Impacts of Global Warming on Polar Ecosystems

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

by

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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.

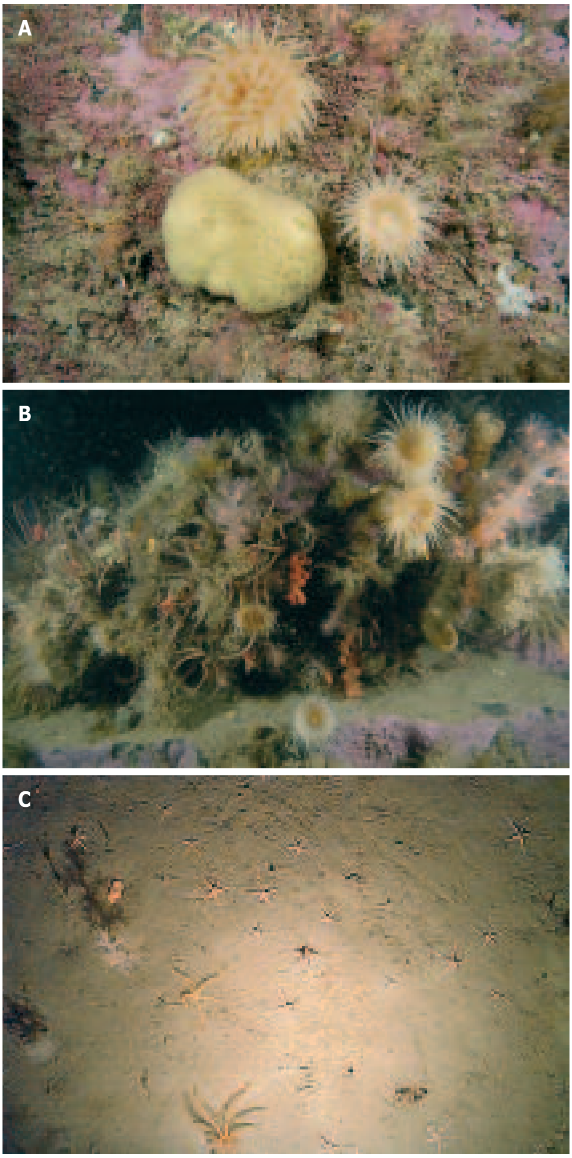


Photo 5.3: High-latitude benthic communities boast a rich diversity of species with important functions in the Arctic ecosystem

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

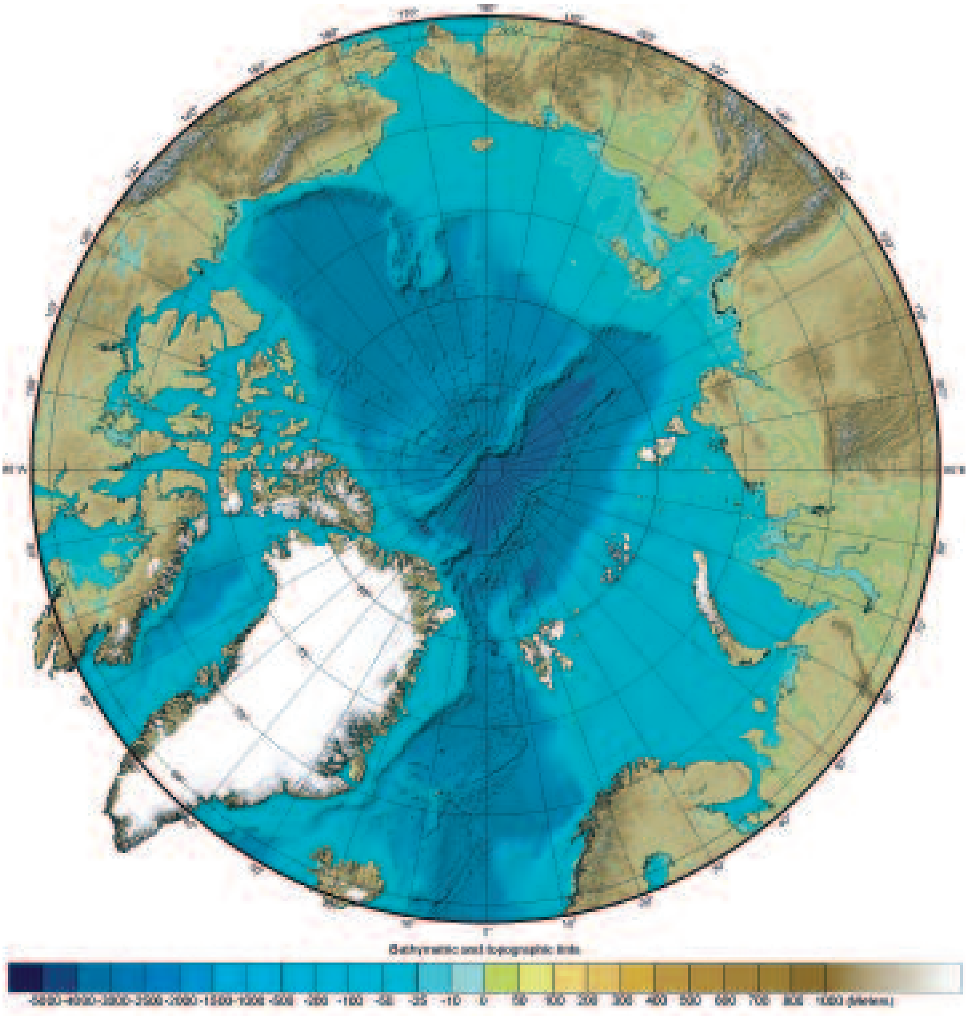
Arctic benthic ecology has been the subject of recent reviews (see Piepenburg 2005), and it is not our purpose here to duplicate these efforts. Instead, our goal is to predict potential effects of climate change on benthic communities and their consequences for Arctic marine ecosystems in general. Not 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.

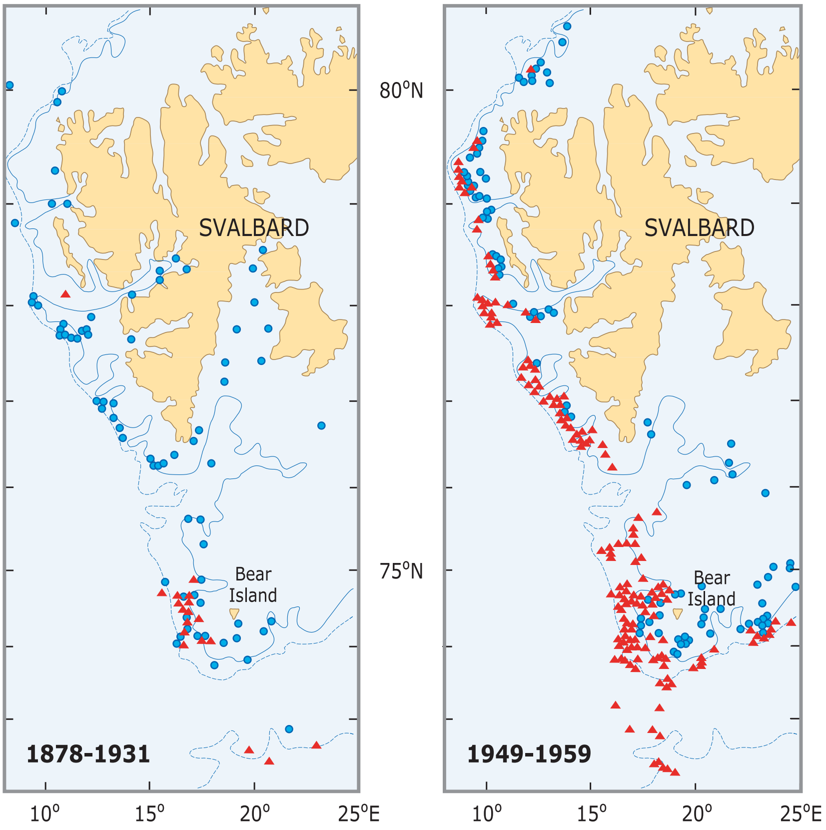
Fishing and hunting of marine mammals, therefore, may have already had significant impacts on high-latitude ecosystems through its removal of top predatory species. Fishing activities continue and may be expected to increase in a warmer, ice-free Arctic, applying further pressure on the system. This "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.

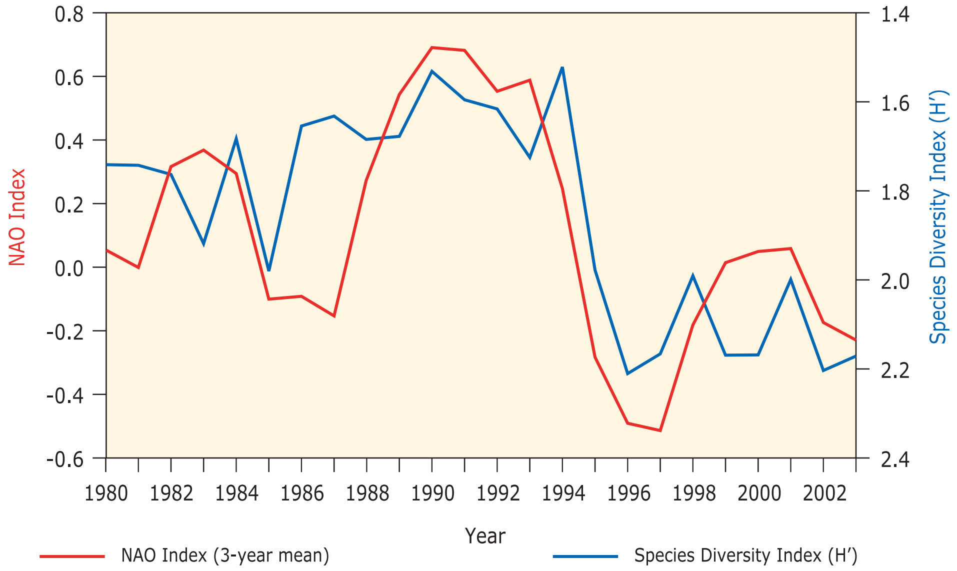
increased light penetration and water-column stratification, which lead to enhanced phytoplankton production (the "spring bloom"), with ice-edge areas exporting large amounts of their primary production to the sea floor (Gradinger 1995; Wassmann 2004).

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.

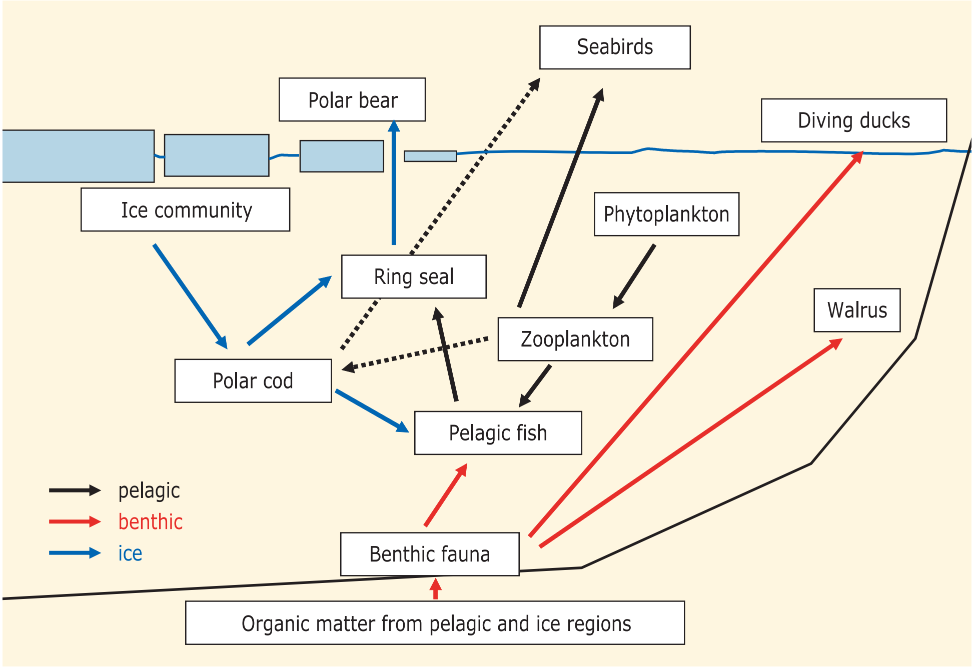
5.6.3. Reproduction

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).

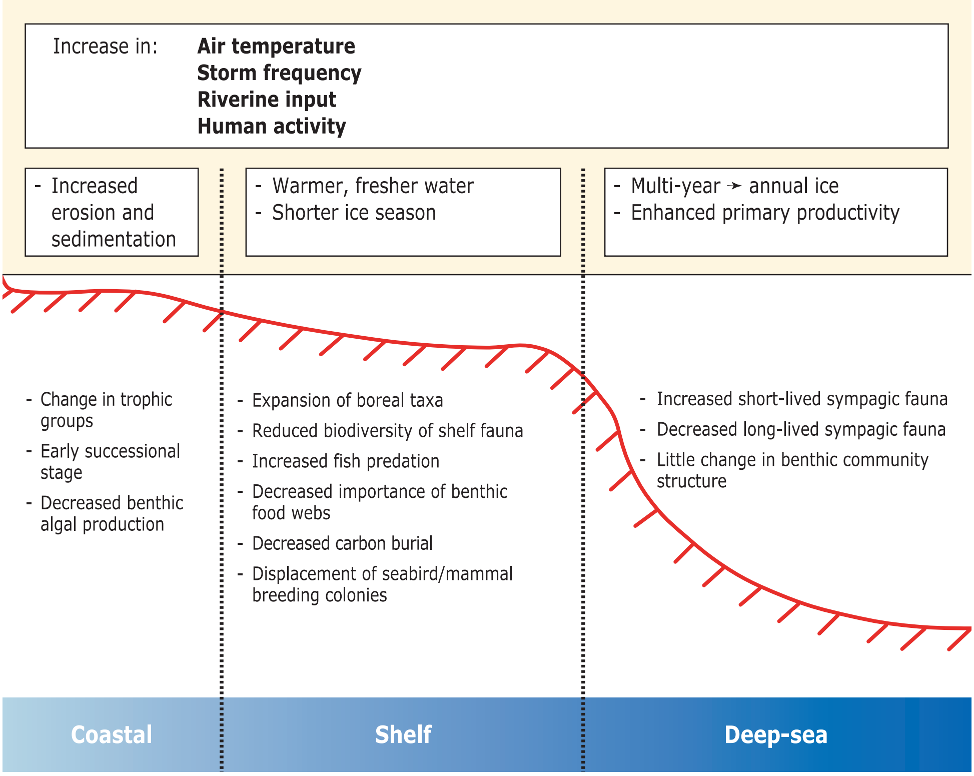
As discussed above, the sediment record preserves proxies of oceanographic conditions and provides valuable insight into the effects of climate change on benthic communities over many time scales. In addition, ecological conditions responsible for the growth of benthic organisms are recorded in their 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.

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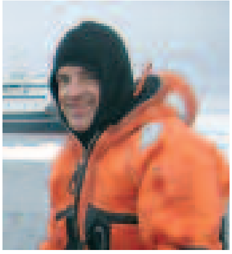

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