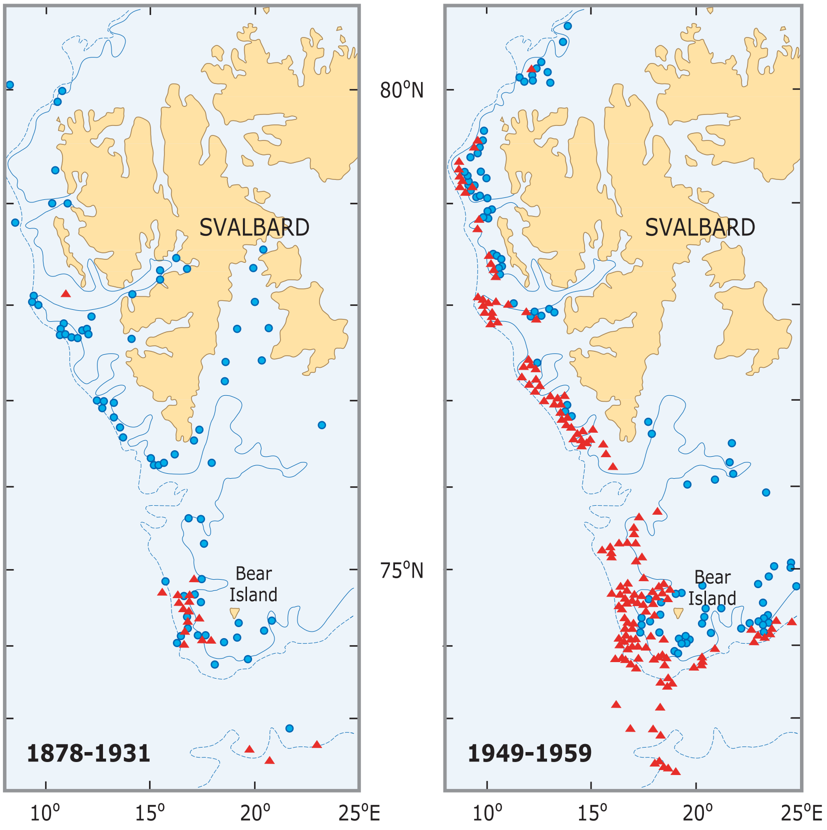
Fishing and hunting of marine mammals, therefore, may have already had significant impacts on high-latitude ecosystems through its removal of top predatory species. Fishing activities continue and may be expected to increase in a warmer, ice-free Arctic, applying further pressure on the system. This “top-down” effect may also be accompanied by an as yet unexplored “bottom-up” effect as climate change alters geographic ranges of food resources for numerous pelagic and benthic species that constitute the bottom of Arctic food chains.

5.5.3. Case Study 3: the 1920s and 1930s warming period

In the early 20th century, the North Atlantic experienced a general warming event that lasted for 30-40 years and serves as our best indicator of ecosystem response to global warming. In general, sea surface temperatures were elevated by 0.5 – 2°C compared to long-term averages, with some areas experiencing increases 2-3 times higher (Drinkwater 2006). While it is unclear how much warmer the Arctic will become due to the present warming, studies conducted over the first half of the 20th century provide insight into at least the initial changes to be expected over the next 30-50 years.

Drinkwater (2006) provides an enlightening review of ecosystem changes during this period. In general, northward expansion in the ranges of boreal fish

Map 5.2: Arctic fauna (blue circles) and boreal fauna (red triangles) of the Svalbard archipelago (Norway) in two time periods: 1878-1931 (left) and 1949-1959 (right)



These two maps chart the expansion of boreal fauna and the contraction of Arctic fauna following the warming period of the 1920s and 1930s.

Source: Redrafted from Blacker (1965) and published by kind permission of the editor of *Int. Commission. NW Atl. Fish Spec. Pub.*

and invertebrate species was observed throughout the region. Cod spread nearly 1200 km northward along the west coast of Greenland where a fishery for the species was established (Hansen 1949). Many other fish and benthic invertebrate species also expanded their ranges around Greenland (Hansen 1949; Tåning 1949; Cushing 1982), Svalbard (map 5.2; Blacker 1957, 1965) and in the central Barents Sea (Nesis 1960; Galkin 1998). These observations prompted the suggestion that long-lived benthic fauna integrate hydrographic processes over several years and that their distributions may be an excellent tool to assess long-term change in systems characterised by considerable short-term (daily to seasonal) variability (Blacker 1957). In fact, studies using perhaps the two longest benthic time series confirm this, tracking cyclical changes in benthos over 100-year time series in the south-central Barents Sea (Galkin 1998) and the English Channel (Southward et al. 2005). Both studies identify clear changes associated with the 1920s and 30s warming period and the preceding and following cool periods.

The warming period has been attributed to regional changes in atmospheric pressure fields and has led to increased storminess and warmer ocean temperatures in the Arctic region (Brooks 1938). Similar causes and consequences have been predicted for the current global warming phase (Hassol 2004). Drawing on modelling studies (Slagstad and Wassmann 1997), Drinkwater (2006) concluded that the ecosystem was responding to increased primary production ("bottom-up" effects). This retrospective analysis highlights just how drastic ecosystem reorganisation can be in response to climate change, and how benthic fauna will both be affected by and be useful indicators of large-scale climate change.

5.5.4. Case Study 4: regime shift in the Bering Sea

Recent events in the northern Bering Sea give another strong indication of what global warming may mean for ecosystem structure and function in Arctic marginal seas. Beginning in the late 1970s, and intensifying in the late 1980s, atmospheric conditions changed in the region, leading to a warming of 0.5-2.0°C (Overland and Stabeno 2004; Grebmeier et al. 2006). This has led to direct and indirect effects throughout the ecosystem, where biological communities and geochemical cycling pathways have changed dramatically. Such fundamental change over a broad geographical region has been termed a "regime shift".

The northern Bering Sea has shown signs of shifting from an Arctic sea with relatively low zooplankton stocks and considerable energy being processed by the benthos, to a system dominated by pelagic food webs (Overland et al. 2004). Food supply to benthic communities has been decreasing (Smith and Kaufmann 1999), leading to lower benthic community biomass and sediment carbon uptake (Grebmeier et al. 2006). Increases in pelagic fish, especially pollack, and zooplankton, and a sharp decrease in the abundance of benthic fish like the Greenland turbot (Brodeur and Ware 1992; Francis et al. 1998), have been accompanied by reductions in benthic-feeding mammals and seabirds (Francis et al. 1998). Sea ice is retreating earlier in the spring and impacting walrus behaviour and, potentially, their feeding and breeding suc-

Photo 5.5: Walrus (*Odobenus rosmarus*). This marine mammal depends for its food on the expanse of the shallow Arctic shelves.

cess (Grebmeier et al. 2006). It is unclear when this trend will slow or reverse, but climate models predict intensified warming over the next 50 years around the Arctic.

What will be the fate of the rest of the Arctic? What about just the European Arctic; another system with strong benthic-related fisheries and structuring by seasonal ice cover? If the Bering Sea model applies to the Barents Sea region, enhanced pelagic fisheries could provide significant economic benefit, but benthic shrimp and halibut stocks would decline strongly (Carroll and Carroll 2003). Rich benthic communities characterised by Arctic species would retreat northwards, with some loss of biodiversity possible, and birds and mammals dependent on benthic prey would also suffer. Conversely, the deeper Barents Sea may respond to climate warming in a different manner to the shallow Bering Sea. Clearly, ocean temperatures elevated only 2°C above current values are sufficient to have been linked with regime shifts over the past 3 million years. Human activities are another factor in determining the nature of ecosystem change and should be regulated with ecosystem impacts in mind. Research results from historical studies provide a valuable model to help predict the future of Arctic shelf ecosystems and must be combined with system-specific knowledge from other shelf regions to build reasonable models of ecosystem response to climate change.

5.6. IMPACTS ON THE ECOLOGY OF ARCTIC COMMUNITIES

The ecosystems of Arctic shelf seas are dynamic and productive, and their structure reflects the many interactions among organisms and the environment operating over different temporal and spatial scales. In addition, the structure and function of many Arctic shelf benthic communities are strongly linked to ocean currents, primary production, grazing and carbon flux taking place in the overlying water (Piepenburg et al. 1997). Since many effects of climate change on the benthos must also reflect impacts on the pelagic communities, predicting ecological response at the sea floor is a significant challenge. However, the integrative nature of benthic communities affords the opportunity to assess potential effects of climate scenarios.

5.6.1. Biodiversity and community structure

Contrary to earlier beliefs, the Arctic is not an area of particularly low benthic biodiversity (see Piepenburg 2005). Like most deep-sea areas, deep Arctic basins are generally low in biomass and abundance of meiofaunal (defined as 63-250 µm) (Vanreusel et al. 2000; Wollenburg and Kuhnt 2000) and macrofaunal (> 250 µm) (Kröncke 1994, 1998; Clough et al. 1997; Deubel 2000; Bluhm et al. 2005) taxa relative to nearby shelf sites. Differences in abundance, biomass and diversity within the deep Arctic basin have been linked to ecological factors such as food supply (Kröncke 1994, Wollenburg and Kuhnt 2000, Clough, Renaud and Ambrose 2005; Renaud et al. 2006a). Benthic communities on Arctic shelves have also been shown to be largely structured by food supply from the overlying water column (see Peterson and Curtis 1980; Grebmeier, Feder and McRoy 1989; Ambrose and Renaud 1995; Piepenburg et al. 1997), with some Arctic communities as productive as those at any latitude (Highsmith and Coyle 1990). Little endemism is evident on shelves or within the deep basins (Golikov and Scarlato 1989), and, as in many areas of the world's oceans, Arctic macrofaunal benthos is dominated by polychaete worms, molluscs, crustaceans and echinoderms. There is, however, a characteristic Arctic shelf fauna that does not tolerate temperatures above 2°C for extended periods of time and is adapted to ice-covered seas.

Ice cover, either seasonal or year-round, is one of the most striking characteristics of the Arctic and one affecting physical and biological characteristics of the marine habitat. Ice itself is a habitat for a wide variety of organisms ranging from microbes, algae and crustaceans to fish, seals and bears (Gradinger 1995). For two to three months each year, algae living within and attached to the sea ice provide food for ice-associated animals. This sympagic (ice-associated) food web is characterised by grazing amphipod crustaceans that in turn are prey for seabirds, seals and polar cod. The polar cod (*Boreogadus saida*) lives closely associated with the Arctic ice and is a key link in Arctic food webs between zooplankton species and higher trophic levels, including birds and mammals (Bradstreet et al. 1986; Lønne and Gulliksen 1989). Ice algae can become dislodged by currents or during ice melt (photo 5.6) and can be an important food source for benthic organisms (Legendre et al. 1992; McMahon et al. 2006), and cue rapid and significant increases in benthic respiration (Renaud et al. 2006b). Ice melt results in

Photo 5.6: Release of large quantities of ice algae (brown colouration in the water) during the break-up of an ice floe in the Barents Sea, in the Arctic Ocean. Ice algae nourish a rich under-ice (sympagic) community and, upon release from the ice, can sink rapidly to the sea floor, providing a rich early-season food supply to the benthos.

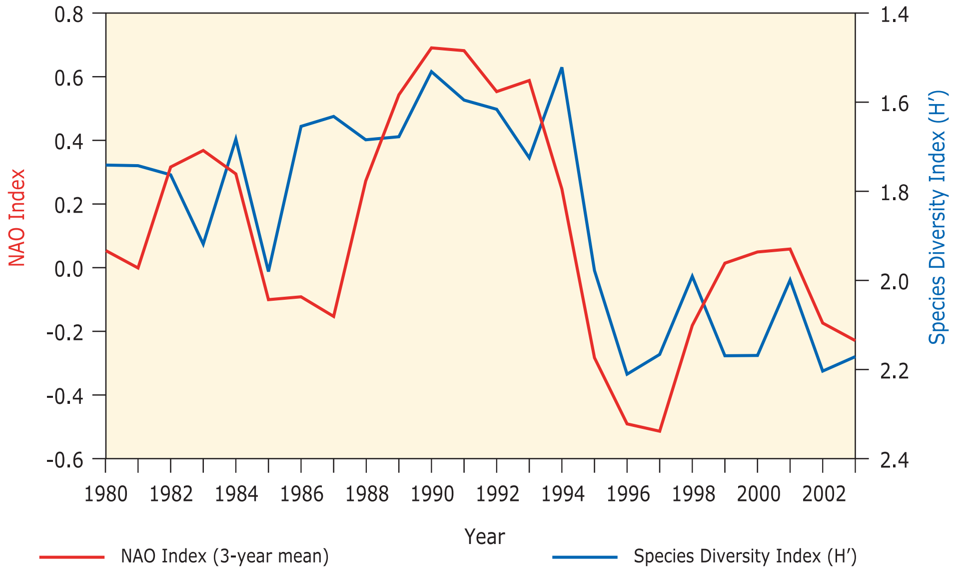
increased light penetration and water-column stratification, which lead to enhanced phytoplankton production (the “spring bloom”), with ice-edge areas exporting large amounts of their primary production to the sea floor (Gradinger 1995; Wassmann 2004).

A shift from today’s system of a multi-year ice pack in the Arctic basin and annual ice over the shelf regions to one of annual ice with ice-free summers will have major impacts on the biodiversity and structure of sea-ice communities, pelagic production regimes and benthic food supply. Thinner ice may permit better ice algal growth, but more rapid spring melting may reduce their growing season. Obligate ice taxa, especially those like the long-lived and ecologically important amphipod *Gammarus wilkitzkii* will decline. Mammal and seabird colonies relying on polar cod and sympagic fauna will have to change their foraging and perhaps breeding areas as prey items decline and aggregation patterns change (Gradinger 1995; Tynan and DeMaster 1997). Early ice break-up and reduction in seal populations will lead to declining health, mobility and population sizes of polar bears (Stirling, Lunn and Iacozza 1999; Derocher, Lunn and Stirling 2004). Ice-edge blooms will be displaced progressively northwards. This may continue to supply the shelf benthos with high quality food in the short term, but if the ice edge retreats past the shelf break, shelf communities will no longer benefit from this food source. Gradinger (1995) predicts increased phytoplankton production with less ice, but it is unclear that the benthos will benefit from this production if, as in the warming period of the 1920s and 1930s, pelagic food webs become more productive and “intercept” this food before it reaches the sea floor. Seabirds and mammals depend on the production of ice communities, as well as the ice itself as a habitat. Significant loss of ice as predicted by climate change models will undoubtedly have major impacts on these ecosystem components (see Ray et al. 2006).

Regional warming is likely to have important consequences for the physical characteristics of sea water, including temperature and salinity. Greater local warming and northward intrusion of Atlantic and Pacific waters onto Arctic shelves will result in warmer average temperatures for benthic organisms. Arctic species will likely not tolerate temperatures much above 2°C for extended periods of time, as has been noted by Nesis (1960). Warmer water will allow northward expansion of the ranges of boreal species (Berge et al. 2005), and the potential for increased commercial and recreational shipping traffic presents new vectors for the introduction of expatriate species from other oceans to the Arctic. Temperature change associated with climate oscillation was found to affect patterns in a hard-bottom macrobenthic community in Svalbard, as local diversity was positively correlated with water temperature (figure 5.1; Beuchel, Gulliksen and Carroll 2006). This study shows that benthic systems are resilient to natural climate oscillations over decadal scales. Projected warming trajectories, however, exceed the intensity and time scales for which communities have been shown to recover. Retreat of Arctic shelf fauna with incursion of boreal taxa can only proceed so far. Once boreal taxa have colonised to the shelf break, there will remain few refugia from which Arctic taxa can recolonise. Under a worst-case scenario, but one that is distinctly possible based on current models, many Arctic shelf-benthos taxa could become extinct if they are unable to survive in slope or deep-sea habitats.

Coastal environments are predicted to experience decreased salinities, due not only to increased ice melt, but also from considerably higher riverine dis-

Figure 5.1: Trends from 1980 to 2003 of the North Atlantic Oscillation (NAO) and of the Shannon-Wiener (H') species diversity index of hard-bottom benthic communities in Kongsfjorden (Svalbard, Norway)



The NAO index is a three-year running mean, and a value of 0 indicates the average for the index for the time period studied. The close correlation between it and the Shannon-Wiener index suggests that diversity is related to NAO climate forcing. According to a paper published by Beuchel, Gulliksen and Carroll (2006), water temperature has a strong positive relationship with the NAO index.

Source: Figure reprinted from Beuchel, Gulliksen and Carroll (2006), with permission from Elsevier.

charges as the ice pack and permafrost melt and regional precipitation increases (Hassol 2004). Benthic organisms in coastal habitats, especially along the Siberian and Beaufort Sea shelves where major rivers enter the Arctic Ocean, will suffer from this in several ways. Direct mortality is likely as salinities decrease, especially within and immediately adjacent to river plumes. Benthic fauna with pelagic larvae may be excluded from areas with surface salinities below larval tolerances, even if bottom waters are adequate for adult survival. Finally, effects on pelagic primary production may influence the quality and quantity of food for benthic organisms.

Increased storminess and river discharge will have an additional effect on coastal benthos. Higher wave action and reduced ice cover will enhance erosion of coastal environments and is already doing so in some areas of the Arctic (Hassol 2004). Increased turbidity from both erosion and riverine sediment loads will reduce the light available for pelagic and benthic algal production, as well as restricting benthic communities to those functional groups able to tolerate heavy sediment loads. This effect may exclude long-lived species, including filter-feeding bivalves important for walrus and diving birds, from impacted habitats. Reduced benthic biodiversity is a likely consequence, as demonstrated in a comparative study by Wlodarska-Kowalczuk and Weslawski (2001).

5.6.2. Carbon cycling

Community structure dictates how that community will function ecologically. A primary function of benthic communities throughout the world's oceans is to process (cycle) organic carbon, thus regenerating inorganic constituents (CO_2, ammonium, silicate) for use by primary producers. This is an especially important role of the benthos in Arctic ecosystems because, firstly, a relatively high proportion of fixed carbon sinks to the sea floor and, secondly, recycled dissolved and particulate material exiting the Arctic Ocean enters the global thermohaline circulation; an engine of heat transport for the entire planet and an important mechanism for storing anthropogenic CO_2. Currently, much of the modification of organic matter going into and coming out of the Arctic Ocean takes place in its marginal shelf seas.

Little is known about carbon cycling by benthos within the deep Arctic Ocean (see Clough, Renaud and Ambrose 2005), but benthic carbon cycling can respond rapidly to food inputs (Svalbard fjord: McMahon et al. 2006; Beaufort Sea: Renaud et al. 2006b), and rates are within the range of those measured from lower latitudes (Glud et al. 1998, Clough, Renaud and Ambrose 2005). While cycling rates depend on how the benthic community is structured, it is clear that the pelagic community may also be important in determining cycling rates. Climate warming, leading to altered ice algal abundance, zooplankton community composition and timing of algal blooms, will impact how much organic matter reaches the benthos. If zooplankton are able to overwinter on warmer Arctic shelves, then their populations may be better matched to phytoplankton blooms, resulting in less food for the benthos. Alternatively, peak primary production earlier in the year may lead to a wider "mismatch" in the two populations and delivery of more organic matter to the sea floor. Clearly, this is a question of particular importance for benthic communities, but one requiring more data before reasonable predictions can be made.

Finally, one reason that macrofauna are so important on Arctic shelves is that bacterial communities are less active in cold habitats with low food concentrations (see Rysgaard et al 1998). Increased food deposition—from pelagic productivity and riverine discharges—and an increase in bottom-water temperature will likely result in higher bacterial cycling of carbon. In some areas, less than 10% of the carbon reaching the seafloor may be permanently buried (Glud et al. 1998). If a significant fraction of that carbon is recycled in a warmer Arctic, then less atmospheric CO_2 will be absorbed by the ocean. This positive feedback could result in an escalating impact of anthropogenic CO_2 emissions, intensifying global warming.

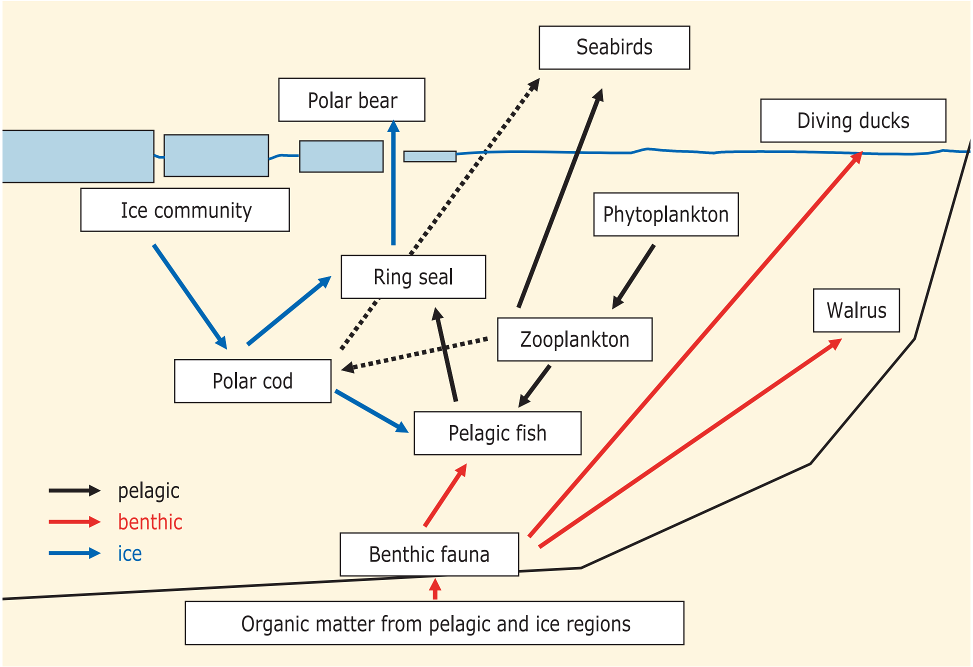
5.6.3. Reproduction

Little work has been conducted on the reproduction of Arctic benthos since the mid-1900s, but there is evidence that some benthic organisms may time various stages in their reproductive cycle to coincide with peak periods of organic matter deposition (Ambrose and Renaud 1997). A change in seasonality, quantity or quality of deposition may create a mismatch with faunal reproductive cycles. On the other hand, it has been proposed that deposition may serve as a cue for reproductive activity in some benthic taxa (Renaud et al. 2006b), in which case fauna may be more flexible in their response to changing conditions. Once larvae are produced, a warmer, more productive water column may result in faster growth, a larger size at settlement and perhaps better survivorship. This all depends upon a number of factors related to mortality and competition for food in the pelagic system, however, and no data exist on these topics from the Arctic.

5.6.4. Trophic interactions

The flow of energy within an ecosystem is mediated through trophic (predator-prey) interactions among community members. Changes in predominance of certain trophic pathways can have cascading ecological effects on the entire community (figure 5.2). These changes can arise from a change in predator populations (top-down) or variation in prey abundance (bottom-up). As discussed above, climate warming can lead to either, or both, of these effects. Warmer ocean temperatures and retreat of sea ice may increase predator pressure on benthic amphipod populations in the Bering Sea as the system becomes more pelagic-driven (Coyle and Highsmith 1994). These dense amphipod beds are important food resources for migrating grey whales, so increased fish predation could have impacts reaching to the top of the food web. Fish predation in this region has already been implicated as an agent of change in benthic community structure, as predatory fish populations increase during warm periods and decrease in cooler periods (Coyle et al. 2007). Per-

Figure 5.2: Simplified Arctic food web showing major links of the ice- (blue), pelagic- (black), and benthic- (red) based food chains



This shows the implications for higher trophic levels of a hypothesised reduction in the importance of ice and benthic food webs that may be a consequence of climate warming.

sistent warming in this region may, then, shunt energy from grey whales and other benthic predators (walrus, crabs) to fish.

Declining ice cover will initially serve to concentrate food resources associated with the ice habitat. Ice fauna and predators of ice fauna (polar cod, seals) will, in the short term, have improved feeding and, presumably, reproductive success. Increased density of seals in good condition will be reflected at the next step in the food web as the hunting success of polar bears increases (Rosing-Asvid 2006). Prolonged ice loss, however, will have negative "bottom-up" consequences for predators as the density and condition of prey species declines (photo 5.7). This points out the potentially conflicting effects of short- and long-term ecosystem response to climate change.

Coastal benthic communities may experience higher sedimentation and decreased sediment stability as storms and riverine runoff increase. The resulting community shift toward short-lived, opportunistic surface-burrowing taxa will reduce food resources for walrus and diving birds feeding

Photo 5.7: Polar bears feeding on a ringed seal on a Barents Sea ice floe, in the Arctic Ocean. In addition to its impact on food supplies for pelagic and benthic components of the food web, sea-ice distribution is an important regulator of the foraging success and population dynamics of top predators. This image highlights one mechanism whereby climate warming has ecological consequences across the Arctic ecosystem.

on the benthos. These higher predators consume long-lived benthic bivalves and crustaceans, many of which could be lost under high sedimentation regimes. Walrus, already at risk because of decline in their ice habitat, play an important ecosystem role as their foraging activities maintain benthic-habitat heterogeneity, and therefore local biodiversity, and enhance nutrient release from sediments for use by phytoplankton (Ray et al. 2006). The potential cascading effects of their decline illustrate the closely linked nature of Arctic ecosystems.

Ecological processes studied across the Arctic over a wide range of scales, therefore, can be used to predict impacts of global warming on the structure and function of benthic communities and the consequences for higher trophic levels. Ecosystems operate at the interface of physics, chemistry and biology, with both complementary and contradictory interactions. The studies cited here by no means represent a consensus, or results that can be clearly extrapolated across all scales of space and time. Still, they are, along with historical studies, the best tools ecosystem scientists have to inform models of climate change across this multidisciplinary interface.

5.7. RESEARCH RECOMMENDATIONS

Climate change, long a research focus of scientists, has captured the attention of the public and the media, but also scientific funding agencies around the world. International Polar Year 2007-2008 will provide a frame for unprecedented research efforts, many aimed at identifying the potential consequences of global warming in the Arctic. Decisions about which regions, processes and communities will be most productive to focus upon, and the scales in time and space to conduct the studies, must be informed by our current knowledge base—and perhaps a few “best guesses”. A combination of long-term monitoring, proxy studies and manipulative experiments should provide input data for a growing number and variety of ecosystem models. Concerted efforts across the pan-Arctic domain will be required to obtain the necessary perspective with which to make meaningful predictions.

Observational mooring networks armed with arrays of physical and biological sampling equipment are already coming into place. Situated in areas critical for hydrological and biological exchange, these networks can provide multi-annual records of water mass distributions and vertical and horizontal transport. Long time series currently conducted at “Hausgarten,” a research site in the northern Greenland Sea (Soltwedel et al. 2005), augment instrumental data with process studies. Other time series include national fisheries surveys, satellite-based remote sensing and many projects conducted by researchers around the Arctic on specific taxa or groups of organisms. Long-term studies of benthic communities are necessary to detect long-term patterns of change against a background of interannual variability and decadal oscillations. Examples of such studies include soft-sediment benthic community studies conducted over more than 20 years in Svalbard fjords (see Renaud et al. 2006c), an over 25-year survey of hard-bottom benthic communities (Beuchel, Gulliksen and Carroll 2006) and more than 100 years of benthic studies in the Barents Sea (Galkin 1998). Comparisons with studies dating back to the mid-19th century are possible in some areas (Mørch 1869).

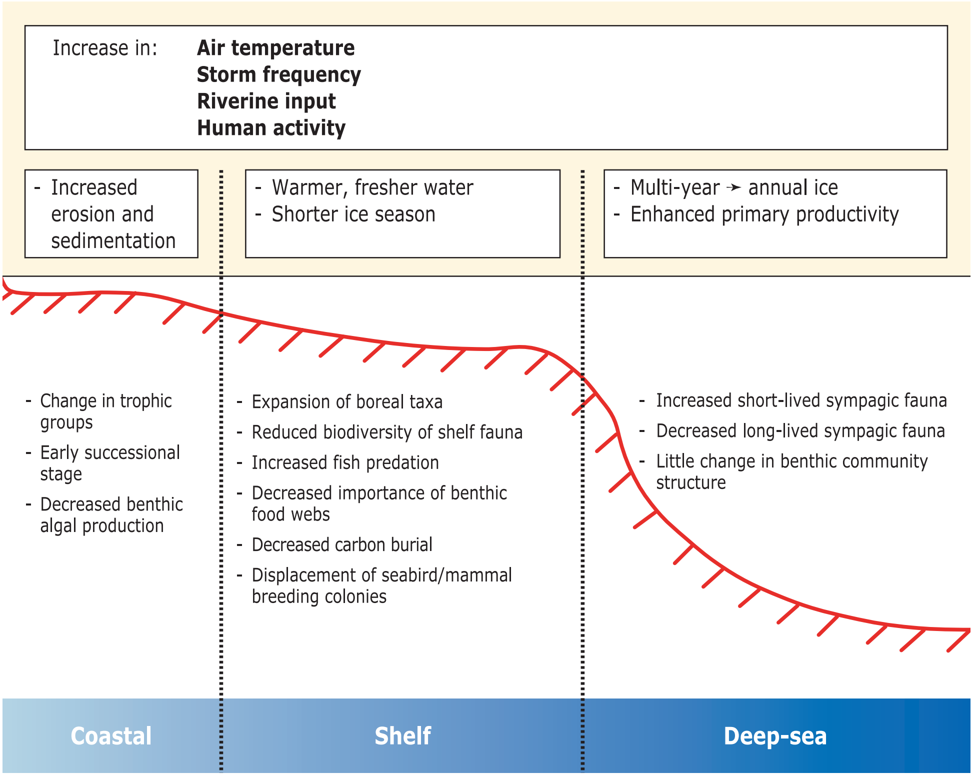
As discussed above, the sediment record preserves proxies of oceanographic conditions and provides valuable insight into the effects of climate change on benthic communities over many time scales. In addition, ecological conditions responsible for the growth of benthic organisms are recorded in their skeletal components. Ambrose et al. (2006) have linked variability in the growth of an Arctic bivalve mollusc with climatic oscillations. Long-lived benthic fauna, such as molluscs and corals, that preserve these records in their skeletons can be used to identify ecologically relevant changes occurring from the present day back hundreds of years or longer. Shells from dated storm deposits and historical collections can add to that record, possibly linking with data of paleoceanographers and creating a long-term continuous record.

Experimental studies offer the opportunity to investigate in detail specific processes of ecosystem significance. “Natural experiments” use fjords, ice-edge areas or polynyas to compare possible future scenarios with present-day conditions; that is, substituting space for time (see, for example, Wlodarska-Kowalczuk and Weslawski 2001). Studies of iceberg-scour disturbances may provide insight into benthic response to increased bottom fishing. Manipulative experiments are used to identify the mechanisms by which climate change may act on the benthos. Examples include thermal tolerance studies on Arctic species, consequences of sedimentation on feeding efficiency of benthic taxa, feeding preference experiments and studies of the relative food values of ice algae and phytoplankton for benthic fauna. Experimental studies of any type should select taxa and locations that play important roles in Arctic ecosystem function and are expected to be most sensitive or useful as sentinels of system change.

5.8. CONCLUSIONS

Emerging evidence from studies of Arctic shelf seas indicates that benthic processes in these regions have global significance in terms of ecology and oceanography and as a resource for human populations. Climate oscillations over different scales of time and space have impacted Arctic ecosystems for millennia and continue to do so. Historical studies suggest a modest increase in ocean temperature (+2°C) is sufficient to cause major ecological regime shifts. The current global-warming scenarios predict disproportionately intense effects for much of the Arctic, and it is unclear how long these new climate patterns will influence the region. It is likely that boreal taxa will spread northwards, displacing Arctic fauna across wide areas of continental shelf. Regional, and perhaps global, biodiversity will suffer should boreal taxa spread to the shelf break, leav-

Figure 5.3: Predicted direct effects of climate change (top box), impacts on regions within the Arctic (centre), and responses of the benthic communities in the three depth-defined domains



These predictions are based on responses to historical climate change and results of monitoring and experimental results of recent scientific studies.

ing few refuges for Arctic shelf fauna. Indirect effects of warming on salinity, turbidity and sedimentation will further influence the community structure of coastal benthos. Energy flow may be redirected from food webs with considerable amounts of energy currently being cycled through the benthos to more pelagic-dominated food webs. Ecological regime shifts coupled with altered sea-ice dynamics will have important implications for seabirds and marine mammals feeding on benthic and ice-associated organisms. Changes in the timing, quality and quantity of food supply to the sea floor are also likely, with consequences for carbon cycling and burial processes (figure 5.3).

These potential ecosystem changes for Arctic benthic communities can be moderated or enhanced, depending upon the human response to warnings about global warming. A warmer Arctic could increase shipping traffic and the harvesting of biological and petroleum resources, increasing disturbance of the sea floor and the potential for the introduction of exotic species. Scientific efforts to establish observatories and other long-term monitoring programs, and to conduct experimental studies, will only track changes as they occur, but they will increase our predictive capabilities. A precautionary principle informed by scientific data must guide environmental decisions. Political and economic policies concerning control of emissions and management of development hold the possibility of slowing current warming trends and returning systems to natural variability cycles.

ACKNOWLEDGEMENTS

We are grateful to Fundación BBVA for sponsoring this debate and to debate organisers C. Duarte and S. Agustí. This chapter benefited from comments from M. Degerlund, K. Sandøy, and L. Seuthe. V. Savinov and L. Seuthe provided graphics support, and K. Nolan and P. Schüle assisted with the preparation of photo 5.2. Preparation of this article was supported in part by the U.S. National Science Foundation (OPP-0326371 to PER, and OPP-0138596 and OPP-0222423 to WGA), the Norwegian Research Council (NORKLIMA Programme, 150356-S30 to MLC) and Akvaplan-niva. The first author acknowledges the support of the MarBEF Network of Excellence “Marine Biodiversity and Ecosystem Functioning” which is funded by the Sustainable Development, Global Change and Ecosystems Programme of the European Community’s Sixth Framework Programme (contract no. GOCE-CT-2003-505446). This publication is a contribution to the MarBEF Responsive Mode Programme ArctEco. The chapter also benefited from discussions to plan the Arctic Tipping Points project, funded by the European Commission.

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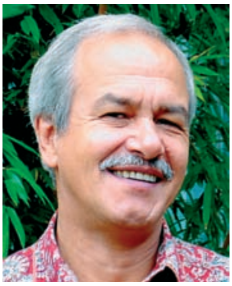

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