Marine Systems

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9.1. Introduction

Approximately two-thirds of the area addressed by the Arctic Climate Impact Assessment is ocean. This includes the Arctic Ocean and its adjacent shelf seas, as well as the Nordic Seas, the Labrador Sea, and the Bering Sea. These are very important areas from a climate change perspective since processes occurring in the Arctic affect the rate of deep-water formation in the convective regions of the North Atlantic, thereby influencing the global ocean circulation. Also, climate models consistently show the Arctic to be one of the most sensitive regions to climate change.

Many arctic life forms, including humans, are directly or indirectly dependent on productivity from the sea. Several physical factors combine to make arctic marine systems unique including: a very high proportion of continental shelves and shallow water; a dramatic seasonality and overall low level of sunlight; extremely low water temperatures; presence of extensive areas of multi-year and seasonal sea-ice cover; and a strong influence from freshwater, coming from rivers and ice melt. Such factors represent harsh conditions for many types of marine life. In geological terms, the arctic fauna is young; recent glaciations resulted in major losses in biodiversity, and recolonization has been slow owing to the extreme environmental conditions and low productivity of the arctic system. This has resulted in arctic ecosystems, in a global sense, being considered "simple". They largely comprise specialist species that have been able to adapt to the extreme conditions, and overall species diversity is low. The large seasonal pulse of summer production in the Arctic, which occurs during the period of 24 hours light, is particularly pronounced near the ice edge and in shallow seas such as the Barents and Bering Seas. This attracts seasonal migrants that travel long distances to take advantage of the arctic summers and then return south to overwinter.

This assessment has also considered the effects of changes in ultraviolet (UV) radiation. However, although UV-B radiation can result in negative impacts on marine organisms and populations, it is only one of many environmental factors that can result in the types of mortality typically observed. It is thus important to assess the relative importance, and hence potential impact, of ozone depletion-related increases in solar UV-B radiation on arctic marine ecosystems.

The Arctic Ocean has not been considered a significant sink for carbon. This is because its extensive sea-ice cover constrains atmosphere—ocean exchange, and because levels of biological production under multi-year sea ice were believed low. Under warmer climate conditions, however, the amount of carbon sequestered by the Arctic Ocean may increase significantly. In addition, the Arctic's role as a source of carbon (methane and carbon dioxide, $\mathrm{CH_4}$ and $\mathrm{CO_2}$ respectively) is poorly understood owing to frozen reserves in permafrost and gas hydrate layers.

This chapter addresses physical features and processes related to marine climate and their impact on the marine ecosystem. Climate change scenarios for the ocean are very uncertain as most models focus mainly on changes in the atmosphere. Such models are not definitive about changes to ocean circulation, deepwater formation, or the fate of major ocean fronts. Therefore, the conclusions drawn in this chapter regarding likely changes in the marine ecosystem are based on scenarios determined from the projected changes in the atmosphere coupled with the present understanding of how atmospheric forcing influences the ocean, as well as the output from a few ocean models.

9.2. Physical oceanography

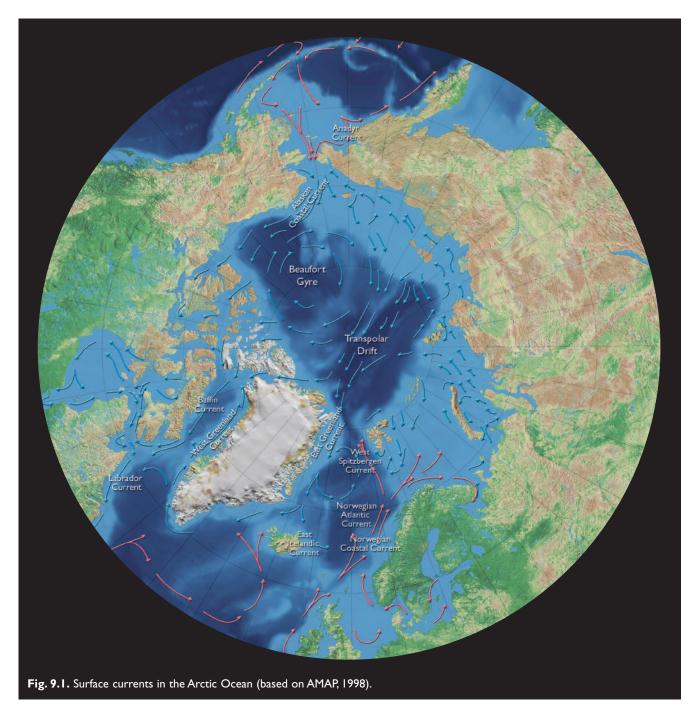
Climate changes impact upon the marine ecosystem mainly through their effects on the physical oceanography. This section provides an overview of the physical oceanography of the Arctic sufficient to enable an examination of potential impacts on the biological system. It also addresses the feedback mechanisms between the atmosphere and the ocean through which changes in the oceanography of the Arctic could have global consequences for the atmosphere.

9.2.1. General features

The marine Arctic is defined within this assessment as comprising the Arctic Ocean, including the deep Eurasian and Canadian Basins and the surrounding continental shelf seas (Barents, White, Kara, Laptev, East Siberian, Chukchi, and Beaufort Seas), the Canadian Archipelago, and the transitional regions to the south through which exchanges between temperate and arctic waters occur. The latter includes the Bering Sea in the Pacific Ocean and large parts of the northern North Atlantic Ocean, including the Nordic, Iceland, and Labrador Seas, and Baffin Bay. Also included are the Canadian inland seas of Foxe Basin, Hudson Bay, and Hudson Strait. Those arctic areas that receive most of the heat input from inflowing warm Atlantic water, i.e., the eastern parts of the Nordic Seas and the Arctic Ocean, are collectively referred to as the Arctic Mediterranean. A detailed description of the topography, water properties, and circulation of these areas is given in Chapter 2. The present chapter presents a brief summary of some of the salient features.

Sea ice is one of the dominant physical features for most of these areas, with coverage ranging from year-round cover in the central Arctic Ocean to seasonal cover in most of the remaining areas. Exceptions occur over the deep basins, which are ice-free throughout the year, e.g., the Nordic Seas and the Labrador Sea, and the deep parts of the Bering Sea.

Relatively warm waters from the Atlantic flow through the Nordic Seas into the Arctic Ocean via the Barents Sea and through Fram Strait while the warm Pacific waters flow across the Bering Sea and enter the Arctic



through the Bering Strait (Fig. 9.1). Approximately ten to twenty times more Atlantic water than Pacific water by volume enters the Arctic Ocean. Within the Arctic Ocean the dominant features of the surface circulation are the clockwise Beaufort Gyre, extending over the Canadian Basin, and the Transpolar Drift that flows from the Siberian coast out through Fram Strait. Both features are strongly influenced by wind forcing. The surface currents along the coast are principally counterclockwise, moving from Atlantic to Pacific on the Eurasian side and from Pacific to Atlantic on the North American side. The subsurface circulation is also counterclockwise and influenced by the inflows from the Atlantic and Pacific Oceans. Waters exit the Arctic Ocean primarily through Fram Strait and the Canadian Archipelago. The arctic waters leaving through Fram Strait are then transported southward along East Greenland, and around the

Labrador Sea and Baffin Bay where they merge with the arctic waters flowing out through the Canadian Archipelago before continuing southward.

The temperature and salinity levels of the various water bodies in the marine Arctic vary considerably, reflecting the extent of the Pacific and Atlantic influence, heat exchange with the atmosphere, direct precipitation, freshwater runoff, and the melting and freezing of sea ice. In the Arctic Ocean, the surface waters are generally near the freezing point owing to the ice cover, whereas the salinity levels exhibit seasonal and spatial fluctuations caused by the freezing and melting of sea ice and river runoff. Density stratification within the Arctic Ocean is principally due to vertical salinity differences. The layer containing the greatest change in salinity is called the halocline. Its characteristics vary across the Arctic Ocean

and are largely characterized by the presence or absence of Pacific-origin water. Waters below the halocline are modified Atlantic waters that flowed into the Arctic through Fram Strait and the Barents Sea. The Atlantic and Pacific inflows carry relatively warm and saline waters into the Arctic and their vertical density stratification is usually controlled more by temperature than salinity differences. As these inflows move northward they are cooled by the atmosphere and freshened by river runoff. Mixing with ambient waters also generally leads to cooling and freshening. The waters leaving the Arctic Ocean also mix with ambient waters, in this case becoming warmer and saltier.

9.2.2. Sea ice

Sea ice controls the exchange of heat and other properties between the atmosphere and ocean and, together with snow cover, determines the penetration of light into the sea. Sea ice also provides a surface for particle and snow deposition, a habitat for plankton, and contributes to stratification through ice melt. The zone seaward of the ice edge is important for plankton production and planktivorous fish. For some marine mammals sea ice provides a place for birth and also functions as a nursery area.

This section describes features of sea ice that are important for physical oceanographic processes and the marine ecosystem. More detailed information about sea ice is given in Chapter 6.

9.2.2.1. Seasonal cycle

Sea-ice extent in the Arctic has a clear seasonal cycle and is at its maximum (14–15 million km²) in March and minimum (6–7 million km²) in September (Parkinson et al., 1999). There is considerable interannual variability both in the maximum and minimum coverage. In addition, there are decadal and inter-decadal fluctuations in

the areal sea-ice extent due to changes in atmospheric pressure patterns and their associated winds, continental discharge, and influx of Atlantic and Pacific waters (Gloersen, 1995; Mysak and Manak, 1989; Polyakov et al., 2003; Rigor et al., 2002; Zakharov, 1994).

At the time of maximum advance, sea ice covers the entire Arctic Basin and the Siberian shelf seas (Fig. 9.2). The warm inflow of Atlantic water keeps the southern part of the Barents Sea open, but in cold years even its shallow areas in the southeast are covered by sea ice. Also, the west coast of Spitsbergen generally remains free of ice. It is here that open water is found closest to the Pole in winter, beyond 81° N in some years (Wadhams, 2000). Sea ice from the Arctic Ocean is transported out through Fram Strait and advected southward by the East Greenland Current to cover the entire east coast of Greenland, although in mild winters it does not reach the southern tip of Greenland. In cold years, the sea ice may also extend south to the northern and eastern coasts of Iceland. In most years there is a thin band of sea ice off West Greenland, which is a continuation of the sea ice from East Greenland and is known as "Storis". Only rarely does the Storis meet the dense sea-ice cover of Baffin Bay and Davis Strait to completely surround Greenland. The whole of the Canadian Archipelago, as well as Hudson Bay and Hudson Strait are usually icecovered (Wadhams, 2000). The Labrador Shelf is also covered by sea ice and the Labrador Current transports this southward to Newfoundland. Further west, a complete sea-ice cover extends across the arctic coasts of northwestern Canada and Alaska and fills the Bering Sea as far south as the shelf break (Wadhams, 2000).

In March or April, the sea ice begins to retreat from its low latitude extremes. By May the coast off northeastern Newfoundland is clear, as is much of the Bering Sea. By June the area south of the Bering Strait is ice-free and open water is found in Hudson Bay and at several arctic coastal locations. August and September are

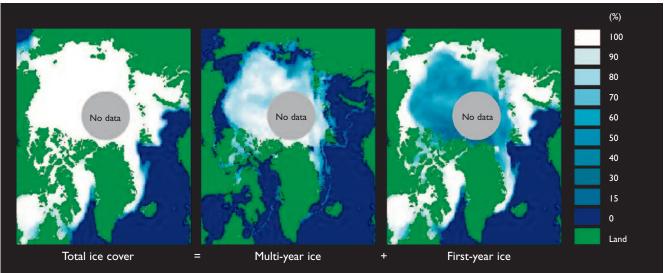


Fig. 9.2. Average sea-ice cover in winter based on data from satellite microwave sensors (Johannessen O. and Miles, 2000). The illustration shows total sea-ice cover, plus the distribution of its two components; multi-year ice and first-year ice. The multi-year ice represents the minimum sea-ice extent in summer.

the months of greatest retreat. At this time most of the Barents and Kara Seas are free of sea ice as far as the northern shelf break. The Laptev Sea and part of the East Siberian Sea have open water along their coastline. In East Greenland, the ice has retreated northward to about 72–73° N, while Baffin Bay, Hudson Bay, and the Labrador Sea become ice-free. In the Canadian Archipelago the winter fast ice usually breaks up. North of Alaska, some open water is typically found along the coast (Wadhams, 2000).

By October, new sea ice has formed in areas that were open in summer, especially around the Arctic Ocean coasts, and in November to January there is a steady advance everywhere toward the winter peak.

9.2.2.2. Fast ice and polynyas

Fast ice grows seaward from a coast and remains in place throughout the winter. Typically, it is stabilized by grounded pressure ridges at its outer edge, and therefore extends to the draft limit of such ridges, usually about 20 to 30 m. Fast ice is found along the whole Siberian coast, the White Sea, north of Greenland, the Canadian Archipelago, Hudson Bay, and north of Alaska.

Polynyas are semi-permanent open water regions ranging in area up to thousands of square kilometers. Flaw leads occur at the border of fast ice when offshore winds separate the drift ice from the fast ice. Polynyas and flaw leads are environmentally important for several reasons (AMAP, 1998):

- they are areas of high heat loss to the atmosphere;
- they typically form the locus of sea-ice breakup in spring;
- they are often locations of intense biological activity; and
- they are regions of deep-water formation.

9.2.2.3. Distribution and thickness

From a combination of satellite observations and historical records, the area covered by sea ice in the Arctic during the summer has been reported to have decreased by about 3% per decade during recent decades (Cavalieri et al., 1997). Multi-year ice is reported to have declined at an even greater rate; 7% per decade during the last 20 years or approximately 600 000 km² (Johannessen O. et al., 1999). Combined, these results imply that the area of first-year ice has been increasing. Sea-ice distribution within subregions of the Arctic has also changed dramatically in the past. For example, warming in the Barents Sea in the 1920s and 1930s reduced sea-ice extent there by approximately 15%. This warming was nearly as great as the warming observed over the last 20 years (see section 9.2.4.2, Barents Sea).

In addition to the recent general decrease in sea-ice coverage, submarine observations suggest that the sea ice over the deep Arctic Ocean thinned from an average

thickness of about 3.1 m (1958-1976) to about 1.8 m (1993-1997), or about 15% per decade (Rothrock et al., 1999). In addition, the ice thinned at all 26 sites examined. Overall, the arctic sea ice is estimated to have lost 40% of its volume in less than three decades. However, according to some models (Holloway and Sou, 2002; Polyakov and Johnson, 2000), the submarine observations may have been conducted over part of the ocean that underwent thinning through shifting sea ice in response to changing winds associated with a high Arctic Oscillation (AO) index (see Chapter 2 for descriptions of the AO and the associated North Atlantic Oscillation). Thus, the conclusion of reduced sea-ice thickness, while valid for the domain of submarine measurements, may not necessarily be true for the Arctic Ocean as a whole and an alternative hypothesis that sea-ice thickness distribution changed in response to the AO but that sea-ice *volume* may not have changed needs to be carefully evaluated.

Scientific debate continues as to the cause of the areal shrinkage of the arctic sea ice. There is some support for the idea that it is probably part of a natural fluctuation in polar climate (Rothrock et al., 1999), while others claim it is another indication of the response to global warming due to increased levels of greenhouse gases (GHGs; Vinnikov et al., 1999).

9.2.2.4. Length of melt season

Smith D. (1998) used satellite data, predominantly from the Beaufort Sea, to estimate that the melt season increased by about 5.3 days per decade during 1979 to 1996. Rigor et al. (2000) found an increase of about 2.6 days per decade in the length of the melt season in the eastern Arctic but a shortening in the western Arctic of about 0.4 days per decade. These trends parallel general observations of a 1 °C per decade *increase* in air temperature in the eastern Arctic compared to a 1 °C per decade *decrease* in the western Arctic for the same time period (Rigor et al., 2000).

9.2.2.5. Sea-ice drift

General sea-ice motion in the Arctic Ocean is organized by the Transpolar Drift in the Eurasian Basin and by the Beaufort Gyre in Canada Basin (Fig. 9.1). Although it has long been recognized that large-scale ice-drift patterns in the Arctic undergo interannual changes, it was not until the International Arctic Buoy Programme (IABP) that sufficient data became available to map the ice drift in detail and thereby directly link changes in sea-ice trajectories to the AO. The IABP data from 1979 to 1998 suggest two characteristic modes of arctic sea-ice motion (Fig. 9.3), one during a low AO index (AO⁻) and the other during a high AO index (AO⁺) (Macdonald et al., 2003a; Rigor et al., 2002). The ice motion revealed by drifting buoys released onto the ice is reasonably well simulated by models (Maslowski et al., 2000; Polyakov and Johnson, 2000). There are two principal differences between the two modes. First, during pronounced AOconditions (Fig. 9.3a), sea ice in the Transpolar Drift

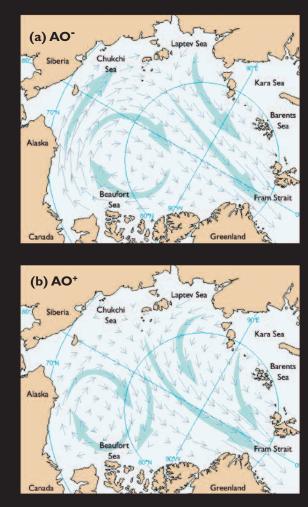


Fig. 9.3. Sea-ice drift patterns for years with (a) pronounced AO⁺ (anticyclonic) conditions and (b) pronounced AO⁺ (cyclonic) conditions (after Maslowski et al., 2000; Polyakov and Johnson, 2000; Rigor et al., 2002). The small arrows show the detailed ice drift trajectories based on an analysis of sea level pressure (Rigor et al., 2002). The large arrows show the general ice drift patterns.

tends to move directly from the Laptev Sea across the Eurasian Basin and out into the Greenland Sea, whereas during pronounced AO⁺ conditions (Fig. 9.3b), ice in the Transpolar Drift takes a cyclonic diversion across the Lomonosov Ridge and into Canada Basin (Mysak, 2001). Second, during pronounced AO⁺ conditions (Fig. 9.3b), the Beaufort Gyre shrinks back into the Beaufort Sea and becomes more disconnected from the rest of the Arctic Ocean, exporting less sea ice to the East Siberian Sea and importing little sea ice from the region to the north of the Canadian Archipelago that contains the Arctic's thickest multi-year ice (Bourke and Garrett, 1987). These changes in sea-ice drift are principally due to the different wind patterns associated with the two AO modes.

During AO⁻ conditions the East Siberian Sea receives much of its ice from the Beaufort Sea and there is an efficient route to carry ice clockwise around the arctic margin of the East Siberian Sea and out toward Fram Strait. Under the strong AO⁺ conditions of the early 1990s, the Beaufort Sea ice became more isolated whereas sea ice from the Kara, Laptev, and East Siberian

Seas was displaced into the central Arctic and toward the Canadian Archipelago. It is not clear from the IABP data how much sea ice from the Russian shelves might be transported into the Canadian Archipelago or the Beaufort Gyre under AO⁺ conditions, but models (Maslowski et al., 2000; Polyakov and Johnson, 2000) suggest that such transport may be important at times.

Fram Strait is the main gateway for arctic ice export. Satellite data, drifting buoys, numerical models, and budgets have been used to construct estimates of the sea-ice flux through Fram Strait (Kwok and Rothrock, 1999; Vinje et al., 1998). Widell et al. (2003) observed a mean sea-ice thickness of 1.8 m and a monthly mean volume flux of 200 km³ for the period 1990 to 1999. They found no trends in ice thickness and volume flux. The maximum sea-ice volume flux occurred in 1994/95 due to strong winds, combined with relatively thick ice.

9.2.3. Ocean processes of climatic importance

The marine Arctic plays an important role in the global climate system (Box 9.1). A number of physical processes will be affected by the changes anticipated in global climate during the 21st century, but this assessment focuses on those that are expected to have strong impacts on the climate or biology of the Arctic. These include the effects of wind on the transport and mixing of water, and the circulation systems generated by freshwater input and thermohaline ventilation (Fig. 9.4). A key issue is the extent to which each of these processes contributes to driving the inflow of Atlantic water to the Arctic. Models (Seager et al., 2002) have shown that the heat transported by this inflow in some areas elevates the sea surface temperature to a greater extent than the temperature increase projected for the 21st century (see Chapter 4). A weakening of the inflow could therefore significantly reduce warming in these areas and might even induce regional cooling, especially in parts of the Nordic Seas. Thus, special attention is paid to the processes that affect the inflow, especially the thermohaline circulation (see section 9.2.3.4).

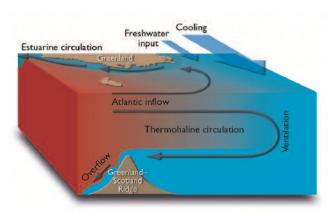
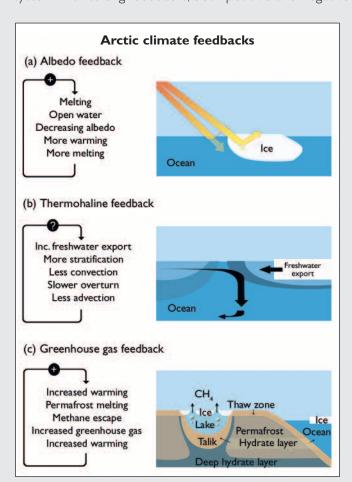


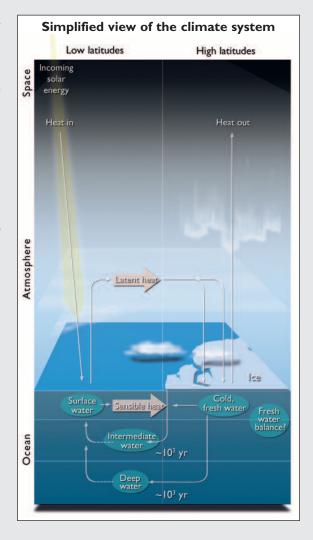
Fig. 9.4. Two types of processes create unique current systems and conditions in the marine Arctic. The input of freshwater, its outflow to the Atlantic, and the en-route entrainment of ambient water create an estuarine type of circulation within the marine Arctic. In addition to this horizontal circulation system, thermohaline ventilation creates a vertical circulation system. Both patterns of circulation are sensitive to climate change.

Box 9.1. Role of the marine Arctic in the global climate system

The marine Arctic is an interconnected component of the global climate system whose primary role is to balance heat gain at low latitudes and heat loss at high latitudes. At low latitudes about half the excess heat is sent poleward as warm (and salty) water in ocean currents (sensible heat, Q_s) and the other half is sent poleward as water vapor in the atmosphere (latent heat, Q₁). At low latitudes the subtropical gyres in the ocean collect excess heat and salt, the western boundary currents carry them poleward, and the Atlantic inflow brings them into the marine Arctic. Heat carried by the atmosphere is released at high latitudes by condensation, thus supplying freshwater to the ocean through precipitation and runoff. Freshwater is stored in the surface and halocline layers of the marine Arctic. To prevent the build-up of salt (by evaporation) at low latitudes, freshwater is exported from the high latitudes, thus completing the hydrological cycle by reuniting the atmospheric water content and the salty ocean water. At high latitudes the return flows include export by ice and transport in low-salinity boundary currents, intermediate water (which forms and sinks along the subpolar fronts), and deep water (which sinks on shelves and in gyres). Export of these low-salinity waters southward couples the Arctic to the world thermohaline circulation (THC) through intermediate and deep-water formation. The role of intermediate water in governing THC is unclear.

The marine Arctic plays an active role in the global climate system with strong feedbacks, both positive and negative.





For example: albedo feedback, thermohaline feedback, and greenhouse gas feedback.

Albedo feedback – Ice and snow reflect most of the solar radiation back into space. With initial warming and sea-ice melting, more heat enters the ocean, thus melting more sea ice and increasing warming.

Thermohaline feedback — If the export of freshwater from the Arctic Ocean should increase, then stratification of the North Atlantic would probably increase, and this could slow the THC. A decrease in the THC would then draw less Atlantic water into high latitudes, leading to a slowdown in the global overturning cell and subsequent localized cooling. (This scenario does not take into account the formation of intermediate water.)

Greenhouse gas feedback – Vast amounts of methane and carbon dioxide are currently trapped in the permafrost and hydrate layers of the arctic margins (Zimov et al., 1997). With warming, arctic coastal lakes will act as a thermal drill to tap this greenhouse gas source and further exacerbate warming.

9.2.3.1. Freshwater and entrainment

Freshwater is delivered to the marine Arctic by atmospheric transport through precipitation and by ocean currents, and to the coastal regions through river inflows (Lewis et al., 2000). Further net distillation of freshwater may occur within the region during the melt/ freeze cycle of sea ice, provided that the ice and rejected brine formed by freezing in winter can be separated and exported before they are reunited by melting and mixing the following summer (Aagaard and Carmack, 1989; Carmack, 2000).

The freshwater has decisive influences on stratification and water column stability as well as on ice formation. Without the freshwater input, there would be less freezing, less ice cover, and less brine rejection (Rudels, 1989). This is also illustrated by the difference between the temperature-stratified low latitude oceanic regime and the salinity-stratified high latitude oceanic regime (Carmack, 2000; Rudels, 1993).

In the Arctic Ocean, freshwater is stored within the various layers above and within the halocline, the latter serving as an extremely complex and poorly understood reservoir. This is especially true for the Beaufort Gyre, which represents the largest and most variable reservoir of freshwater storage in the marine Arctic. The ultimate sink for freshwater is its export southward into the North Atlantic to replace the freshwater evaporating from low latitude oceans and to close the global freshwater budget. This southward transport occurs partly through the THC since the overflow from the Nordic Seas into the Atlantic is less saline than the inflowing Atlantic water. The role of the freshwater is illustrated in Fig. 9.5. The figure shows the processes responsible for the development of the horizontal and vertical circulation systems unique to the marine Arctic.

Most of the freshwater in the Arctic Ocean returns southward in the surface outflows of the East Greenland Current and through the Canadian Archipelago. These flows carry low-salinity water as well as sea ice. They include most of the water that enters the Arctic Ocean

through the Bering Strait and water of Atlantic origin entrained into the surface flow. Since the estimated total volume flux of the surface outflows greatly exceeds the combined fluxes of the Bering Strait inflow and the freshwater input, most of the surface outflows must derive from entrained Atlantic water. This process therefore induces an inflow of Atlantic water to the Arctic, which by analogy to the flows in estuaries is usually termed "estuarine circulation". This estuarine-type circulation is sensitive to climate change.

9.2.3.2. Mixed-layer depth

The vertical extent of the surface mixed layer is critical to the primary production and depends on the vertical density stratification and the energy input, especially from the wind. Density stratification is affected by heat and freshwater fluxes from the atmosphere or by advection from surrounding ocean areas. Some areas, for example the Arctic Ocean, are salt-stratified whereas other areas, such as the Nordic Seas and the Bering Sea, are temperature-stratified. In a classic study, Morison and Smith (1981) found that seasonal variations in mixed-layer depth are largely controlled by buoyancy (i.e., heat and salt) fluxes.

Winds blowing over the sea surface transfer energy to the surface mixed layer. In ice-free areas, increased winds would tend to deepen the surface mixed layer, depending upon the strength of the vertical density stratification. In the presence of sea ice, however, the efficiency of energy transfer from wind to water is a complex function of sea-ice roughness and internal ice stress which, in turn, is a function of sea-ice concentration and compactness (see McPhee and Morison, 2001). Because warming will decrease sea-ice concentrations (and so decrease internal ice stress) and increase the duration of "summer" conditions (i.e., earlier breakup and later freeze-up), the efficiency of wind mixing in summer is likely to increase. This is especially true for late summer in the Arctic Ocean when energy input from storms is greatest. However, owing to the poorly understood role of air-ice-ocean coupling and the present level of salt-stratification, this increased exposure

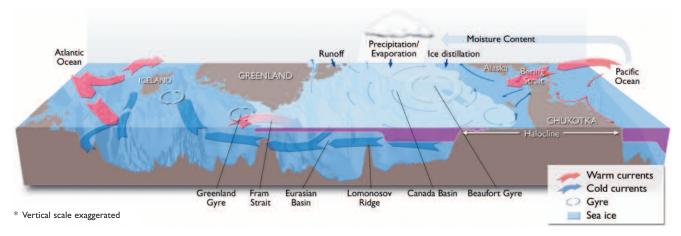


Fig. 9.5. The freshwater budget of the Arctic Ocean. Low salinity waters are added to the surface and halocline layers via precipitation and runoff, Pacific inflow via the Bering Strait, and the sea-ice distillation process. Low salinity waters and sea ice are subsequently advected through Fram Strait and the Canadian Archipelago into the convective regions of the North Atlantic.

will not necessarily lead to significant increases in mixed-layer depth. Furthermore, the role that lateral advection plays in establishing the underlying halocline structure of the Arctic Ocean must also be considered.

9.2.3.3. Wind-driven transport and upwelling

A number of studies have shown the effect of wind stress on the circulation of particular regions within the marine Arctic (e.g., Aagaard, 1970; Isachsen et al., 2003; Jónsson, 1991). Winds have also been shown to have a strong influence on exchanges between regions (e.g., Ingvaldsen, 2002; Morison, 1991; Orvik and Skagseth, 2003; Roach et al., 1995). If winds were to change significantly, wind-driven currents and exchanges would also change. These wind-induced changes in turn would redistribute the water masses associated with the different currents, thereby affecting the location and strength of the fronts separating the water masses (Maslowski et al., 2000, 2001; Zhang J. et al., 2000).

Retraction of the multi-year ice cover seaward of the shelf break in the Arctic Ocean may lead to wind-induced upwelling at the shelf break, which is currently not happening. This process might substantially increase the rate of exchange between the shelf and deep basin waters, the rate of nutrient upwelling onto the shelves, and the rate of carbon export to the deep basin (Carmack and Chapman, 2003).

9.2.3.4. Thermohaline circulation

Thermohaline circulation is initiated when cooling and freezing of sea water increase the density of surface waters to such an extent that they sink and are exchanged with waters at greater depth. This occurs in the Labrador Sea, in the Nordic Seas, and on the arctic shelves. Together, these regions generate the main source water for the North Atlantic Deep Water; the main ingredient of the global ocean "Great Conveyor Belt" (Broecker et al., 1985). All these arctic areas are therefore important for the global THC. More importantly from the perspective of this assessment is the potential impact of a changing THC on flow and conditions within the marine Arctic. Some areas are more sensitive than others, because the oceanic heat transport induced by the THC varies regionally. The most sensitive areas are those that currently receive most of the heat input from inflowing warm Atlantic water, i.e., the eastern parts of the Nordic Seas and the Arctic Ocean (Seager et al., 2002), namely the Arctic Mediterranean.

The THC in the Arctic Mediterranean is often depicted as more or less identical to open-ocean convection in the Greenland Sea. This is a gross over-simplification since, in reality, there are several different processes contributing to the THC and they occur in different areas. The THC can be subdivided into four steps (Fig. 9.4).

 Upper layer inflow of warm, saline Atlantic water into the Arctic Ocean and the Nordic Seas.

- 2. Cooling and brine rejection making the incoming waters denser.
- 3. Vertical transfer of near-surface waters to deeper layers.
- 4. The overflow of the dense waters in the deep layers over the Greenland–Scotland Ridge and their return to the Atlantic.

Although these steps are linked by feedback loops that prevent strict causal relations, the primary processes driving the THC seem to be steps 2 and 3, which are termed thermohaline ventilation. By the action of the thermohaline ventilation, density and pressure fields are generated that drive horizontal exchanges between the Arctic Mediterranean and the Atlantic (steps 1 and 4). Box 9.2 illustrates the basic mechanisms of the thermohaline forcing.

Thermohaline ventilation

The waters of the Arctic Ocean and the Nordic Seas are often classified into various layers and a large number of different water masses (Carmack, 1990; Hopkins, 1991). For the present assessment, it is only necessary to distinguish between "surface" (or upper layer) waters and "dense" waters, which ultimately leave the Arctic Mediterranean as overflow into the North Atlantic. The term "dense waters" is used to refer to deep and intermediate waters collectively and the term "thermohaline ventilation" is used as a collective term for the processes that convert surface waters to dense waters. Thermohaline ventilation is a two-step process that first requires cooling and/or brine rejection to increase the surface density and then a variety of processes that involve vertical transfer.

Cooling and brine rejection

Production of dense waters in the arctic Nordic Seas is due initially to atmospheric cooling, and then to brine rejection during sea-ice formation (Aagaard et al., 1985). The waters flowing into the Nordic Seas from the Atlantic exhibit a range of temperatures depending on location and season. On average, their temperature is close to 8 °C, but it decreases rapidly after entering the Nordic Seas. The temperature decrease is especially large in the southern Norwegian Sea. The simultaneous salinity decrease indicates that some of the temperature decrease may be due to admixture of colder and less saline adjacent water masses. Except for relatively small contributions of freshwater from river inflow and the Pacific-origin waters flowing along the east coast of Greenland, the adjacent water masses are predominantly of Atlantic origin. Thus, atmospheric cooling in the Nordic Seas is the main cause of the decreasing temperature of the inflowing Atlantic water.

Attempts have been made to calculate the heat loss to the atmosphere from climatological data, but the sensitivity of the results to different parameterizations of the heat flux makes these estimates fairly uncertain (Simonsen and

Haugan, 1996). Most of the heat loss from the ocean to the atmosphere occurs in ice-free areas of the Nordic and Barents Seas (Simonsen and Haugan, 1996).

Brine rejection, however, is intimately associated with sea-ice formation (Carmack, 1986). When ice forms at the ocean surface, only a small fraction of the salt follows the freezing water into the solid phase, the remainder flowing into the underlying water. Brine also continues to drain from the recently formed ice. Both processes increase the salinity, and therefore density, of the ambient water. In a stationary state, the salinity increase due to brine rejection in cold periods is compensated for

by freshwater input from melting ice in warm periods, but freezing and melting often occur in different regions. For example, on the shallow shelves surrounding the arctic basins rejected brine results in shelf waters sufficiently dense to drain off the shelves, thus becoming separated from the overlying ice (Anderson L. et al., 1999). Winds can also remove newly formed ice from an area while leaving behind the high salinity water.

Vertical transfer of water

The second step in thermohaline ventilation is the vertical descent of the surface waters made denser by cool-

Box 9.2. Thermohaline forcing of Atlantic inflow to the Arctic

The processes by which thermohaline ventilation induces Atlantic inflow to the Arctic Mediterranean can be illustrated by a simple model where the Arctic Mediterranean is separated from the Atlantic by a ridge (the Greenland–Scotland Ridge). South of the ridge, Atlantic water (red) with uniform temperature, salinity, and density (ρ) extends to large depths. North of the ridge, the deep layers (blue) are less saline, but they are also much colder than the Atlantic water and therefore denser ($\rho+\Delta\rho$). Above this deep, dense layer is the inflowing Atlantic water, which is modified by cooling and brine rejection to become increasingly similar to the deep layer as it proceeds away from the ridge. The causal links between the processes involved can be broken into three steps.

Thermohaline ventilation — Cooling and brine rejection make the inflowing Atlantic water progressively denser until it has reached the density of the deeper layer. At that stage, the upper-layer water sinks and is transferred to the deeper layer. This is equivalent to raising the interface between the two layers in the ventilation areas, which are far from the ridge.

Overflow – When ventilation has been active for some time, the interface will be lifted in the ventilation areas and will slope down towards the ridge. Other things being equal, this implies that the pressure in deep water will be higher in the ventilation

Atlantic

Arctic Mediterranean

Cooling and brine rejection

Barotropic pressure gradient

Atlantic inflow

Density:

Overflow

Density:

Density:

Density:

Atlantic Mediterranean

Cooling and brine rejection

Interface height

areas than at the same depth close to the ridge. A horizontal internal (so-called baroclinic) pressure gradient will therefore develop which forces the deep water towards and across the ridge. In this simple model, the overflow is assumed to pass through a channel, sufficiently narrow to allow neglect of geostrophic effects. If the rate at which upper-layer water is converted to deeper-layer water is constant, the interface will rise until it can drive an overflow with a volume flux that equals the ventilation rate.

Sea-level drop – When thermohaline ventilation has initiated a steady overflow, there will be a continuous removal of water from the Arctic Mediterranean. Without a compensating inflow, the sea level would drop rapidly north of the ridge. Thus an uncompensated overflow of the present-day magnitude would make the average sea level in the Arctic Mediterranean sink by more than one meter a month. As soon as the water starts sinking north of the ridge, there will, however, develop a sea-level drop across the ridge. This sea-level drop implies that water in the upper layer north of the ridge will experience lower pressure than water at the same level in the Atlantic. A sea surface (so-called barotropic) pressure gradient therefore develops that pushes water northward across the ridge. The amount of Atlantic water transported in this way increases with the magnitude of the sea-level drop. In the steady state, the sea-level drop is just sufficient to drive an Atlantic inflow of the same volume flux as the overflow and the ventilation rate.

When upper-layer water is converted to deeper-layer water at a certain ventilation rate (in m³/s), an overflow and an Atlantic inflow are therefore generated which have the same volume flux on long timescales. In the present state, these fluxes must equal the estimated overflow flux of about 6 Sv. Simple, non-frictional, models indicate that the required interface rise is several hundred meters, as is observed, while the required sea-level drop is only of the order of 1 cm.

ing and brine rejection. Several processes contribute to the transfer. These include the sinking of the boundary current as it flows around the Arctic Mediterranean, open-ocean convection, and shelf convection as well as other ventilation processes (Fig. 9.6).

- 1. The boundary current enters the Arctic Mediterranean as pure Atlantic water with relatively high temperature (>8 °C) and salinity (>35.2). It enters mainly through the Faroe-Shetland Channel and within the Channel joins with part of the Iceland-Faroe Atlantic inflow. Part of the boundary current continues as an upper-layer flow along the continental slope to Fram Strait. There, one branch moves toward Greenland while the other enters the Arctic Ocean and flows sub-surface along its slope to join the first branch as it exits again through Fram Strait. The flow continues as a subsurface boundary current over the slope off East Greenland all the way to Denmark Strait with the core descending en route (Rudels et al., 2002). While circulating through the Arctic Mediterranean, boundary current waters experience a large temperature decrease, much of it during the initial flow along the Norwegian shelf. While the associated density increase is partly offset by a salinity decrease, there is still a considerable net density increase. After passing Fram Strait, both branches are submerged without direct contact to the atmosphere such that temperature and salinity changes occur mainly through isopycnal mixing with surrounding waters. Isopycnal mixing occurs between waters of the same density but different temperatures and salinities.
- 2. Open-ocean convection is very different from boundary current deepening, being essentially a vertical process. After a pre-conditioning phase in which the waters are cooled and mixed, further intensive cooling events may trigger localized intense descending plumes or eddies with horizontal scales of the order of a few kilometers or less (Budéus et al., 1998; Gascard et al., 2002; Marshall and Schott, 1999; Watson et al., 1999). They have strong vertical velocities (of the order

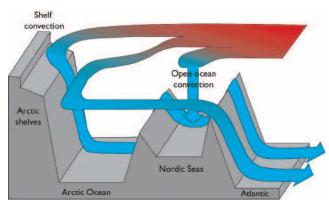


Fig. 9.6. Three of the thermohaline ventilation processes that occur in the Arctic Mediterranean: boundary current deepening, open-ocean convection, and shelf convection.

- of a few hundredths of a meter per second), but do not represent an appreciable net volume flux since they induce upward motion in the surrounding water (Marshall and Schott, 1999). They do, however, exchange various properties (such as CO₂) between the deep and near-surface layers as well as to the atmosphere. They also help maintain a high density at depth. Open-ocean convection is assumed to occur to mid-depths in the Iceland Sea (Swift and Aagaard, 1981). In the Greenland Sea, convective vortices have been observed to reach depths of more than 2000 m (Gascard et al., 2002) and it is assumed that convection in earlier periods penetrated all the way to the bottom layers to produce the very cold Greenland Sea Deep Water, as observed in 1971 (Malmberg, 1983).
- 3. Shelf convection results from brine rejection and convection, and can lead to the accumulation of high salinity water on the shelf bottom (Jones et al., 1995; Rudels et al., 1994, 1999). Freezing of surface waters limits the temperature decrease, but if winds or other factors remove the sea ice while leaving the brine-enriched water behind, prolonged cooling can produce a high salinity water mass close to the freezing point. Eventually, gravity results in this saline, dense water mass flowing off the shelf and sinking into the arctic abyss. As it sinks, it entrains ambient waters and its characteristics change (Jones et al., 1995; Quadfasel et al., 1988; Rudels, 1986; Rudels et al., 1994). Shelf convection is the only deep-reaching thermohaline ventilation process presumed to enter the Arctic Ocean and hence is responsible for local deepwater formation.

There are at least two additional sinking mechanisms (not included in Fig. 9.6) that may transfer dense water downward; isopycnal sinking and frontal sinking. Overflow water is often defined as water denser than σ_{θ} =27.8 (Dickson and Brown, 1994) and such water is widely found in the Arctic Ocean and the Nordic Seas, close to the surface. During winter, mixing and cooling result in surface densities up to and above this value. This water can therefore flow over the ridge, sinking below the top of the ridge but without crossing isopycnals. This is termed "isopycnal sinking". A somewhat-related mechanism has been termed "frontal sinking", which indicates that nearsurface water from the dense side of a front can sink in the frontal region and flow under the less dense water. In the Nordic Seas, this has been observed in the form of low-salinity plumes sinking at fronts between Arctic and Atlantic waters (Blindheim and Ådlandsvik, 1995).

Horizontal water exchange

The Nordic Seas and the Arctic Ocean are connected to the rest of the World Ocean through the Canadian Archipelago, across the Greenland—Scotland Ridge, and through the Bering Strait, and they exchange water and various properties with the World Ocean through these gaps. Four exchange branches can be distinguished (Fig. 9.7). The near-surface outflow from the Arctic Ocean through the Canadian Archipelago and Denmark Strait, and the Bering Strait inflow to the Arctic Ocean from the Pacific are important in connection with freshwater flow through the Arctic Ocean and the Nordic Seas. For the THC, the overflow of cold and dense water from the Nordic Seas into the Atlantic and the inflow of Atlantic water to the Nordic Seas and the Arctic Ocean are the most important factors.

Overflow

The term overflow is used here to describe near-bottom flow of cold, dense (σ_{θ} >27.8; Dickson and Brown, 1994) water from the Arctic Mediterranean across the Greenland–Scotland Ridge into the Atlantic. It occurs in several regions. In terms of volume flux, the most important overflow site is the Denmark Strait, a deep channel between Greenland and Iceland with a sill depth of 620 m. The transport in this branch is estimated at 3 Sv, or about half the total overflow flux (Dickson and Brown, 1994). Mauritzen C. (1996) and Rudels et al. (2002) argue that water from the East Greenland Current forms the major part of this flow. Other sources contribute, however (Strass et al., 1993); some workers suggest the Iceland Sea as the primary source for the Denmark Strait overflow (Jónsson, 1999; Swift and Aagaard, 1981).

The Faroe Bank Channel is the deepest passage across the Greenland–Scotland Ridge and the overflow through the channel is estimated to be the second largest in terms of volume flux, approximately 2 Sv (Saunders, 2001). Owing to the difference in sill depth, the deepest water flowing through the Faroe Bank Channel is usually colder than water flowing through the Denmark Strait and the Faroe Bank Channel is thus the main outlet for the densest water produced in the Arctic Mediterranean.

Overflow has also been observed to cross the Iceland– Faroe Ridge at several sites, as well as the Wyville– Thomson Ridge, but more intermittently. The total overflow across these two ridges has been estimated at slightly above 1 Sv, but this value is fairly uncertain compared to the more reliable estimates for the Denmark Strait and Faroe Bank Channel overflow branches (Hansen and Østerhus, 2000).

As the overflow waters pass over the ridge, their temperature varies from about -0.5 °C upward. A large proportion of the water is significantly colder than the 3 °C value often used as a limit for the overflow (approximately equivalent to $\sigma_{\theta} > 27.8$). After crossing the ridge, most of the overflow continues in two density-driven bottom currents that are constrained by the effects of the earth's rotation (i.e., the Coriolis force) to follow the topography, although gradually descending. The bottom current waters undergo intensive mixing and entrain ambient waters from the Atlantic Ocean, which increases the water temperature. When the Denmark Strait and Faroe Bank Channel overflow waters join in the region southeast of Greenland, they have been warmed to 2 to 3 °C, typical of the North Atlantic Deep Water. Through entrainment, enough Atlantic water is added to approximately double their volume transport.

Atlantic inflow

Inflow of Atlantic water to the Nordic Seas occurs across the Greenland–Scotland Ridge along its total extent except for the westernmost part of the Denmark Strait. Iceland and the Faroe Islands divide this flow into three branches (Fig. 9.7); the Iceland branch (Jónsson and Briem, 2003), the Faroe branch (Hansen et al., 2003), and the Shetland branch (Turrell et al., 2003). There is a gradual change in water mass characteristics with the most southeastern inflow being the warmest (and most saline). There is also a difference in the volume fluxes, with that for the Iceland branch being much less than for the other two, which are similar in magnitude.

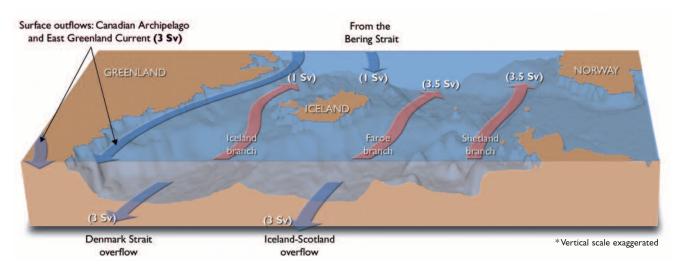


Fig. 9.7. The Arctic Mediterranean has four current branches that import water into the upper layers; three from the Atlantic (the Iceland, Faroe, and Shetland branches), and one from the Pacific. The outflow occurs partly at depth through the overflows and partly as surface (or upper-layer) outflow through the Canadian Archipelago and the East Greenland Current. The numbers indicate volume flux in Sverdrups (10⁶ m³/s) rounded to half-integer values and are based on observations, with the exception of the surface outflow, which is adjusted to balance (based on Hansen and Østerhus, 2000).

The Iceland branch flows northward on the eastern side of the Denmark Strait. North of Iceland, it turns east and flows toward the Norwegian Sea, but the heat and salt content of this branch are mixed with ambient water of polar or Arctic Ocean origin and freshwater runoff from land. By the time it reaches the east coast of Iceland it has lost most of its Atlantic character. The Faroe and Shetland branches flow directly into the Norwegian Sea. On their way they exchange water, but still appear as two separate current branches off the coast of northern Norway. Their relative contribution to various regions is not clarified in detail but the Barents Sea is clearly most affected by the inner (Shetland) branch, while the western Norwegian Sea and the Iceland Sea receive most of their Atlantic water from the outer (Faroe) branch.

Budgets

The horizontal exchanges between the Arctic and oceans to the south transfer water, heat, salt, and other properties such as nutrients and CO₂. Since typical temperatures, salinities, and concentrations of various properties are known, quantifying the exchanges is mainly a question of quantifying volume fluxes.

The water budget for the Arctic Ocean and the Nordic Seas as a whole is dominated by the Atlantic inflow and the overflow (Fig. 9.7). The Bering Strait inflow is fairly fresh (S<33) and most of it can be assumed to leave the Arctic Mediterranean in the surface outflow (Rudels, 1989). The deeper overflow is formed from Atlantic water, which means that 75% of the Atlantic inflow is ventilated in the Arctic Ocean and the Nordic Seas. Errors in the flux estimates may alter this ratio somewhat, but are not likely to change the conclusion that most of the Atlantic inflow exits via the deep overflow rather than in the surface outflow.

The question as to how the thermohaline ventilation is split between the Nordic Seas and the Arctic Ocean and its shelves can be addressed in different ways. One method is to measure the fluxes of the various current branches that flow between these two ocean areas; another is to estimate the amount of water produced by shelf convection. Both methods involve large uncertainties, but generally imply that most of the ventilation occurs in the Nordic Seas with perhaps up to 40% of the overflow water produced in the Arctic Ocean (Rudels et al., 1999). That most of the heat loss also appears to occur in the Nordic and Barents Seas (Simonsen and Haugan, 1996) highlights the importance of these areas for the THC.

9.2.3.5. What drives the Atlantic inflow to the Arctic Mediterranean?

The Atlantic inflow is responsible for maintaining high temperatures in parts of the marine Arctic and potential changes in the Atlantic inflow depend on the forces driving the flow. The few contributions to this discus-

sion to be found in the literature (e.g., Hopkins, 1991) generally cite direct forcing by wind stress, estuarine circulation, or thermohaline circulation as being the main driving forces.

The freshwater input combined with entrainment generates southward outflows from the Arctic Mediterranean in the upper layers, which for continuity reasons require an inflow (estuarine circulation). Similarly, thermohaline ventilation generates overflows, which also require inflow (thermohaline circulation). If inflows do not match outflows, sea-level changes are induced, which generate pressure gradients that tend to restore the balance (Box 9.2). To the extent that the water budget (Fig. 9.7) is reliable, it is therefore evident that the processes that generate the estuarine circulation can account for 2 Sv of the Atlantic inflow, whereas thermohaline ventilation is responsible for an additional 6 Sv. This has led some workers to claim thermohaline ventilation as the main driving force for the Atlantic inflow (Hansen and Østerhus, 2000).

Wind affects both the estuarine and the thermohaline circulation systems in many different ways (e.g., through entrainment, cooling, brine rejection, flow paths). Direct forcing by wind stress has also been shown to affect several current branches carrying Atlantic water (Ingvaldsen et al., 2002; Isachsen et al., 2003; Morison, 1991; Orvik and Skagseth, 2003), but there is no observational evidence for a strong direct effect of wind stress on the total Atlantic inflow to the Nordic Seas. On the contrary, Turrell et al. (2003) and Hansen et al. (2003) found that seasonal variation in the volume flux for the two main inflow branches (the Faroe Branch and Shetland Branch on Fig. 9.7) was negligible, in contrast to the strong seasonal variation in the wind stress. Thermohaline ventilation is also seasonal, but its effect is buffered by the large storage of dense water in the Arctic Mediterranean, which explains why the total overflow and hence also thermohaline forcing of the Atlantic inflow has only a small seasonal variation (Dickson and Brown, 1994; Hansen et al., 2001; Jónsson, 1999). In a recent modeling study, Nilsen et al. (2003) found high correlations between the North Atlantic Oscillation (NAO) index and the volume flux of Atlantic inflow branches, but that variations in the total inflow were small in relation to the average value.

These studies indicate that the Atlantic inflow to the Arctic Mediterranean is mainly driven by thermohaline (Box 9.2) and estuarine forcing, but that fluctuations at annual and shorter timescales are strongly affected by wind stress. Variations in wind stress also have a large influence on how the Atlantic water is distributed within the Arctic Mediterranean.

9.2.4. Variability in hydrographic properties and currents

Ocean climate changes on geological time scales in the Arctic are briefly discussed in Box 9.3.

Box 9.3. Arctic climate – a long-term perspective

At the start of large-scale glaciation around 3 million years ago, the Arctic was relatively warm with forests growing along the shores of the Arctic Ocean (Funder et al., 1985; Knies et al. 2002). About 2.75 million years ago a marked phase of global cooling set in, leading to a widespread expansion of ice sheets across northern Eurasia and North America (Jansen et al., 2000). Before this marked cooling, climates were only cold enough to sustain glaciers on Greenland, indicating that the ocean was warmer and the sea-ice cover less than at present (Fronval and Jansen, 1996; Larsen et al., 1994). This cooling is believed due to reduced northward heat transport to the Arctic. After this cooling event, multi-year sea-ice cover and cold conditions probably existed throughout the Arctic, however, less freshwater influx may have reduced surface ocean stratification and open areas and polynyas may have prevailed. Lower sea level also left major portions of the shelf areas exposed.

The next major change occurred approximately I million years ago. Glacial episodes became longer, with a distinct 100000 year periodicity and glaciation more severe. Yet between the glacial periods, warmer but short interglacial periods persisted, due to stronger inflow of warm Atlantic waters to the Nordic Seas (Berger and Jansen, 1994; Jansen et al., 2000). The long-term effects of sea-level change through ice sheet erosion affected the ocean exchange with the Arctic. For example, water mass exchange could take place between the Atlantic and the Arctic through the Barents Sea when it changed from a land area to a sea.

After the last glacial period, which ended about 11000 years ago, the marginal ice zone was farther north than at present since the summer insolation was higher in the Northern Hemisphere than now. In the early phase of the postglacial period (Holocene), 8000 to 6000 years ago, mollusks with affinities for ice-free waters were common in Spitsbergen and along the east coast of Greenland. Summer temperatures over Greenland and the Canadian Arctic were at their highest, 3 °C above present values (Dahl-Jensen et al., 1998). The sea-ice cover expanded southward again in the Barents and Greenland Seas 6000 to 4000 years ago, concomitant with the expansion of glaciers in Europe. This expansion was most likely to be a response to the diminishing summer insolation.

Superimposed on these long-term trends, there is evidence of high amplitude millennial- to century-scale climate variability. The millennial-scale events are recorded globally and shifts in temperature and precipitation occurred with startling speed, with changes in annual mean temperature of 5 to 10 °C over one to two decades (Alley et al., 2003; Dansgaard et al., 1993; Haflidason et al., 1995; Koc et al., 1993). These abrupt climate changes occurred repeatedly during glacial periods with a temporal spacing of 2000 to 10000 years. The latest was the Younger Dryas cooling about 12000 years ago, which was followed by two cold phases of lower amplitude, the last 8200 years ago. Cooling periods in the regions surrounding the Arctic were associated with widespread drought over Asia and Africa, as well as changes in the Pacific circulation. Mid-latitude regions were most affected, while the amplitudes of these climate shifts were lower in the high Arctic.

The rapid climate shifts were accompanied by changes in the deep-water formation in the Arctic and the northward protrusion of warm water towards the Arctic (Dokken and Jansen, 1999), yet it would be wrong to say that they shut off entirely during the rapid change events. Instead they were characterized by shifts in the strength and in the depth and location of ocean overturning. The high amplitude climate shifts are hypothesized to be caused by, or at least amplified by, freshwater release from calving and melting of ice sheets in the Arctic.

Bond et al. (2001) identified events when icebergs originating from Greenland were more strongly advected into the North Atlantic and proposed that changes in insolation may have been the cause. Some of these events coincide with known climate periods, such as the Medieval Warm Period and an increase in icebergs during the following cooling period, known as the Little Ice Age. Temperature data from the Greenland Ice Sheet show a general warmer phase (800 to 1200 AD) and a general cold phase (1300 to 1900 AD) during these periods, respectively (Dahl-Jensen et al., 1998). Proxy data with higher temporal resolution from the Nordic Seas suggest similar temperature trends there, but it is clear that neither the Medieval Warm Period nor the Little Ice Age was monotonously warm or cold (Koc and Jansen, 2002).

9.2.4.1. Seasonal variability

Upper-layer waters in the Arctic Ocean that are open or seasonally ice-free experience seasonal fluctuations in temperature due to the annual cycle of atmospheric heating and cooling. The extent of the summer temperature rise depends on the amount of heat used to melt sea

ice (and hence not used for heating the water) and the depth of the surface mixed layer. For shallow mixed layers caused by ice melt, surface temperatures can rise substantially during the summer. Seasonal temperature ranges in the near-surface waters generally tend to increase southward. The melting and formation of sea ice leads to seasonal changes in salinity. Salt is rejected

from newly formed ice, which increases the salinity of the underlying water. This water sinks as it is denser than its surroundings. Salinity changes in some coastal regions are governed more by the annual cycle of freshwater runoff than by ice, e.g., along the Norwegian coast, in the Bering Sea, and Hudson Bay. Except for areas in which brine rejection from sea-ice formation occurs annually, seasonal changes in temperature and salinity below the mixed layer are usually small.

9.2.4.2. Interannual to decadal variability

Variability observed at interannual to decadal time scales is important as a guide for predicting the possible effect of future climate change scenarios on the physical oceanography of the Arctic.

Arctic Ocean

Long-term oceanographic time series from the Arctic Ocean deep basins are scarce. Data collections have been infrequent, although there was a major increase in shipboard observations during the 1990s (Dickson et al., 2000). These efforts identified an increased presence of Atlantic-derived upper ocean water relative to Pacificderived water (Carmack et al., 1995; Morison et al., 1998). Temperatures and salinities rose, especially in the Eurasian Basin. The rise in temperature for the Atlantic waters of the arctic basins ranged from 0.5 to 2 °C. The major cause of the warming is attributed to increased transport of Atlantic waters in the early 1990s and to the higher temperatures of the inflowing Atlantic water (Dickson et al., 2000; Grotefendt et al., 1998). At the same time, the front between the Atlantic- and Pacificcharacter waters moved 600 km closer to the Pacific from the Lomonosov Ridge to the Alpha-Mendeleyev Ridge (Carmack et al., 1995; McLaughlin et al., 1996; Morison et al., 1998). This represented an approximate 20% increase in the extent of the Atlantic-derived surface waters in the Arctic Ocean. In addition, the Atlantic Halocline Layer, which insulates the Atlantic waters from the near-surface polar waters, became thinner (Morison et al., 2000; Steele and Boyd, 1998). As the Atlantic-derived waters increased their dominance in the Arctic Ocean, there was an observed shrinking of the Beaufort Gyre and a weakening and eastward deflection of the Transpolar Drift (Kwok, 2000; Morison et al., 2000). These were shown to be a direct response to changes in the wind forcing over the Arctic associated with variability in the AO (Maslowski et al., 2000, 2001; Zhang et al., 2000).

Barents Sea

Inflow to the Arctic via the Barents Sea undergoes large variability on interannual to decadal time scales (Ingvaldsen et al., 1999, 2003; Loeng et al., 1997). The inflows change in response to varying atmospheric pressure patterns, both local (Ådlandsvik and Loeng, 1991) and large-scale, as represented by the NAO, with a larger transport associated with a higher index (Dickson et al., 2000; Dippner and Ottersen, 2001; Ingvaldsen et al.,

2003). The Shetland Branch of the Atlantic inflow (Fig. 9.7; also known as the Norwegian Atlantic Current) is a major contributor to the inflow to the Barents Sea. It is strongly correlated with the North Atlantic wind stress curl with the current lagging the wind stress curl by 15 months (Orvik and Skagseth, 2003).

Variability in both the volume and temperature of the incoming Atlantic water to the Barents Sea strongly affects sea temperatures. A series of hydrographic stations along a line north of the Kola Peninsula in northwest Russia has been monitored for over 100 years. Annual mean temperatures for this section show relatively warm conditions since the 1990s. It was also warm between 1930 and 1960, but generally cold prior to the 1930s and through much of the period between 1960 and 1990 (Fig. 9.8). Since the mid-1970s there has been a trend of increasing temperature, although the warmest decade during the last century was the 1930s (Ingvaldsen et al., 2003). Also evident are the strong near-decadal oscillations since the 1960s and prior to the 1950s. Annual ocean temperatures in the Barents Sea are correlated with the NAO; higher temperatures are generally associated with the positive phase of the NAO (Ingvaldsen et al., 2003; Ottersen and Stenseth, 2001). The correlation is higher after the early 1970s, which is attributed to an eastward shift in the Icelandic Low (Dickson et al., 2000; Ottersen et al., 2003).

Willem Barentsz was the first to provide information on sea ice conditions in the northern Barents Sea when he discovered Spitsbergen in 1596 (de Veer, 1609). Observations became more frequent when whaling and sealing started early in the 17th century (Vinje, 2001) and since 1740 there have been almost annual observations of seaice conditions. Typically, interannual variation in the position of the monthly mean ice edges is about 3 to 4 degrees of latitude. Variations on decadal and centennial scales are also observed. In all probability, the extreme northern position of the ice edge in summer coincides with an increased influx of Atlantic water entering the Arctic Ocean north of Svalbard. Complete disintegration of the sea ice in the Barents Sea proper (south of 80° N) was reported between 1660 and 1750. A similar north-

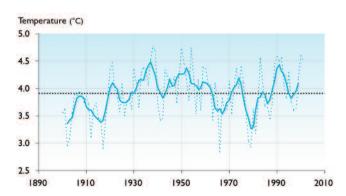


Fig. 9.8. Annual and five-year running means in sea temperature (at 50–200 m) from a series of hydrographic stations along a line north of the Kola Peninsula in northwest Russia (based on data supplied by the Knipovich Polar Research Institute of Marine Fisheries and Oceanography, Russia).

ern retreat of the sea ice was seen again in recent decades (after 1937). In contrast, sea ice completely covered the Barents Sea, as well as the Greenland and Iceland Seas, and the northern part of the Norwegian Sea, during 1881. This coincided with the lowest mean winter air temperature on record.

Northern North Atlantic

In the 1910s and 1920s, a major and rapid atmospheric warming took place over the North Atlantic and Arctic, with the greatest changes occurring north of 60° N (Fig. 9.9; Johannessen O. et al., 2004; Rogers, 1985). Warm conditions generally continued through to the 1950s and 1960s. Sea ice thinned and the maximum extent of the seasonal ice edge retracted northward (Ahlmann, 1949). Increases in surface temperature were reported over the northern North Atlantic (Smed, 1949) and throughout the water column over the shelf off West Greenland (Jensen, 1939). Higher temperatures between the 1930s and 1960s were also observed in the Barents Sea along the Kola Section (Fig. 9.8). The cause of this warming is uncertain although a recent hypothesis suggests that it was due to an increase in the transport of the North Atlantic Current into the Arctic (Johannessen O. et al., 2004).

At the end of this warm period, water temperatures declined rapidly. For example, at a monitoring site off northern Iceland, temperatures (at 50 m) suddenly declined in 1964 by 1 to 2 °C (Malmberg and Blindheim, 1994). This was caused by the replacement of the warm Atlantic inflow by the cold waters of the East Greenland Current. Also, the front to the east of Iceland between the warm Atlantic waters and the cold arctic water moved southward. These observations signified that the cooling had coincided with large-scale changes in circulation.

In the Labrador Sea, temperatures reached maximum values in the 1960s and did not decline substantially until the early 1970s. Shelf temperatures on the western Grand Banks at a site 10 km off St. John's, Newfoundland have been monitored since the late 1940s. Low-frequency subsurface temperature trends at this site are representative of the Grand Banks to southern Labrador (Petrie et al., 1992). Temperatures

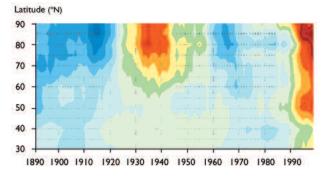


Fig. 9.9. Observed time—latitude variability in surface air temperature anomalies north of 30° N (Johannessen O. et al., 2004).

continued a general decline superimposed upon by quasi-decadal oscillations until the mid-1990s. Temperature minima were observed near the mid-1970s, mid-1980s, and mid-1990s that correspond to peaks in the NAO index (Colbourne and Anderson, 2003). After the mid-1990s, temperatures rose. Winter temperatures off Newfoundland are negatively correlated with those in the Barents Sea (Fig. 9.10) and linked through their opposite responses to the NAO. The Barents Sea and Newfoundland temperatures however have only been closely linked to the NAO since the 1960s (Ottersen et al., 2003).

During the 1970s, an upper-layer surface salinity minimum was observed in different regions of the North Atlantic (e.g., Dickson and Blindheim, 1984; Dooley et al., 1984; Malmberg, 1984). The generally accepted explanation for this observation was given by Dickson et al. (1988). During the 1960s, an intense and persistent high-pressure anomaly became established over Greenland. As the northerly winds increased through to a peak in the late 1960s, there was a pulse of sea ice and freshwater out of the Arctic via Fram Strait with the result that the waters in the East Greenland Current and the East Icelandic Current became colder and fresher. In addition, convective overturning north of Iceland and in the Labrador Sea was minimal, preserving the fresh characteristics of the upper layer. Beginning in the Greenland Sea in 1968, significant quantities of freshwater were advected via Denmark Strait into the Subpolar Gyre. The low salinity waters (called the Great Salinity Anomaly) were tracked around the Labrador Sea, across the Atlantic, and around the Nordic Sea before returning to the Greenland Sea by 1981–1982. Similar transport of low salinity features around the Subpolar Gyre was suggested to have occurred in the early 1900s (Dickson et al., 1988) and in the mid-1980s (Belkin et al., 1998). Belkin et al. (1998) proposed that the source of the mid-1980s salinity anomaly originated in Baffin Bay.

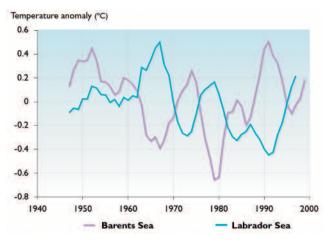


Fig. 9.10. Five-year average winter temperature anomalies (relative to the mean for 1971 to 2000) for the Barents Sea (the Kola Section off northwestern Russia, 0–200 m mean) and the Labrador Sea (Station 27 on the western Grand Bank off Newfoundland, near bottom at 175 m).

The deep water of the Norwegian Sea has for a long time been considered to have a relatively stable temperature. However, since the mid-1980s there has been a steady increase of more than 0.05 °C for the waters between 1200 m and 2000 m, and even the deepest water has shown a small temperature increase (Østerhus and Gammelsrød, 1999). In the surface layer there has been a steady decrease in salinity. In the deep, southflowing waters of the Greenland Sea there has been a 40-year trend toward decreasing salinity and this trend toward decreasing salinity has spread throughout much of the northern North Atlantic (Dickson et al., 2002). Dickson et al. (2003) suggest this may correspond to a general freshening of the whole Atlantic.

Interannual variability in the depth of convection in the Greenland Sea (Budéus et al., 1998; Meincke et al., 1992) and Labrador Sea (Lazier, 1980, 1995) depends upon wind, air temperature, upper layer salinity and temperature, and the pre-winter density structure. Dickson et al. (1996) and Dickson (1997) found the convective activity in the two areas to be of opposite phase, linked to shifting atmospheric circulation as reflected in the NAO index. In the late 1960s when the NAO index was low, there was intense convection in the Greenland Sea and little convection in the Labrador Sea owing to reduced winds and freshwater accumulation at the surface. In contrast, in the late 1990s when the NAO index was high, the reverse occurred with deep convection in the Labrador Sea and minimal convection in the Greenland Sea. Deep-reaching convection in the Greenland Sea contributes to overflow waters but Hansen et al. (2001) did not observe any NAO-like variations in their 50-year time series of Faroe Bank Channel overflow. However, deep convection is only one of several ventilation processes affecting the overflow (see section 9.2.3.4, vertical transfer of water). Hansen et al. (2001) did however find a general decreasing trend in the overflow, as was observed for the overflows across the southern part of the Iceland-Faroe Ridge and the Wyville-Thompson Ridge (Hansen et al., 2003). In the 1990s, higher temperatures offset the corresponding reduced Atlantic inflow to the Nordic Seas such that there was no net change in the heat flux but Turrell et al. (2003) suggested that a reduced salt flux may account for some of the freshening observed in large parts of the Nordic Seas.

Hudson Bay and Hudson Strait

The timing of the sea-ice advance and retreat in Hudson Bay and Hudson Strait varies between years by up to a month from their long-term means. This sea-ice variability has been linked to dominant large-scale atmospheric modes, in particular the NAO and the El Niño—Southern Oscillation (ENSO; Mysak et al., 1996; Wang J. et al., 1994). In years of high positive NAO and ENSO indices, heavy ice conditions occur in Hudson Bay as well as in Baffin Bay and the Labrador Sea. This increase in sea ice is attributed to cold air masses and stronger northwesterly winds over the region.

Between 1981 and the late 1990s air temperatures over Hudson Bay and Hudson Strait increased. This led to an earlier breakup of sea ice (Stirling et al., 1999) and an earlier spring runoff of river discharge into Hudson Bay (Gagnon and Gough, 2001).

Bering Sea

At decadal and longer timescales, the Bering Sea responds to two dominant climate patterns: the Pacific Decadal Oscillation (PDO) and the AO (see Chapter 2 for a detailed discussion). The PDO is strongly coupled to the sea level pressure pattern with stronger winds in the Aleutian low-pressure system during its positive phase (Mantua et al., 1997). It has a major impact on the southern Bering Sea. Thus the 40- to 50-year oscillation in the PDO led to higher sea surface temperatures in the North Pacific from 1925 to 1947 and 1977 to 1998, and cold conditions in 1899 to 1924 and 1948 to 1976. The AO had major shifts around 1977 and 1989 and there has been a long-term strengthening from the 1960s through the 1990s. Heavy sea-ice years in the Bering Sea generally coincide with negative values of the PDO, such as occurred in the early 1970s. The late 1970s and 1980 were warm years with reduced sea-ice cover. Heavy sea ice was again observed in the 1990s, but was not as extensive as in the early 1970s. In the 1990s, there was a shift toward warmer spring temperatures that resulted in sea ice in the Bering Sea melting one week earlier than in the 1980s, and the snow melting up to two weeks earlier (Stabeno and Overland, 2001).

9.2.5. Anticipated changes in physical conditions

During the 1990s it became apparent that global warming would occur more rapidly and with greater impact in the high latitudes (Morison et al., 2000; SEARCH, 2001). Observations showed substantial variability in the arctic water column, atmosphere, ice cover, and export to the North Atlantic (e.g., Belkin et al., 1998; Carmack et al., 1995; Morison et al., 1998; Rothrock et al., 1999; Walsh J.E. et al., 1996). This variability spans temporal scales that include interannual fluctuations, interdecadal patterns, and long-term trends. The first challenge is to define the temporal scales and magnitudes of arctic variability, for example to distinguish recurrent modes from trends and to separate natural from anthropogenic climate forcing. The second challenge is to understand and predict the impact of changes in the physical environment on the biota.

This section links the various sub-components of the physical system (e.g., land/ocean exchanges, shelf/basin interactions, inter-basin fronts, and the transport of ice and water properties) to climate-scale forcing at seasonal and decadal timescales. The assessment is based on the outcome of Chapter 4, plus the most recent results from the Intergovernmental Panel on Climate Change (IPCC, 2001) and information from the peer-reviewed literature.

9.2.5.1. Atmospheric circulation

General features of projected changes in the arctic atmosphere relevant to marine processes are summarized in Table 9.1. Air temperatures are very likely to increase by 4 to 5 °C over most of the Arctic by 2080. As air temperatures are very likely to increase more in winter than in summer there is very likely to be an associated decrease in the amplitude of the seasonal cycle. The IPCC (2001) reported that some studies have shown increasingly positive trends in the indices of the NAO/ AO in simulations with increased concentrations of GHGs. The magnitude and character of the changes vary for the different models. In general, the intensity of winter storms and the zonal temperature gradient are likely to decrease. However, in some regions (e.g., the Labrador, Nordic, Bering, and Beaufort Seas) an increase in storm activity is likely. Storm tracks are likely to shift northward under stronger AO and NAO conditions. Christensen and Christensen (2003) projected that the atmosphere will contain more water under a warmer climate, making more water available for precipitation. Model scenarios project an increase in precipitation of 10% by 2080 and an increase in cloud cover of 8%.

Paeth et al. (1999) assessed changes in the mean and variance of the NAO at decadal scales. They predicted

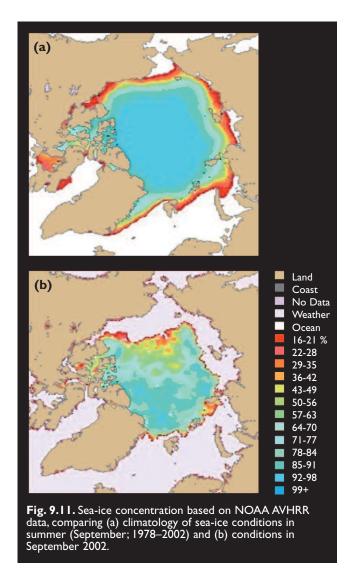
that the mean value will increase, while the variance will decrease, suggesting that the NAO will stabilize in the positive phase. The consequences of such a scenario are likely to be more westerly winds and milder weather over Europe during winter, while the Labrador Sea would be likely to experience more northwesterly winds and colder conditions. Shindell et al. (1999) and Fyfe et al. (1999) also predicted a positive trend in the NAO index. Ulbrich and Chrisroph (1999) concluded that there will be a northeastward shift of the NAO's northern variability center from a position close to the east coast of Greenland to the Norwegian Sea while Shindell (2003) stated that if the dynamic strengthening of the arctic vortex continues the Northern Hemisphere is likely to continue to warm up rapidly during winter.

Despite present uncertainties, it can be concluded that if the NAO increased, it would be likely to lead to increased westerly winds over the North Atlantic and more frequent storm patterns. Any trend toward positive AO conditions would be very likely to result in a weakening of the Beaufort High and increased cyclonicity over Canada Basin, as noted by Proshutinsky and Johnson (1997). Winds over the Bering/Chukchi Seas would probably also weaken. Changes in atmospheric forcing will impact upon most of the features discussed in the following sections; sea-ice conditions, ocean cir-

Table 9.1. Changes in surface and boundary forcing based on model projections and/or extrapolation of observed trends. Unless otherwise specified these projected changes are very likely to happen.

	2020	2050	2080
Air temperature			
annual meana	I-I.5 °C increase	2-3 °C increase	4-5 °C increase
winter	2.5 °C increase	4 °C increase	6 °C increase in the central Arctic
summer	0.5 °C increase	0.5-1.0 °C increase	I °C increase
seasonality	Reduced sea	sonality (warmer winters compa	red to summer)
interannual variability	No change	No change	No change
Wind			
means	While changes in winds are expected, there is at present no consistent agreement from general circulation models as to the magnitude of the changes in either speed or direction		
storm frequency	Possible increase in storm intensity regionally (Labrador, Beaufort, Nordic Seas); in general, winter storms will decrease slightly in intensity because the pole to equator temperature gradient decreases		
storm tracks	Probable northward shift in storm tracks		
regional issues	In areas of sea-ice retreat, there will be an increase in wind-driven effects (currents, waves) because of longer fetch and higher air–sea exchange		
Precipitation/runoff			
mean ^b	2% increase	6% increase	10% increase
seasonality	Decreased seasonality in runo	off related to earlier snow melt. S	easonality in precipitation unclear
snow on ice	I-2% increase	3-5% increase	6-8% increase
ea level	5 cm rise	15 cm rise	25 cm rise
Cloud cover			
general	3% increase	5% increase	8% increase
spring, autumn	4-5% increase	5-7% increase	8-12% increase
winter, summer	I-2% increase	3-5% increase	4-8% increase
Cloud albedo	Not available	Not available	Not available

^aThese numbers are averages and should be higher in the central Arctic and lower over southern regions; ^bbased on the estimates of precipitation minus evaporation i Chapter 6.



culation and water properties, ocean fronts, and thermohaline circulation.

9.2.5.2. Sea-ice conditions

Under scenarios of climate warming, sea-ice cover is expected to "retreat" further into the Arctic Basin, to breakup earlier and freeze-up later, and to become thinner and more mobile. For example, substantial differences in sea-ice conditions were observed in summer 2002 compared to the climatology of sea-ice conditions in summer

Table 9.2. Sea-ice extent in March (10^6 km^2) as projected by the five ACIA-designated models.

Model	1981-2000	2011-2030	2041-2060	2071-2090
CGCM2	16.14	15.14	13.94	13.26
CSM_I.4	16.32	15.00	14.16	14.01
ECHAM4/ OPYC3	16.19	15.62	14.97	14.38
GFDL- R30_c	16.17	15.60	14.86	14.52
HadCM3	16.32	15.53	14.87	13.74

CGCM2: Canadian Centre for Climate Modelling and Analysis; CSM_I.4: National Center for Atmospheric Research; ECHAM4/OPYC3: Max-Planck Institute for Meteorology; GFDL-R30_c: Geophysical Fluid Dynamics Laboratory; HadCM3: Hadley Centre for Climate Prediction and Research.

for the period 1978 to 2002 (Fig. 9.11, see also Serreze et al., 2003). Substantial changes in sea-ice conditions are evident in Canada Basin north of the Chukchi Sea, and in the sea-ice extent in Fram Strait and north of Svalbard.

Projected changes in sea-ice conditions for the 21st century are summarized in Chapter 6 based on output from the five ACIA-designated global climate models. Tables 9.2 and 9.3 show the maximum and minimum values for sea-ice extent projected by these five models, respectively. The values shown are the adjusted model values, meaning that the data have been "normalized" by forcing a fit to the 1981-2000 baseline observations. The projections vary widely, especially for the summer. The CSM_1.4 (National Center for Atmospheric Research) model consistently projects the greatest sea-ice extent and the least amount of change, while the CGCM2 (Canadian Centre for Climate Modelling and Analysis) model consistently projects the least sea ice and the greatest amount of change. However, all five ACIAdesignated models agree in projecting that sea-ice coverage will decrease both in summer and winter.

Areal ice extent

Increases in the AO index are likely to result in the Transpolar Drift taking a strongly cyclonic diversion across the Lomonosov Ridge and into Canada Basin and the Beaufort Gyre shrinking back into the Beaufort Sea (section 9.2.2.5; Fig. 9.3). This is very likely to alter the advective pathways and basin residence times of sea ice formed in winter on the Eurasian shelves. Furthermore, the ice extent in early autumn is also likely to be reduced, due to expected changes in wind forcing and winter air temperature in the eastern Russian Arctic (Rigor et al., 2002). By 2050, the CGCM2 model, which results in the greatest rate of sea-ice melt, projects that the entire marine Arctic may be sea-ice free in summer (Table 9.3). The other four models agree in projecting the presence of summer sea ice, at least until the end of the 21st century, but disagree in their projections of the extent of areal coverage. While the changes in winter sea-ice coverage are generally projected to be much smaller than in summer (Table 9.2), it is likely that the Barents Sea and most of the Bering Sea may be totally ice free by 2050 (see Chapter 6).

Table 9.3. Sea-ice extent in September (10^6 km^2) as projected by the five ACIA-designated models.

Model	1981-2000	2011–2030	2041-2060	2071-2090
CGCM2	7.28	3.33	0.55	0.05
CSM_I.4	7.22	7.00	6.72	6.59
ECHAM4/ OPYC3	7.02	6.03	4.06	2.68
GFDL- R30_c	7.28	5.91	4.33	2.91
HadCM3	7.41	6.22	5.12	3.22

CGCM2: Canadian Centre for Climate Modelling and Analysis; CSM_1.4: National Center for Atmospheric Research; ECHAM4/OPYC3: Max-Planck Institute for Meteorology; GFDL-R30_c: Geophysical Fluid Dynamics Laboratory; HadCM3: Hadley Centre for Climate Prediction and Research.

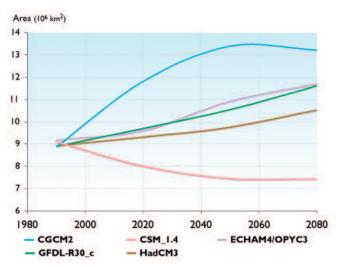


Fig. 9.12. Changes in the areal coverage of the seasonal sea-ice zone over the 21st century as projected by the five ACIA-designated models. The illustration is based on the values in Tables 9.2 and 9.3.

Seasonal sea-ice zone

Every year around 7 to 9 million km² of sea ice freezes and melts in the Arctic (Parkinson et al., 1999). Four of the five ACIA-designated models project that the seasonal sea-ice zone is likely to increase in the future because sea-ice coverage will decrease more during summer than winter (Fig. 9.12). This suggests that seaice thickness is also likely to decrease because a single winter of sea-ice growth is an insufficient period to reach equilibrium thickness. There is very likely to be a shorter period of sea-ice cover due to earlier breakup and later freeze-up. Longer ice-free periods will significantly increase sub-surface light availability. (At present, sea ice lingers in the Arctic Ocean through May and June, months of high levels of insolation.) A delayed freeze-up will also expose more open water to forcing by autumn storms. Retreat of the seasonal sea-ice zone northward into the central arctic basins will affect nutrient and light availability on the continental shelves during summer and autumn by increasing the areas of open water, wind mixing, and upwelling.

Fast ice is not explicitly included in climate model scenarios. Although reductions in the extent, thickness, and stability of fast ice are likely to occur, the implications of climate change for fast ice is recognized as a gap in knowledge.

9.2.5.3. Ocean circulation and water properties

Changes in the surface and boundary forcing (Table 9.1) will probably result in changes in ocean circulation, water mass properties, and ocean processes (section 9.2.3). Sea surface temperatures are likely to increase by approximately the same amount as air temperatures in areas that are sea-ice free, but are very likely to remain the same (i.e., near freezing) in ice-covered waters. By 2020 the upper water layer of all arctic shelves is very likely to exhibit stronger seasonality in

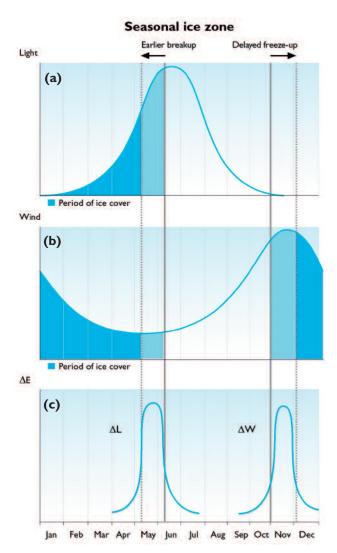


Fig. 9.13. The annual pattern of (a) incoming solar radiation, (b) wind speed, and (c) incremental changes in incoming solar radiation (Δ L) and wind energy (Δ W) to the water column from earlier breakup and delayed freeze-up. Earlier breakup allows a disproportionate amount of solar energy into the water column, while delayed freeze-up exposes the water column to autumn storms.

terms of sea-ice cover, and by 2080, 50 to 100% of the Arctic Ocean is likely to undergo such variability. Whether or not there is a concurrent increase in mixed-layer depth in summer depends on the relative coupling of wind and ocean in the presence or absence of sea ice, which in turn depends on the magnitude of internal ice stress (Wadhams, 2000). McPhee and Morison (2001) argue that, away from coastal areas, in summer most of the wind momentum transferred to the sea ice is subsequently passed on to the water and that sea ice may even serve to enhance the coupling of wind to water. Mixed-layer deepening is also very likely to be influenced by increased river discharge. Sub-sea light levels will increase in areas where sea ice is absent, but are very likely to decrease where sea ice remains due to increased snow.

General circulation models project a strengthening of the AO leading to increased atmospheric cyclonicity over the Arctic Ocean during the 21st century (Fyfe et al.,

1999). This, in turn, is very likely to affect the sea-ice drift and surface currents in the Arctic Basin. With increased cyclonicity the Transpolar Drift is very likely to shift eastward to favor drift directly toward Fram Strait (Rigor et al., 2002). The Beaufort Gyre is very likely to weaken and retreat into Canada Basin, following the "cyclonic mode" discussed by Proshutinsky and Johnson (1997) and Polyakov and Johnson (2000). In turn, changes in the Beaufort Gyre are very likely to affect the storage and release of freshwater in Canada Basin (Proshutinsky et al., 2002). Under this scenario the position of the Atlantic/Pacific Front will tend to align with the Alpha-Mendeleyev Ridge rather than the Lomonosov Ridge (McLaughlin et al., 1996; Morison et al., 1998) and perhaps retreat further into Canada Basin. Modeling studies by Zhang and Hunke (2001) and Maslowski et al. (2000) are in general agreement.

Relatively small changes in the timing of sea-ice breakup and freeze-up (of the order of a few weeks) are very likely to have a disproportionate effect on the physical forcing of arctic waters (Fig. 9.13). For example, under present-day conditions, much of the incoming solar radiation during the long summer days is reflected back by the ice and snow and so does not reach the water column to warm it. A later freeze-up will mean that the ocean surface is exposed to wind forcing by autumn storms for a longer period of time. Combined with prolonged exposure of the shelf break to wind forcing, this is very likely to enhance vertical mixing and the shelf—basin exchange of heat, salt, nutrients, and carbon.

Thresholds for change in the Arctic Ocean

Three potential thresholds for substantial changes in ocean circulation and water mass properties are described in this section (also see Box 9.4).

- 1. If and when the seasonal sea-ice zone retreats annually beyond the shelf break.
- 2. If and when the Arctic Ocean becomes sea-ice free in summer.
- 3. If and when parts of the deep arctic basins (e.g., the western Nansen Basin and western Canada Basin) remain sea-ice free in winter.

The seasonal retreat of sea ice from shelf domains to the deep Arctic Basin, anticipated as soon as 2020 (Tables 9.2 and 9.3, and Chapter 6), will expose the shelf-break region to upwelling- and downwellingfavorable winds, both for longer and more often. The coupling of wind and water in the presence of sea ice is not straightforward and can be of greater significance than in sea-ice free waters if internal ice stress (a function of ice concentration and compactness) is sufficiently small (McPhee and Morison, 2001). It is thus likely that a zone of maximum coupling exists in the transition from full sea-ice cover to open water, and that if this zone were located over the shelf break, then shelf-basin exchange would also increase (Carmack and Chapman, 2003). Such exchange would draw more Pacific- and Atlantic-origin waters onto the shelves, with an associated increase in the delivery of salt, heat, and nutrients.

Box 9.4. Effects of climate change in the Arctic on global ocean circulation and climate

The Arctic plays a key role in the global climate through its production of North Atlantic Deep Water (NADW). North Atlantic Deep Water is formed by the mixture of waters produced by thermohaline ventilation in the Arctic Mediterranean, entrained Atlantic water, and water convected in the Labrador Sea. Once formed the NADW flows southward through the Atlantic Ocean and, together with the denser Antarctic Bottom Water (AABW), forms the source of all the deep and bottom waters of the World Ocean. NADW is of considerable significance for the global thermohaline circulation (THC).

If climate change should result in reduced thermohaline ventilation in the Arctic, there is considerable – although not unambiguous - evidence for a reduced NADW-THC through the Atlantic (Ganachaud and Wunsch, 2000; Munk and Wunsch, 1998; Rahmstorf and England, 1997; Toggweiler and Samuels, 1995). A proper understanding of this scenario requires an understanding of the relative magnitudes of the NADW and the AABW contributions to the global THC. Traditional estimates of NADW production (e.g., Schmitz and McCartney, 1993) are of the order of 15 Sv and this is supported by modern estimates based on the WOCE (World Ocean Circulation Experiment) data set (Ganachaud and Wunsch, 2000). Estimates of AABW production are less consistent, but even the highest estimates (Broecker et al., 1999) indicate that AABW production is currently significantly less than NADW production. The NADW is therefore considered to account for more than half the deep-water production of the World Ocean at present. The latest IPCC assessment (IPCC, 2001) concludes that most models show a weakening of the Northern Hemisphere THC, which contributes to a reduction in surface warming in the northern North Atlantic. The more extreme scenario of a complete shutdown of the THC would have a dramatic impact on the climate of the North Atlantic region, on the north-south distribution of warming and precipitation, on sea-level rise, and on biogeochemical cycles (IPCC, 2001). The IPCC concluded this to be a less likely, but not impossible, scenario. More reliable estimates of its likelihood and consequences require more reliable coupled ocean-atmosphere models than are presently available (see section 9.7).

(°C)

-1.1

-1.2

-1.3

-1.4

-1.5

-1.6

Box 9.5. The Chukchi albedo feedback loop: An Achilles Heel in the sea-ice cover of the western Arctic?

Attention has long focused on the role of Atlantic inflow waters in the transport of heat within the Arctic Basin, and its potential to impact upon the overlying sea ice should the arctic halocline weaken or break down. This box highlights the potential for Pacific inflow waters to impact upon the overlying sea ice, and the potential for this inflow to amplify locally the well-known albedo feedback mechanism.

Pacific inflow waters are warmed in summer as they travel northward across the seasonally ice-free parts of the Bering and Chukchi Seas. On reaching the shelf break, these waters subduct below the polar mixed layer and enter the arctic halocline, forming Pacific Summer Water (PSW), identified by a shallow temperature maximum at depths 40 to 60 m and salinities near 31.5. The water at the temperature maximum may be higher in years with extensive open waters over the Bering and Chukchi Seas. Summer climatological data (see panel, Timokhov and Tanis, 1998; Shimada et al., 2001) demonstrates the accumulation of such water within the Beaufort Gyre over the eastern flank of the Northwind Ridge.

One possibility for the fate of this stored heat within the PSW in the southwestern Canada Basin is that it acts to retard the growth of sea ice during the subsequent winter. Therefore, the amount of summer melting (freshwater addition) and winter freezing (freshwater removal) are not balanced, and ice floes drifting over the "warm patch" will be thinner than in surrounding waters. The thin sea ice observed east of the Northwind Ridge, also noted by Bourke and Garrett (1987), is evidence of local PSW influence. When winter sea-ice growth falls below a critical (and unknown) value at the start of the melt season, the thickness and concentration of sea ice over the region would be sufficient to reduce albedo and initiate further sea-ice reduction, thus initiating a feedback. An alternate explanation for the record low sea-ice con-

centrations in summer 2002 is given by Serreze et al. (2003).

The disappearance of sea-ice cover in the Arctic in summer, as projected by the CGCM2 model by 2050, will have far reaching effects on upper-layer circulation and water properties. Direct exposure of surface waters to wind will enhance wind-driven circulation. Also, it is probable that wind-driven vertical mixing will increase the depth of the surface mixed layer, depending upon the strength of local stratification. For example, wind-driven deepening of the mixed layer is very likely to be more pronounced in the more weakly stratified Nansen Basin than in Canada Basin with its strong Pacific influence. Concurrently, the seasonal sea-ice zone is very likely to increase (perhaps by 10 million km²) owing to projections that the rate of decrease in sea-ice cover for summer will be greater than for winter (Fig. 9.12; Tables 9.2 and 9.3).

Some model scenarios project that by 2080 the formation of sea ice in winter will no longer completely cover the Arctic Basin. If this does occur, two parts of the Arctic Basin are potential sites for sea-ice free or at least

decreased ice concentrations in winter: the western Nansen Basin and western Canada Basin.

The first site is the weakly stratified western Nansen Basin adjacent to the inflow and subduction of Atlantic waters (Martinson and Steele, 2001). Here the incoming waters are warmest and the overlying halocline is weakest. At present, this region has the deepest winter mixed layer in the central Arctic Ocean. Under the extreme climate change scenario in which sea ice in winter no longer completely covers the Arctic Basin, the Nansen Basin is likely to become a region of strong convection and deepwater formation. However, the dynamics are more likely to resemble the present day Nordic Sea system, i.e., with deeper mixed-layer ventilation or convection (see Muench et al., 1992 and Rudels et al., 2000 for a discussion of water masses). However, this argument supposes an increased transport of warmer Atlantic water into the Arctic whereas some models (e.g., Rahmsdorf, 1999) suggest a weakening or southward shift of the THC.

The second site is located in the western Canada Basin immediately north of the Chukchi Sea and above the Northwind Ridge (Box 9.5). This area is adjacent to the inflow of shallow and relatively warm summer water through the Bering Strait and across the Chukchi Sea. The spread of this relatively warm water takes place within the Beaufort Gyre at depths of 40 to 60 m, and is thus within the limits of winter haline convection (Shimada et al., 2001).

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At both sites, it is their proximity to warm inflows from the Atlantic and Pacific that establishes conditions that may reduce winter sea-ice cover. It is not clear, however, if release of heat from subsurface sources would serve to melt the sea ice, or merely keep new ice from forming. In either case ecosystems currently located in the Nordic and Bering Seas are very likely to shift northward.

Changes in the Nordic and the Barents Seas

An 80-year CMIP2 integration (1% per year increase in the atmospheric ${\rm CO}_2$ concentration) with the Bergen Climate Model (BCM) was used to estimate changes in the Nordic and Barents Seas (Furevik et al., 2003). This model has a relatively high spatial resolution in

these areas and is believed to give as reliable projections for these areas as can be obtained at present. However, in common with other such models, its predictive capability is limited and the results presented should be seen as possible, rather than likely outcomes.

The evolution of the winter sea surface temperature field is shown in Fig. 9.14. From the present to 2020 a minor cooling is projected over most of the area. The greatest decrease is projected to occur along the marginal ice zone in the Barents Sea and off the East Greenland coast, with a maximum decrease of more than 1 °C projected in Denmark Strait. Some of this cooling is likely to be associated with the weaker westerlies projected for this period (Furevik et al., 2002). In the central Nordic Seas a warming of 0.5 °C is projected. By 2050, the entire Nordic Seas are projected to become warmer with the exception of a small area in Denmark Strait. The largest warming is projected to occur in the northeastern Barents Sea and to the south of Iceland. With the doubling of the atmospheric CO₂ concentration assumed by 2070, surface temperatures in the Nordic Seas are projected to increase by 1 to 2 °C, with the highest values in the Barents Sea. Minimum warming (<0.5 °C) is projected in the Denmark Strait.

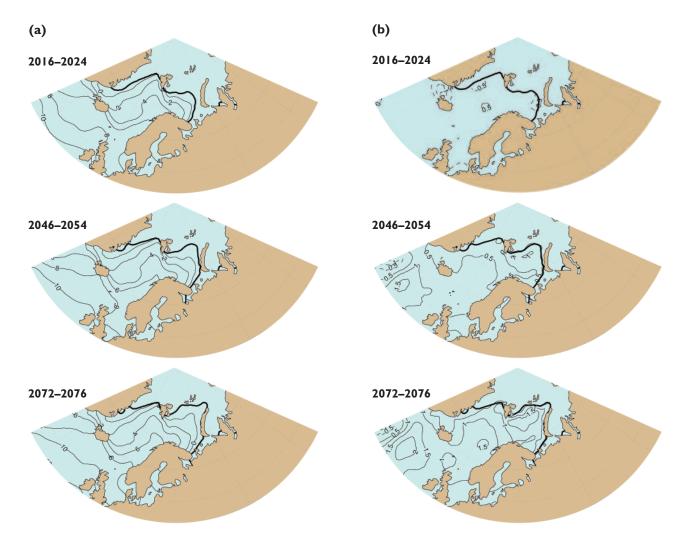


Fig. 9.14. Evolution of the sea surface temperatures and the sea-ice edge (heavy black line) in the BCM CMIP2 integration; (a) shows the March sea surface temperatures and sea-ice distribution around the years 2020, 2050, and 2075, (b) shows projected changes from 2000 to 2020, 2050, and 2075, respectively (Furevik et al., 2002).

Projected salinity changes in the Nordic Seas are generally small, except for areas influenced by coastal runoff and the melting of sea ice. By 2020, there is projected to be a freshening (a salinity decrease of 0.1 to 0.3) in the southeast Barents Sea and the Kara Sea, and a weak freshening along the East Greenland coast. The freshening continues to the 2050s, with salinity reductions north of Siberia in the range 0.1 to 0.5. A significant freshening is also projected in the Arctic Ocean (a salinity decrease of 0.3 to 0.5), which is advected southward with the East Greenland Current into the Denmark Strait and East Icelandic Current. The arctic waters are projected to become slightly more saline, but not exceeding a salinity increase of 0.1. By the 2070s, the model output suggests 0.1 to 0.2 more saline water south of the inflow area, and less than 0.1 more saline arctic waters in the Nordic Seas. North of Siberia and in the Arctic Ocean, salinities are projected to decrease by 0.5 to 1.0, and a tongue of fresher water is projected along the East Greenland Coast.

In terms of volume flow, from 2000 to 2020 the Bergen Climate Model projects a small (<10%) increase in the net Atlantic inflow through the Iceland–Scotland Gap, mainly near Iceland, and a corresponding increase in the Denmark Strait outflow. There is generally a weakening by a few percent of the cyclonic gyre in the Nordic Seas. By 2050, the Nordic Seas gyre is projected to have weakened by a further 10%. A greater inflow of arctic

waters is projected via the eastern branch (east of the Faroe Islands), and less via the western. No significant changes are projected for the Barents Sea. Toward 2070 a further reduction in the internal cyclonic flow in the Nordic Seas is projected. There is also a strengthening (~0.25 Sv, ~12%) in the transport of arctic waters through the Barents Sea with a compensating reduction through Fram Strait (Furevik et al., 2002).

Seas of the North American Arctic

Projections of change in the Bering, Chukchi, and Beaufort Seas, the Canadian Archipelago, Baffin and Hudson Bays, and the Labrador Sea are highly uncertain as many important aspects of these regions (e.g., the presence of fast ice, strong seasonality, complex water mass structure, through flow) are not included in the current global climate models. The following discussion is thus highly speculative.

These seas are expected to experience the general changes in sea ice, sea surface temperature, mixed-layer depth, currents, fronts, nutrient and light levels, air temperature, winds, precipitation and runoff, sea level, and cloud cover summarized in Tables 9.1 and 9.4, but owing to their more southerly latitude and contact with terrestrial systems, the changes may be greater and perhaps faster. Because the Bering/Chukchi shelf is very shallow the effects of the albedo feedback mechanism

Table 9.4. Summary of changes projected in ocean conditions according to the five ACIA-designated models relative to baseline conditions. Unless otherwise specified these projected changes are very likely to happen.

	2020	2050	2080
Sea ice			
duration	Shorter by 10 days	Shorter by 15-20 days	Shorter by 20–30 days
winter extent	6–10% reduction	15–20% reduction	Probable open areas in high Arctic (Barents Sea and possibly Nansen Basin)
summer extent	Shelves likely to be ice free	30-50% reduction from present	50-100% reduction from present
export to North Atlantic	No change	Reduction beginning	Strongly reduced
type	Some reduction in multi-year ice, especially on shelves	Significant loss of multi-year ice, with no multi-year ice on shelves	Little or no multi-year ice
landfast ice	Possible thinning and a retreat in southern regions	Probable thinning and further retreat in southern regions	Possible thinning and reduction in extent in all arctic marine areas
Sea surface temperature			
winter/summer (outside THC regions and depending upon stratification and advection)	An increase by about the same amount as the air temperatures in ice-free regions. No change in ice-covered regions		
seasonality	All shelf seas to undergo seasonal changes	30–50% of Arctic Ocean to undergo seasonal changes	50–100% of Arctic Ocean to undergo seasonal changes
Mixed-layer depth	Increase during summer in areas with reduced ice cover and increased wind		
Currents	In regions affected by THC, modifications to the THC will change the strength of the currents		
Ocean fronts	nts Fronts are often tied to topography but with altered current flows, may rapidly shift their position		
Light exposure	With decreasing ice duration and areal extent, more areas to be exposed to direct sunlight		
Nutrient levels	Substantial increases over the shelf regions due to retreat of the sea ice beyond the shelf break	higher levels due to deep	and in deep arctic basins; per mixed layer in areas of ice cover

are likely to be amplified as water moves across ice-free parts of the shelves. Preconditioning of Pacific inflow waters during their transport across the shelf supplies a reservoir of heat at shallow depths within the offshore halocline, which may affect conditions to the east on the Beaufort Shelf (Box 9.5). Such heat could potentially retard sea-ice growth the following winter.

The Canadian Archipelago is a large (~2.9 million km², including Foxe Basin and Hudson Strait) and complex shelf domain for which it is particularly difficult to draw conclusions regarding global warming (Melling, 2000). Sea ice remains landfast for more than half the year there, but the presence of fast ice is not included in the global climate models. The general trends projected by the ACIA-designated models and summarized in Table 9.1 are likely to be representative for this region. Two additional features of the Canadian Archipelago are (1) that it serves as a passageway for water masses moving from the Arctic Ocean to the North Atlantic via Baffin Bay and the Labrador Sea, and (2) that its sea-ice domain is a variable mixture of local growth and floes imported from the Arctic Basin, and that transport through the Canadian Archipelago is governed in the present climate by ice bridges across connecting channels (Melling, 2002).

Large uncertainties exist in the changes projected for the Labrador Sea. If the NAO increases as some models project, then there are likely to be stronger northwesterly winds and colder air masses over this region. This would lead to increased sea-ice cover, colder water temperatures, and increased deep convection. Conversely, general atmospheric warming would lead to warmer water temperatures, decreased sea-ice cover, and decreased convection. The slight increase in precipitation may possibly lower salinities over the Labrador Sea, with the largest decline occurring over the shelves due to the accumulation of river discharges. Temperatures in the region are also likely to be greatly influenced by the relatively warm Irminger Current inflow but given the poor understanding of future wind fields, changes in its strength are highly uncertain. Polynyas, such as the North Water Polynya in northern Baffin Bay, owe their existence, at least in part, to winds that move sea ice from the area of its formation southward, so maintaining the area as open water even in the middle of winter. If the winds change, the number and size of polynyas are also likely to change.

9.2.5.4. Ocean fronts

Open ocean fronts generally separate water masses, are associated with strong current flows, and act as barriers for marine organisms. It is difficult, however, to provide reliable estimates of how fronts will respond to climate change since few models provide such information. Most of the deep ocean fronts are linked to bottom topography and so it is likely that these will maintain their present positions, e.g., along the Mohn Ridge in the Greenland Sea and around the Svalbard Bank in the

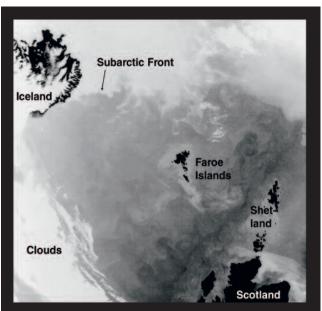


Fig. 9.15. Infrared satellite image showing the position of the Subarctic Front (also called the Iceland–Faroe Front in this region) between Iceland and Scotland on 18 May 1980. Dark areas indicate warm water, and light areas indicate cold water, except where cloud cover occurs (satellite image supplied by University of Dundee, UK).

Barents Sea. However, where topographic steering is weak, fronts may disappear or be displaced. The eastern part of the Polar Front in the Barents Sea is very likely to disappear as a result of climate change (Loeng, 2001). In the Norwegian Sea, the front to the east of Iceland is likely to move northeastward to the position it occupied during the warm period at Iceland between 1920 and 1964.

The reduced inflow of Atlantic water projected by some models would be very likely to shift ocean fronts toward the continental slope region. For example, in the Norwegian Sea the Subarctic Front separates Atlantic and arctic waters, typically lies a few hundred kilometers north of the Faroe Islands (Fig. 9.15), and reduced inflow would be likely to move the front closer to or even onto the Faroe Shelf. If such a shift takes place a cooling of the order of 5 °C would possibly occur in the areas affected. Assessing the likelihood of its occurrence is, however, far beyond the capability of present-day models.

9.2.5.5. Possibility and consequences of altered thermohaline circulation

A major uncertainty in projecting the extent of climate change in the Arctic concerns the response of the THC to altered freshwater flux. In turn, the THC of the Arctic is an integral part of the global THC (see Boxes 9.2 and 9.4). At present, climate models do not generate unambiguous results. Some project a significant weakening, or even collapse, of the THC, while others project a stable THC. An alternative view is that the THC will not weaken or shut down, but that the sites of ventilation will relocate north or south within the system (Aagaard and Carmack, 1994; Ganopolski and Rahmstorf, 2001).

Several coupled atmosphere-ocean general circulation models have been used to simulate the effects of increased GHG emissions on the North Atlantic THC. Rahmstorf (1999) summarized the outcome of six such simulations, all of which projected a weakening of the Atlantic overturning. Latif et al. (2000), however, did not find weakening of the overturning in their model. The models tend to agree that global climate change is very likely to include increased freshwater input to the Arctic Mediterranean, but tend to disagree on the associated consequences. Much of the uncertainty involves the response of the Atlantic inflow and the positive feedback mechanism that it can induce through salt advection. In the simulation by Latif et al. (2000), the feedback mechanism was counteracted by the increased salinity of the Atlantic inflow to the Arctic Mediterranean. The salinity increase in their model was explained by increased freshwater transport from the Atlantic to the Pacific in the tropical atmosphere. Latif (2001) used the observed salinity increase at Bermuda to support their conclusions. In the Nordic Seas, observations indicate the opposite with a general freshening in the upper layers (Blindheim et al., 1999; Verduin and Quadfasel, 1999).

Most of the general circulation models that project a weakening of the THC project a reduction of no more than 50% for the 21st century (IPCC, 2001). Some, however, project instabilities and the possibility of a more or less total collapse of the THC when the intensity of the circulation falls below a certain threshold (Tziperman, 2000). Although such results may explain the instabilities reported for the glacial climate state, their applicability to a GHG-warming scenario cannot be assessed objectively at present.

Observations of the salinity of overflow water in the Atlantic confirm a long-term decrease (Dickson et al., 2002). However, observational evidence for or against a reduction in the THC itself is uncertain. While many observations indicate a reduction in deep convection in the Greenland Sea since 1970, deep convection to depths below the sill level of the Greenland–Scotland Ridge is still occurring (Budéus et al., 1998; Gascard et al., 2002; Meincke et al., 1997) and there are also

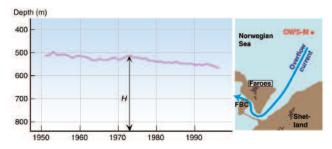


Fig. 9.16. Temporal variability in the intensity of the overflow through the Faroe Bank Channel. The lavender line shows the five-year running mean for the depth of the 28.0 density surface ($\gamma_e = 28.0 \text{ kg/m}^3$) at Ocean Weather Ship M (OWS-M). This surface is considered the upper limit of the dense overflow water and its height (H) above the sill level of the Faroe Bank Channel (FBC) is used as an indicator for overflow intensity. A deepening trend in the density surface implies a decreasing overflow intensity through this channel (Hansen et al., 2001).

other sources of dense water. Observations of the Faroe Bank Channel overflow (Fig. 9.16) indicate significant decreases in volume flux during the latter half of the 20th century, especially since 1970 (Hansen et al., 2001). A lack of similar data for the Denmark Strait overflow leaves open the question as to whether the change in the Faroe Bank Channel overflow is representative of the total overflow flux.

A significantly weakened THC in the Nordic Seas is thus a possible scenario. Reduced ventilation implies reduced renewal rates for deep water in some of the basins, and this seems to be happening in the Norwegian Basin (Østerhus and Gammelsrød, 1999). These changes are slow, however. The magnitude of the inflow weakening and its spatial extent will possibly be influenced by changes in the wind field (Blindheim et al., 1999). The waters most likely to be affected in this scenario are those to the north of Iceland and the Faroe Islands, those in the southern Norwegian Sea, and those in the Barents Sea.

The situation in the waters to the north of Iceland, where the present-day climate is associated with a highly variable Atlantic inflow, can be used to illustrate a potential impact of climate change. Hydrographic investigations show clear seasonal variation in this inflow, with a maximum inflow in summer. There are, however, pronounced interannual differences in the variability of the inflow that affect the temperature, salinity, and stability of the water column (Astthórsson and Vilhjálmsson, 2002; Thordardóttir, 1977). Most of the Atlantic inflow (80–90%, see Fig. 9.7) enters the Arctic Mediterranean through the Norwegian Sea. This region is characterized by abnormally high sea surface temperatures (up to almost 10 °C) compared to zonal averages (Rahmstorf and Ganopolski, 1999). Much of this elevation is due to the heat flux from the inflowing Atlantic water. The temperature decrease in some areas, especially in winter, resulting from a severely weakened Atlantic inflow would thus be much larger than the projected warming (Chapter 4) by the end of the 21st century according to certain models (Seager et al., 2002). Thus, there is the possibility that some areas of the Arctic Ocean will experience significant regional cooling rather than warming, but present models can assess neither the probability of this occurring, nor its extent and magnitude. According to Rahmstorf (2003) the extent to which Europe's mild winters depend on the transport of heat by the North Atlantic Current is presently unknown.

9.3. Biota

Following a general introduction to the biota of the marine Arctic, this section reviews the dominant species and, where possible, presents relevant life history and ecological information. The section then addresses the influence of physical factors on the biota and discusses variations in abundance and distribution observed in response to past climate fluctuations. The section concludes by presenting possible future changes in the arctic biota induced by the projected

changes in the atmospheric forcing functions and potential future sea-ice conditions discussed in Chapter 6. Salmon ecology and response to climate change are addressed in Chapters 8 and 13.

9.3.1. General description of the community

Biological production in the oceans is based primarily on phytoplankton or planktonic algae. These are microscopic unicellular plants that mostly reside within the water column but in the Arctic are also found in and on the sea ice. Through photosynthesis, they reduce ${\rm CO}_2$ while releasing oxygen and producing carbohydrates. The carbohydrates are converted, according to the needs of the algae, into essential compounds such as proteins and nucleic acids by incorporating nitrogen, phosphorus, sulfur, and other elements.

The organic matter produced by the algae is primarily consumed by herbivorous (i.e., plant-eating) animals, mainly zooplankton, which in turn may be eaten by fish. The fish are then consumed by seabirds and mammals, including humans. Each segment of the food web within which organisms take in food in the same manner is called a trophic level. Thus phytoplankton are considered the first tropic level, zooplankton the second, etc. The loss of organic matter between one trophic level and the next is about 75 to 80%. The main losses are associated with respiration (i.e., the burning of food) within the organisms themselves, consumption by bacteria (i.e., microbial degradation) of dissolved organic matter, and sinking cellular remains and fecal pellets (i.e., the body's waste). These processes all result in the release of CO₂ or nutrients. Only a small fraction of the organic matter reaches the seabed – the deeper the water column, the smaller this fraction (Box 9.6).

Table 9.5. Average carbon biomass and annual carbon productivity for different trophic levels within the Barents Sea, compared with that for human populations in Norway and Japan. Data recalculated from Sakshaug et al. (1994).

	Biomass (mg C/m ²)	Productivity (mg C/m²/yr)
Bacteria	400	60 000
Phytoplankton	2000	90000
Zooplankton (copepods and krill)	>3000	9500
Zoobenthosa	5160	1550
Capelin ^b	600	300
Cod ^c	300	100
Minke whales	110	2.6
Seals	30	0.5
Seabirds	2.5	0.4
Polar bears	0.25	0.027
People, Norway	107	1.5
People, Japan	2200	22

 $^{\rm a}$ Interannual biomass variation, 3000–7350 mg C/m² (Denisenko and Titov, 2003); $^{\rm b}$ Interannual biomass variation, 30–700 mg C/m²; $^{\rm c}$ Interannual biomass variation, 150–700 mg C/m².

Pelagic ecosystems are those which occur within the water column of the open ocean away from the ocean floor. Arctic pelagic ecosystems, like pelagic ecosystems elsewhere and in contrast to terrestrial ecosystems, are dominated by animal biomass. In the Barents Sea, for example, the mean annual plant biomass is 2 g C/m² whereas the mean annual animal biomass is at least four times more. Globally, annual marine primary production is about 40 Pg C (i.e., 10^{15} grams) or 40% of the

Box 9.6. Organisms in the food web

Population abundance, whether for algae, fish, or polar bears (*Ursus maritimus*), is dependent on the population growth and death rates. Given a growth rate higher than the death rate, the population size will increase, and *vice versa*. If the two rates are equal, the population is in steady state. Another variable is population migration; stocks may arrive in or leave a given ecosystem. Essentially, a change in any environmental variable, including those affected by climate change, has a direct impact on one or more processes by changing their rate, which in turn causes a change in population biomass. Thus, while the population growth rate is determined by light or nutrient levels (algae), or food availability (animals), the loss rate represents the sum of losses due to natural death, pollution, sedimentation, and being eaten, fished, or hunted.

Populations can be arranged hierarchically within a food web on the basis of what they eat, with the lowest trophic level comprising photosynthetic organisms. Animals can move up the food-web hierarchy as they grow, by becoming able to eat larger prey. Because most of the food intake is spent on maintaining life, reproduction, movements, etc., only 15 to 25% contributes to population growth, which during steady state represents food for the next trophic level. Consequently, marine food chains are short, with a maximum of five trophic levels.

In models, population growth is described by exponential functions in which growth and mortality rates themselves are functions of environmental change, including changes caused by the evolution of the ecosystem itself (feedback). Ideally, ecosystem models should include all trophic levels, including major species as separate entities; however, coupling plankton and fish is difficult, as is the coupling of fish and higher animals.

Box 9.7. Sea-ice communities

Sympagic organisms are those that live in close association with sea ice, either within channels in the ice itself, on the underside of the ice, or at the interface with the water immediately below the ice. The organisms that inhabit this environment are highly specialized, but cover a wide taxonomic range, from bacteria and simple algae, to vertebrate fauna. Some species, particularly microorganisms, become incorporated into the sea ice as the ice crystals grow. While it may seem an inhospitable environment, the sea ice is actually quite a stable and organically-enriched environment for those organisms that can tolerate its extreme conditions. While some organisms occupy the sea ice as it forms, others actively or passively migrate into the ice ecosystems. Organisms that live within the interstitial spaces of sea ice include microfauna such as protists, and larger organisms such as ciliates, nematodes, rotatorians, turbellarians, and copepods. Multi-year sea ice has the most complex communities and often serves as a platform for colonizers to young ice. In addition, the abundance and biomass of the multi-year sea ice organisms can be very high. For example, copepods may easily exceed densities of 150 individuals per square meter. Given the correct conditions vast algal mats can form on the under-surface of sea ice, including both microalgae and macroalgae such as sea-tangle (Fucus distichus), and their associated epiphytic organisms such as Pylaiella littoralis. In comparison, seasonal sea ice normally has lower densities and lower biomasses and tends to support more simple communities.

The spatial distribution of sea-ice fauna is generally patchy, even within single ice fields, because the origin, history, size, snow thickness, and the thickness of the sea ice itself can vary dramatically. Interannual variability within a community is also high. In areas such as the Barents Sea, the size of the Atlantic Water inflow varies from year to year, causing dramatic changes in the sympagic community. Nevertheless, sympagic communities are characterized by fauna that can withstand high levels of variation in food availability and low temperatures. Generally, the older the sea ice, the more complex and established the sympagic community. Ice-living invertebrates tend to have low basal metabolic rates, concomitant slow growth, and long life cycles. For example, some arctic ice amphipods live for five or six years, while their more temperate counterparts, or amphipods in other arctic habitats, have average life spans of two to three years. Large, lipid-rich ice-dwelling amphipods are prime prey for the circumpolar polar cod (Boreogadus saida). This small, arctic fish is an opportunistic feeder that can live pelagically, or in association with sea-ice communities. In ice-filled waters its diet largely comprises Themisto libellula and Apherusa glacialis. The fish capture these small "lipid packages" and convert them into prey that is substantial enough to support higher vertebrates such as seabirds and marine mammals. Some seabirds and marine mammals also eat large invertebrate ice-dwellers directly. Black guillemots (Cepphus grylle) and thickbilled murres (Uria lomvia) feed on the amphipod Gammarus wilkitzkii. Little auks (Alle alle) and ivory gulls (Pagophila eburnea) also eat sympagic amphipods. First-year harp seal (Phoca groenlandica) feed extensively on sympagic amphipods when they start to self-feed. However, the preferred prey within the sympagic community is polar cod for most marine mammals.

Thinning, and reduced coverage of arctic sea ice will have dramatic impacts on the entire sympagic ecosystem, particularly on interstitial organisms as these do not have alternate habitats in which to live. Also, given that the sympagic community is important in providing pelagic and benthic communities with food, particularly during the summer when the sea ice melts, changes in this highly specialized environment are likely to have repercussions throughout the arctic marine community as a whole.

global total (marine plus terrestrial) production. Macroalgal biomass (i.e., large plants such as kelp and sea-tangle) in the Arctic is believed to be small due to habitat restrictions caused by freezing, ice scouring by small icebergs, and local freshwater input. In some areas, however, macroalgal biomass can be large as kelp forests do occur in the Arctic.

Generally, the higher the trophic level, the smaller the production. In the Barents Sea, major pelagic fish species represent a few hundred milligrams of carbon biomass per square meter and seabirds and polar bears, only 2.5 and 0.25 mg C/m², respectively (Table 9.5). The table shows the inverted biomass pyramid which is typical for phytoplankton and zooplankton in the marine pelagic food web. On the Bering Shelf, the annual primary pro-

duction is higher than in the Barents Sea. In the shallow areas of the Bering Sea (40 to 100 m depth), the "rain" of organic particles from the upper layers to the benthic (bottom-dwelling) animals can be higher than the fraction grazed by pelagic animals (Walsh J.J. et al., 1989). This input is also much higher than in the Barents Sea, which has an average depth of 230 m. Benthic biomass and production are lowest in the deep Arctic Ocean.

Box 9.7 reviews the highly specialized communities associated with seasonal and multi-year sea ice.

Although phytoplankton generally grow more slowly in the Arctic than in warmer areas, near-freezing temperatures would not delay the onset of the initial phytoplankton bloom (i.e., period of very high production) by

more than two to three days compared to that at 5 to $10\,^{\circ}$ C. Light- and nutrient-limitation is more important than temperature. Arctic zooplankton, certainly the predominant copepods, have adapted to cold conditions by having life cycles that are two to ten times longer than corresponding species in temperate conditions.

The Arctic Ocean as a whole is not particularly productive yet seasonal productivity in patches of the Barents and Chukchi Seas, and on the Bering Shelf, is among the highest of anywhere in the world (Rysgaard et al., 2001; Sakshaug, 2003; Sakshaug et al., 1994; Springer et al., 1996; Walsh, 1989). In these areas, the primary production supports large populations of migratory seabirds, a large community of various mammals, and some of the world's richest fisheries.

Many seabirds and some marine mammal species either migrate into the Arctic during the summer pulse of productivity or can cope with the long periods when food supplies are limited. Many of the permanent residents store large quantities of reserve energy in the form of lipids (oils) during periods of abundant food supply while others survive winter in a dormant stage.

9.3.1.1. Phytoplankton, microalgae, and macroalgae

Phytoplankton are often classified according to size. Nanoplankton (2–20 μm) are the most abundant yet several microplankton species (>20 µm; some reaching 500-750 µm) can produce intense blooms given sufficient light, nutrients, and stratification. Microalgae can join together and then sink to form thick mats on the bottom in shallow coastal waters (Glud et al., 2002). Among the approximately 300 species of marine phytoplankton known in high northern latitudes, diatoms and dinoflagellates comprise around 160 and 35 species, respectively (Sukhanova et al., 1999). Diatoms have non-growing siliceous shells and thus need silicate for growth while dinoflagellates move by the action of taillike projections called flagella. Diatoms are responsible for most of the primary production in arctic pelagic ecosystems. Within the Arctic, the Arctic Ocean has the lowest number of different species and the western Barents Sea the most (Horner, 1984; Loughlin et al., 1999; Melnikov, 1997).

Prymnesiophytes (another group of swimming flagellates) include the two bloom-forming species; *Phaeocystis pouchetii* and *Emiliania huxleyi* (the latter being an exception among prymnesiophytes by lacking flagella and having a cover of calcite platelets, and as such are highly relevant to the carbon cycle). *Phaeocystis pouchetii* is common throughout the Arctic except in the deep Arctic Ocean (Hasle and Heimdal, 1998; Sukhanova et al., 1999). *Emiliania* blooms have been observed south of Iceland (Holligan et al., 1993), in the Norwegian and Bering seas (Paasche, 1960; Sakshaug et al., 1981; Sukhanova et al., 1999), and in Norwegian fjords (Berge, 1962; Johnsen and Sakshaug, 2000). *Emiliania* huxleyi blooms were first recorded on the southeastern Bering Shelf in 1997 during an extremely bright summer (Napp and Hunt, 2001) and in the Barents Sea in 2000 (Fossum et al., 2002). *Emiliania huxleyi* continues to bloom in both areas.

Dinoflagellates, chrysophytes, cryptophytes, and green flagellates are common in arctic waters. Cyanobacteria (formerly called blue-green algae), common in temperate and tropical waters, are abundant in the deep reaches of the Bering Sea (Sukhanova et al., 1999). They are also transported into the Barents Sea by the Atlantic inflow. Dinoflagellates are particularly important in multi-year ice, and a variety of flagellates thrive in melt ponds on top of the sea ice in summer (Braarud, 1935; Gosselin et al., 1997).

The major species of diatom and prymnesiophyte possess the water-soluble reserve carbohydrate β-1,3 glucan (chrysolaminarin), which is by far the most important carbon source for marine bacteria. Although in most phytoplankton species lipids comprise <10% of dry weight, a large proportion comprises essential polyunsaturated fatty acids that are distributed throughout the ecosystem (Falk-Petersen et al., 1998; Henderson et al., 1998). Healthy phytoplankton cells are protein-rich, with proteins comprising up to 50% of dry weight (Myklestad and Haug, 1972; Sakshaug et al., 1983).

Locally, the hard-bottom intertidal zone in the Arctic Ocean supports beds of sea-tangle (*Fucus distichus*) and in the littoral and sublittoral regions (down to about 40 m in clear water) are kelp forests of *Alaria esculenta*, *Laminaria saccharina*, *L. digitata*, and *L. solidungula* (Borum et al., 2002; Hop et al., 2002; Zenkevich, 1963). *Laminaria saccharina*, *L. digitata*, and the red alga *Ahnfeltia plicata* are commercially important in the northern coastal areas of Russia (Korennikov and Shoshina, 1980).

9.3.1.2. Microheterotrophs

Microheterotrophs are non-photosynthetic microorganisms. Their role is not well documented in the Arctic, but bacterial production is generally thought to be high, albeit somewhat reduced due to the low temperatures (Pomeroy et al., 1990). Rates of bacterial production are mainly determined by the amount of decaying organic matter available, although limitation by mineral nutrients cannot be excluded in some cases (Rich et al., 1997).

There are upward of 10¹¹ to 10¹² bacteria cells per cubic meter in the water column (Steward et al., 1996). Phages, a group of highly species-specific viruses, which are even more abundant than bacteria, attack and kill bacteria and phytoplankton, thus regulating their abundance (Bratbak et al., 1995). A well-developed community of heterotrophic flagellates grazes on the bacteria. These in turn are eaten by a variety of protozoans such as ciliates, which are in turn eaten by copepods. Thus the ciliates form an important link between the microbial (i.e., bacteria-based) and grazing food webs.

Excluding bacteria, the microheterotrophs in sea ice and ice-filled waters comprise 60 to 80 species of flagellate and about 30 species of protozoan, especially ciliates (Ikävalko and Gradinger, 1997). In contrast to first-year ice, multi-year ice has a well-developed microbial community. The abundance of microheterotrophs is particularly high during and immediately after phytoplankton maxima (Booth and Horner, 1997).

9.3.1.3. Zooplankton

Mesozooplankton play a major role in pelagic ecosystems including those of the Arctic, where a diverse array of planktonic animals comprise, on average more than 50% of the total pelagic biomass (Sakshaug et al., 1994). Marine mesozooplankton comprises ~260 species in the Arctic, ranging from less than 40 species in the East Siberian Sea to more than 130 species in the Barents Sea (Zenkevich, 1963).

Herbivorous mesozooplankton belonging to the family Calanoidae in the crustacean order Copepoda are predominant in terms of species richness, abundance, and biomass. Large herbivorous copepods (2-5 mm adult size) can make up 70 to 90% of the mesozooplankton biomass in the arctic seas. The most important are Calanus finmarchicus, C. hyperboreus, and C. glacialis in Atlantic and Arctic Water, and C. marshallae, Eucalanus bungii, Neocalanus spp., Metridia longa, and M. pacifica in the North Pacific and the Bering Sea. Calanus finmarchicus predominates in Atlantic Water, C. hyperboreus is found in both Atlantic and Arctic Water, and C. glacialis is found almost exclusively in Arctic Water. Variations in the distribution and abundance of Calanus species are considered early indicators of climate-induced change in the North Atlantic system (Beaugrand et al., 2002) with major consequences for the recruitment of fish species such as cod, which depend on them (Beaugrand et al., 2003).

The large copepods in the Arctic represent, as elsewhere, important links between primary production and the upper levels of the food web because they store large amounts of lipid for overwintering and reproduction (e.g., Scott et al., 2000). Calanoid copepods overwinter at depths of several hundred meters and then ascend to surface waters in spring to reproduce. Adults and the late copepodite stage V feed on phytoplankton in the surface waters storing lipids through the spring and summer (e.g., Dawson, 1978; Hargrave et al., 1989). Daily vertical migrations, common in most seas, have not been observed in the Arctic, not even under sea ice (Fortier et al., 2002). Many small copepods, <2 mm adult size, are known to be herbivorous while some are carnivorous (Loughlin et al., 1999; Smith and Schnack-Schiel, 1990; Stockwell et al., 2001).

Krill (euphausiids) are swarming shrimp-like crustaceans that are common on the Atlantic side of the Arctic Ocean and in the Bering Sea but are not common in the central Arctic Ocean. They can make up to

45% of mesozooplankton catches by weight (Dalpadado and Skjoldal, 1991, 1996) but are generally less abundant in the Arctic than in some areas of the Southern Ocean (Dalpadado and Skjoldal, 1996; Loughlin et al., 1999; Smith, 1991). Some species, for example Thysanoessa inermis, are herbivorous whereas others are omnivorous or even carnivorous, for example T. raschii, T. longipes, T. longicauda, and Euphausia pacifica. Most graze diatoms and Phaeocystis pouchetii efficiently (Båmstedt and Karlson, 1998; Falk-Petersen et al., 2000; Hamm et al., 2001; Loughlin et al., 1999; Mackas and Tsuda, 1999; Smith, 1991).

Amphipods, another crustacean group, are represented in the Arctic by *Apherusa glacialis*, *Onisimus* spp., *Gammarus wilkitzkii*, and *Themisto libellula*, all of which are associated with sea ice or ice-influenced waters. Except for the latter, they live in the interstitial cavities (brine channels) in the ice and on the underside of the pack ice, where *G. wilkitzkii* constitutes >90% of the amphipod biomass at times. *Apherusa* is common in first-year ice, and *Onisimus* in fast ice (Hop et al., 2000).

Themisto libellula lives in ice-filled waters but is not dependent on sea ice. It is an important food source for the upper trophic levels and is itself carnivorous, feeding on herbivorous copepods and other ice-associated zoo-plankton. It appears to fill the same niche as krill where these are absent (Dunbar, 1957). The largest of the ice amphipods, *Gammarus wilkitzkii*, can reach 3 to 4 cm in length. *Apherusa glacialis* and *G. wilkitzkii*, which are closely associated with multi-year ice, have a high fecundity (Melnikov, 1997; Poltermann et al., 2000).

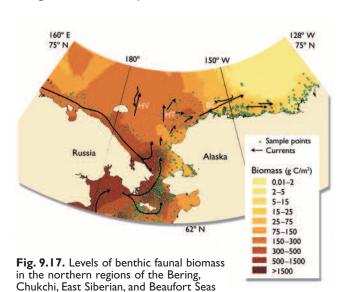
Although copepods, amphipods, and euphausiids are predominant in terms of mesozooplankton biomass in the arctic seas, virtually all major marine zooplankton groups are represented, namely, hydrozoans, ctenophores, polychaetes, decapods, mysids, cumaceans, appendicularians, chaetognaths, and gastropods (Hop et al., 2002; Murray, 1998). Pteropods (planktonic snails) such as *Limacina helicina* occur in vast swarms some years (Grainger, 1989; Kobayashi, 1974).

9.3.1.4. Benthos

The benthic fauna differs substantially between the continental shelves and the abyssal areas of the Arctic due to differences in hydrography, with warmer and more saline water in the deeper areas (Curtis, 1975). The benthos of the Bering Sea and the Canadian Archipelago between the New Siberian Islands and Bathurst Island is primarily Pacific (Dunton, 1992). The Atlantic fauna are carried into the Barents Sea by the Atlantic inflow and into the central Arctic by strong boundary currents. The fauna of the shallow Kara, Laptev, and Pechora Seas has to contend with large seasonally fluctuating physical conditions and massive amounts of freshwater from the Russian rivers. The littoral (i.e., near-coastal) zone varies from the rocky shore of exposed coasts, to sand and mud in sheltered

areas of fjords and bays, and is influenced to varying degrees by ice cover and scouring. Despite the formative studies by Russian workers in the first decades of the twentieth century (summarized by Zenkevich, 1963) detailed quantitative information on the distribution of the benthos and the structure of benthic communities in the Eurasian Arctic (especially in coastal and estuarine areas) is limited. Since around 1980, extensive regions of the North American arctic shelf and fjord areas have been sampled and their communities described and related to environmental influences, see for example studies by Stewart et al. (1985), Aitken and Fournier (1993), Grebmeier et al. (1989), and Feder et al. (1994). The greatest numbers of benthic species are found in areas of mixing between cold polar waters and temperate waters, for example between the Barents Sea and the Bering Sea, and off West Greenland and Iceland. The total number of benthic invertebrate species in the Barents Sea has been estimated at around 1600, but in the western parts of the Bering Sea alone the total number may exceed 2000 (Zenkevich, 1963). In the shallow waters of the Laptev Sea there are 365 benthic species (Zenkevich, 1963) and even fewer in the Beaufort Sea owing to the cold, unproductive arctic water masses, and to the brackish conditions (Curtis, 1975). In the deep Arctic Ocean, the number of benthic macrofauna species varies from 0 to 11 (Kröncke, 1994). The number of species in the intertidal zone of Svalbard (Weslawski et al., 1993), Bjørnøya (Weslawski et al., 1997), Baffin Island (Ellis, 1955), and Greenland (Madsen, 1936) varies between 30 and 50. The low number of benthic macrofauna species in the arctic intertidal zone is usually attributed to ice scouring (Ellis, 1955), a combination of tidal height and ice thickness (Ellis and Wilce, 1961), or heavy wave action (Weslawski et al., 1997).

Most recent benthic research has focused on specific patterns and processes resulting in biological hot spots such as below predictable leads in the sea ice, polynyas, oceanographic fronts, areas of intense mixing, and the marginal ice zone (Dayton et al., 1994).



(Dunton et al., 2003).

Because a relatively large proportion of the primary production in highly productive water columns can potentially reach the bottom, primary and benthic production tends to be coupled. The fraction of sinking matter that reaches the bottom is related to bottom depth; the shallower the water body, the greater the amount of material reaching the bottom. In shallow arctic waters, the benthic food web plays a greater role than in the deep seas or at lower latitudes (Cooper et al., 2002; Grebmeier and Barry, 1991). The Bering Shelf and the southern Chukchi Sea exhibit some of the highest levels of faunal biomass in the world's oceans (Fig. 9.17), supporting a rich fauna of bottom-feeding fish, whales, seals, walruses, and sea ducks (Grebmeier et al., 1995; Hood and Calder, 1981; Joiris et al., 1996; Welch et al., 1992). Other rich benthic communities in the Arctic occur in Lancaster Sound and the shallow parts of the Barents Sea.

The benthic fauna varies with depth and habitat. For example, off Svalbard the most common species in the steep rocky littoral zone include the macroalgae Fucus spp., sessile (i.e., non-mobile) barnacles (Balanus balanoides), and motile (i.e., mobile) gastropods (Littorina saxatilis) and amphipods (Gammarus setosus and G. oceanicus). The tidal flats are inhabited by a rich and diverse non-permanent fauna due to sediment freezing for six to eight months each year (Weslawski et al., 1999). The sediment fauna is dominated by small polychaetes (Scoloplos armiger, Spio filicornis, Chaetozone setosa) and oligochaetes (Weslawski et al., 1993). Sublittoral organisms include the barnacle Balanus balanus that contributes a large proportion of the biomass of sessile species (Jørgensen and Gulliksen, 2001). Other conspicuous, sessile species are the bivalve Hiatella arctica, actinarians Urticina eques and Hormathia nodosa, bryozoans, and Ophiopholis aculeata. Many, small, motile amphipods (Calliopidae sp.), isopods (Munna sp. and Janira maculosa), snails (Alvania sp.) and barnacles (Tonicella sp.), are observed together with infaunal polychaetes, nematodes, bivalves (Thyasira sp.), and amphipods (*Harpinia* spp.). The infauna occur in pockets of sediment on the rocky wall. At depths between 100 and 300 m in soft bottom areas of the northern Barents Sea (Cochrane et al., 1998), the polychaetes Maldane sarsi, Spiochaetopterus typicus, and Chone paucibranchiata are among the dominant species.

Some crustaceans occur or have occurred in the arctic regions at densities sufficient for commercial interest. These include the deepwater prawns *Pandalus borealis* (Aschan and Sunnanå, 1997) and *Pandalopsis dispar*, and several crab species: red king crab (*Paralithodes camtschatica*, Hjelset et al., 2002; Jewett and Feder, 1982), *Lithodes aequispina*, Tanner and snow crab (*Chionoecetes* spp.), and Dungeness crab (*Cancer magister*, Orensanz et al., 1998). Commercially harvested arctic mollusks include clams (*Mya truncata*, *M. arenaria*), blue mussel (*Mytilus edulis*), and Iceland scallop (*Chlamys islandica*). Commercial fisheries and aquaculture are addressed in detail in Chapter 13.

9.3.1.5. Fish

Arctic or Arctic-influenced waters are inhabited by more than 150 species of fish (Murray, 1998). Few are endemic to the Arctic, unlike the situation in the Southern Ocean where endemic species predominate. Most fish species found in the Arctic also live in boreal (northern) and even temperate regions. Arctic fish communities are dominated by a small number of species. The most abundant being Greenland halibut (Reinhardtius hippoglossoides), polar cod, Atlantic and Pacific cod (Gadus morhua and G. macrocephalus), Greenland cod (G. ogac), walleye pollock (Theragra chalcogramma), capelin (Mallotus villosus), long rough dab, also known as American plaice (Hippoglossoides platesoides), yellowfin sole (Pleuronectes asper), Atlantic and Pacific herring (Clupea harengus and C. pallasi), and redfish (Sebastes spp. e.g., S. mentella, S. marinus).

Greenland halibut, polar cod, and capelin have a circumpolar distribution. Greenland cod is a predominantly arctic species that is restricted to Greenland waters. The other species principally occur in waters to the south of the Arctic Ocean, except for parts of the Barents and Chukchi Seas.

Capelin

Capelin is a small circumpolar pelagic fish (Fig. 9.18). It is planktivorous (i.e., eats plankton), feeding mainly on copepods, followed by krill and amphipods. It is particularly abundant in the North Atlantic and the Barents Sea (Gjøsæter, 1995, 1998), and around Iceland (Vilhjálmsson, 1994). In the eastern Bering Sea, capelin tend to occur in cooler or more northerly areas. Capelin populations are subject to extreme fluctuations (e.g., Gjøsæter and Loeng, 1987; Sakshaug et al., 1994) in their distribution and abundance. Capelin is heavily exploited in the Atlantic but not the Pacific sector of the Arctic.



Fig. 9.18. Distribution of capelin (green) (based on Vilhjálmsson, 1994).

Table 9.6. Annual productivity and food requirement of higher trophic levels: average for the whole Barents Sea over several years. Data recalculated from Sakshaug et al. (1994) by Sakshaug and Walsh (2000).

	Annual production (mg C/m²)	Food requirement (mg C/m²)
Capelin	280	
Cod	90	550
Whales	3.6	360
Seals	0.8	95
Seabirds	0.5	78
Capelin fishery		200
Total	375	1280

Capelin is important in the diet of other fishes, marine mammals, and seabirds (e.g., Haug et al., 1995; Lawson and Stensen, 1997; Mehlum and Gabrielsen, 1995) and is thus regarded as a key prey species. Capelin can provide more than 20% of the food required by seabirds, higher predators, and the capelin fishery collectively in an average year (Table 9.6).

Fluctuations in the abundance of capelin have a big impact on their predators, particularly cod, seals, and seabirds. The growth rate of cod and their somatic and liver condition, for example, are correlated with capelin population abundance (Carscadden and Vilhjálmsson, 2002; Vilhjálmsson, 1994, 2002; Yaragina and Marshall, 2000).

Herring

Atlantic herring is generally restricted to waters south of the Polar Front, for example in the Nordic Seas and the Barents Sea (Vilhjálmsson, 1994). Like capelin, Atlantic herring is planktivorous, feeding in highly productive frontal areas of the open sea. Larval herring are important prey for seabirds. Adult herring is an important food item for larger fish and marine mammals.

The principal population of Atlantic herring in the Arctic is the Norwegian spring-spawning stock; one of the largest fish stocks in the world and with a spawning biomass that exceeded ten million tonnes for much of the 20th century. This population, together with the Icelandic spring- and summer-spawning herring make up the Atlanto-Scandian herring group. The migration route from nursery areas to feeding areas to overwintering areas to spawning areas takes the Norwegian spring-spawning herring around the Norwegian Sea (Box 9.8), over a distance of several thousand kilometers, and even into the Icelandic Sea during certain climatic warm periods (see Fig. 9.19 and section 9.3.3.3).

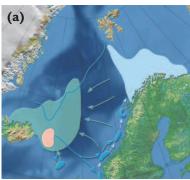
Spawning occurs at many sites along the Norwegian coast between 58° and 70° N. The spawning grounds comprise five main areas, but their relative importance, the time of arrival on the spawning grounds, and the spawning time have often changed (Slotte, 1998). These changes are not solely due to varying environmen-

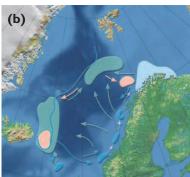
tal conditions, but are also affected by population structure, and the optimum life history strategy for individual fish under varying levels of food supply. Flexibility in spawning behavior offers an adaptive advantage to the population during changing climates.

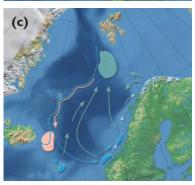
Pacific herring are common in the Bering Sea shelf regions (NRC, 1996). This species is, however, of relatively minor importance for seabirds and marine mammals in that region (Livingston, 1993).

Polar cod

Polar cod is a key species in many arctic food chains and forms a major link in the transfer of energy from zooplankton to top carnivores (Fig. 9.20). Large polar cod (23–27 cm) consume mainly fish and are themselves eaten by a variety







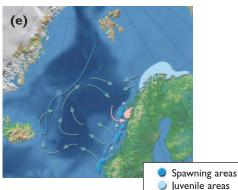
of large fish as well as by many seabird species and most arctic marine mammals (e.g., Dahl T. et al., 2000; Hobson and Welch, 1992; Holst M. et al., 2001; Lawson and Stenson, 1997; Lowry and Frost, 1981; Mehlum et al., 1999; Nilssen et al., 1995; Orr and Bowering, 1997; Rowe et al., 2000; Wathne et al., 2000). Polar cod spend much of their time associated with sea ice and stay in arctic waters throughout their life cycle. This species is broadly distributed, from inshore surface waters to very deep waters (Falk-Petersen et al., 1986; Jarvela and Thorsteinson, 1999; Pedersen and Kanneworff, 1995; Walters V., 1955). Polar cod occur in large schools (Crawford and Jorgenson, 1996; Welch et al., 1993)

Box 9.8. Effects of climate on Norwegian spring-spawning herring

In the Icelandic area, herring was the fish species most affected by the environmental adversities of the 1960s (Dragesund et al., 1980; Jakobsson, 1980; Jakobsson and Østvedt, 1999). This is not surprising since herring are plankton feeders and in Icelandic waters are near their northern limit of distribution. Thus, the traditional feeding migrations of the Norwegian spring-spawning herring stock to the waters off northern Iceland (Fig. 9.19a) stopped completely when the Atlantic plankton community collapsed. In 1965-1966, the oldest herring were instead forced to search for food in the Norwegian Sea near the eastern boundary of the East Icelandic Current, i.e., around 150 to 200 nautical miles farther east than previously (Fig. 9.19b). In 1967–1968, the stock migrated north to feed west of Svalbard during summer (Fig. 9.19c). This was also the case in 1969 when the overwintering grounds also shifted from 50 to 80 nautical miles east of Iceland to the west coast of Norway (Fig. 9.19d). The Norwegian spring-spawning herring stock collapsed in the latter half of the 1960s (Dragesund et al., 1980) and the feeding migrations to the west into the Norwegian Sea ceased altogether (Fig. 9.19e).

The abundance of the Norwegian spring-spawning herring stock increased dramatically in the 1990s. This process has, however, taken about twenty-five years despite a ban on commercial fishing in the period 1973 to 1983. It was not until the mid-1990s that these herring resumed some semblance of their previous feeding pattern. The Norwegian spring-spawning herring still overwinter in fjords in the Lofoten area on the northwest coast of Norway. When and if they will revert completely to the traditional distribution and migration pattern cannot be predicted.



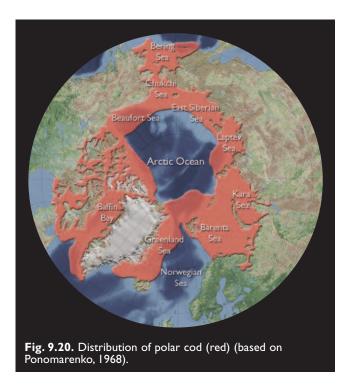


Main feeding areas

Over-wintering area

Spawning migrationsFeeding migrations

Fig. 9.19. Changes in the migration routes, and feeding and wintering areas of Norwegian spring-spawning herring during the latter half of the twentieth century. The plots show (a) the normal migration pattern during the warm period before 1965, (b and c) the pattern following the Great Salinity Anomaly until the stock collapsed in 1968, (d) during years of low stock abundance, and (e) the present migration pattern (based on Vilhjálmsson, 1997).



mostly north of 60° N in the eastern Bering Sea or in the cold pool of the mid-shelf region (Wyllie-Echeverria and Wooster, 1998). The importance of this species is likely to have been underestimated in the past, in part owing to its patchy distribution. Polar cod displays a variety of physiological and biochemical adaptations to life in cold waters, including bioenergetic adjustment to low temperature (Hop et al., 1997; Ingebrigtsen et al., 2000; Steffensen et al., 1994).

\mathbf{Cod}

Cod species found in the Arctic include Atlantic cod, Pacific cod (Bergstad et al., 1987), Pacific tomcod (*Microgadus proximus*), which occurs as far north as the Bering Sea, Greenland cod, and Arctic cod (*Arctogadus glacialis*) that resides in the Arctic Ocean, but about which little is known (Mikhail and Welch, 1989; Morin et al., 1991; Sufke et al., 1998). The majority of these species appear regularly in the diet of marine mammals (e.g., Holst M. et al., 2001; Welch et al., 1992).

Atlantic cod is the most abundant gadoid species in the northern North Atlantic. Like Atlantic herring it occurs mainly to the south of the Polar Front, yet can live in temperatures below 0 $^{\circ}$ C by producing antifreeze proteins.

Four large cod populations occurred in the arctic areas of the North Atlantic during the 20th century. The Northeast Arctic cod spawns along the Norwegian coast, with more than 50% of this occurring in the Lofoten area. Cod from Iceland spawn around the coast with more than 50% of this occurring off the southwest corner. The cod off Greenland have inshore and offshore spawning components, and an immigrant contribution from Icelandic waters. The history of the increase and

collapse of this cod population during the 20th century is described in section 9.3.3.3. The cod population off Newfoundland and Labrador also collapsed during the 1990s, owing to high fishing mortality combined with adverse environmental changes (Drinkwater, 2002).

Pacific cod is a mixed feeder that consumes a wide variety of fish (primarily walleye pollock), shellfish, and invertebrates in the eastern Bering Sea (Livingston et al., 1986).

Walleye pollock

Walleye pollock is the single most abundant fish species in the Bering Sea, comprising the bulk of the commercial catch in this area (Akira et al., 2001; Livingston and Jurado-Molina, 2000; Wespestad et al., 2000). It is mainly semi-pelagic, dominating the outer shelf regions. Walleye pollock is primarily planktivorous, feeding on copepods and euphausiids but adults become cannibalistic, feeding on juveniles seasonally (Dwyer et al., 1987). Juvenile pollock is an important prey item for other fish species, marine mammals, and seabirds (Springer, 1992).

Redfish

Several redfish species are broadly distributed and common in arctic deep waters (100 to >500 m). They are slow-growing and long-lived species. The three common species which are exploited in the northern North Atlantic are *Sebastes marinus*, *S. mentella*, and *S. viviparus*, but the latter, which is the smallest of the three, is not caught in significant amounts (Frimodt and Dore, 1995; Hureau and Litvinenko, 1986; Muus and Nielsen, 1999). There are two distinct populations of *S. mentella*. These vary in their habitat and fishery and are commonly known as deep-sea redfish and oceanic redfish, respectively. The relationship between the two forms and the extent to which the populations are separated spatially is not clear (ICES, 2003).

Oceanic redfish are caught in the Irminger Sea during the summer at depths of 100 to 200 m and water temperatures of 5 to 6 °C. Mature fish feed on krill and small fish such as capelin and herring and undertake extensive feeding migrations. They mate in early winter and the female carries the sperm and eggs, and later larvae, which are born in April/May (Wourms, 1991). The juveniles stay near the bottom, along the edge of the continental shelf.

Greenland halibut

Greenland halibut is commercially important in the North Atlantic and the Pacific, and is an important food item for deep-feeding marine mammals (e.g., narwhal and hooded seals) and sharks feeding on benthos such as the Greenland shark (Somniosus macrocephalus). During their first four to five years as immature fish in the eastern Bering Sea, the Greenland halibut inhabit depths to

200 m. On the Atlantic side, immature fish occur mainly between 200 and 400 m depth. Adults mainly occupy slope waters between 200 and 1000 m or more (Alton et al., 1988). Walleye pollock and squid are the main prey items for Greenland halibut in the eastern Bering Sea (Yang and Livingston, 1988).

Other flatfish

Other arctic flatfish include the long rough dab, which is an abundant bottom-dweller in some parts of the Arctic seas, including the Barents Sea (Albert et al., 1994). On the Pacific side in the eastern Bering Sea, yellowfin sole, flathead sole (Hippoglossoides elassodon), rock sole (Pleuronectes bilineatus), Alaska plaice (Pleuronectes quadrituberculatus), and arrowtooth flounder (Atheresthes stomias) are important members of the groundfish community (Livingston, 1993). Yellowfin sole, Alaska plaice, and rock sole consume mostly infaunal prey such as polychaetes, clams, and echiuran worms. These fish are distributed at depths generally less than 50 m. The highly piscivorous (i.e., fish-eating) arrowtooth flounder is found mostly on the outer shelf area, as is flathead sole, which mainly consumes brittle stars.

9.3.1.6. Marine mammals and seabirds

Arctic marine mammals to a large extent escaped the mass extinctions that affected their terrestrial counterparts at the end of the Pleistocene (Anderson, 2001). Like fish, mammals and birds have the advantage of having great mobility and hence are good colonizers. Thus, it is not surprising that these groups dominate the arctic marine megafauna, represented both by resident and migratory species. Their high abundance was a major attractant for people to this region historically, becoming the mainstay of the diet of coastal communities throughout the Arctic (Chapter 12) and later the subject of extreme levels of commercial exploitation. The massive harvests of marine mammals and seabirds that began in the 1600s and lasted for several hundred years decimated many arctic populations. Bowhead whales (Balaena mysticetus) and sea otters (Enhydra lutris) were almost driven to extinction throughout the Arctic (Burns et al., 1993; Kenyon, 1982), while the great auk (Pinguinus impennis) and Steller sea cow (Hydrodamalis gigas) did become extinct. Walruses (Odobenus rosmarus) were all but extirpated in some arctic regions (Gjertz and Wiig, 1994, 1995). Polar bears, all the great whales, white whales (Dephinapterus leucas), and many species of colonially nesting seabird were dramatically reduced. Harvesting of marine mammals and seabirds is now undertaken in accordance with management schemes based on sustainability in most Arctic countries, although overexploitation of some species is still occurring (CAFF, 2001).

Marine mammals are the top predators in the Arctic other than humans. Virtually all large-scale taxonomic groupings of marine mammals have arctic representatives (Perrin et al., 2002).

Polar bear

The polar bear, the pinnacle predator, has a circumpolar distribution and is dependent on sea ice to provide for most of its needs (Ferguson et al., 2000a,b; Mauritzen M. et al., 2001; Stirling et al., 1993). Polar bears feed almost exclusively on ice-associated seals (e.g., Lønø, 1970; Stirling and Archibald, 1977; Smith T., 1980). Adult bears can swim quite long distances if required, but mothers with cubs depend on ice corridors to move young cubs from terrestrial denning areas to prime hunting areas on the sea ice (Larsen T., 1985, 1986). Pregnant females dig snow dens in the early winter and give birth several months later. This requires a significant depth of snow, thus females return year after year to land sites that accumulate sufficient snow early in the season. A mother that emerges from the den with her young has not eaten for five to seven months (Ramsay and Stirling, 1988). Therefore, successful spring hunting is essential for the family's survival and largely dictates condition, reproductive success, and survival for all polar bears (e.g., Stirling and Archibald, 1977). Factors that influence the distribution, movement, duration, and structure of sea ice profoundly affect the population ecology of polar bears, not least due to their influence on the principal prey species, ringed seal (*Phoca hispida*) (Stirling and Øritsland, 1995; Stirling et al., 1999). The global polar bear population is estimated at 22 000 to 27000 (IUCN, 1998).

Walrus

Walruses, like polar bears, are circumpolar, but with a more disjointed distribution. Two sub-species are recognized: the Pacific walrus (*Odobenus rosmarus divergens*) and the Atlantic walrus (*O. r. rosmarus*) (Fay, 1981, 1982). The global walrus population is estimated at about 250 000, of which 200 000 belong to the Pacific sub-species. The Atlantic walrus is distributed from the central and eastern Canadian Arctic eastward to the Kara Sea (Fay, 1981; Zyryanov and Vorontsov, 1999), including several more or less well-defined sub-



Fig. 9.21. Walrus routinely use sea ice as a haul-out platform in shallow areas where they feed on benthic fauna (photo supplied by Kit Kovacs & Christian Lydersen, Norwegian Polar Institute).

populations (Andersen L. et al., 1998; Buchanan et al., 1998; Outridge and Stewart, 1999). Walruses haul-out on pack ice most months of the year (Fig. 9.21), using land-based sites only during summer when sufficient sea ice is unavailable. Walruses have a narrow ecological niche, depending on the availability of shallow water (<80 m) with bottom substrates that support a high production of bivalves (e.g., Born et al., 2003; Fisher and Stewart, 1997; Wiig et al., 1993).

Seals

Ringed seals represent the "classical" arctic ice seal, being uniquely able to maintain breathing holes in thick sea ice. Thus, they can occupy areas far from sea-ice edges, unreachable by other seal species. They are distributed throughout the Arctic, even at the North Pole (Reeves, 1998). They number in the millions and this is by far the most abundant seal species in the Arctic. This species exclusively uses the sea ice for breeding, molting, and resting (haul-out), and rarely, if ever, moves onto land. Although quite small, ringed seals survive the thermal challenges posed by the arctic winter by building lairs in the snow on top of sea ice, where they rest in inclement weather and where they house their new-born pups (e.g., Lydersen and Kovacs, 1999; Smith T. and Stirling, 1975). Ice amphipods and fish constitute much of their diet (e.g., Gjertz and Lydersen, 1986; Weslawski et al., 1994).

The bearded seal (*Erignathus barbatus*) has a patchy circumpolar Arctic distribution (Burns, 1981a).

This species breeds on drifting sea ice (Kovacs et al., 1996) but occasionally hauls out on land during the summer. These animals are mostly benthic feeders, eating a wide variety of fish, mollusks, and other invertebrates in shallow areas. Some bearded seal populations are thought to be resident throughout the year, while others follow the retreating pack ice in summer, and then move southward again in the late autumn and winter (Burns, 1967; Gjertz et al., 2000). The global population has not been assessed but is thought to number in the hundreds of thousands in the Arctic (Kovacs, 2002a).

Harbour seals (*Phoca vitulina*) have one of the broadest distributions of the pinnipeds, from temperate areas as far south as southern California to arctic waters of the North Atlantic and into the Bering Sea in the Pacific (Bigg, 1969; Rice, 1998). They are coastal, non-migratory, and aggregate in small numbers on rocky outcrops, beaches, or inter-tidal areas (Grellier et al., 1996; Pitcher and McAllister, 1981). They are opportunistic feeders that eat a wide variety of fish species and some cephalopods and crustaceans (Bowen and Harrison, 1996). Harbour seals are not numerous in the Arctic and several of the populations that live north of the Arctic Circle are very small (Boveng et al., 2003; Henriksen et al., 1996).

In the Atlantic sector of the Arctic, there are three additional phocid (i.e., true) seal species: harp seals, hooded

seals (Cystophora cristata), and grey seals (Halichoerus grypus). Harp seals are highly gregarious and migratory, moving southward to three traditional breeding sites (off the east coast of Canada, in the White Sea, and between Jan Mayen and Svalbard) for the birthing period on pack ice in March (Lavigne and Kovacs, 1988). Following the breeding season, harp seals from each population move northward into molting sites before dispersing into the Arctic for the rest of the year (e.g., Folkow and Blix, 1992). Adult harp seals feed mainly on small marine fish such as capelin, herring, sculpins (Cottidae), sand lance (Ammodytes americanus), and polar cod (e.g., Lawson and Stenson, 1997; Lawsen et al., 1995; Nilssen, 1995), and then on krill and amphipods. The global population is thought to exceed seven million animals (Lavigne, 2002).

The hooded seal is a large, pack-ice breeding northern phocid that ranges through a large sector of the North Atlantic. In spring the adults gather to breed in two main groups; one off the east coast of Canada and the other either in Davis Strait or off East Greenland depending on conditions (Lavigne and Kovacs, 1988). Some weeks after breeding, the animals move northward into traditional molting areas before dispersing for the summer and autumn, preferring the outer edges of pack ice (Folkow and Blix, 1995). They feed on a variety of deep-water fishes including Greenland halibut and a range of redfish species, as well as squid (Folkow and Blix, 1999). The global population is very difficult to estimate because hooded seals are difficult to survey, but is certainly in excess of half a million animals (Kovacs, 2002b).

Grey seals were historically abundant in Icelandic waters and along the coastal regions of northern Norway and northeastern Russia (Collett, 1912). They have been depleted through hunting and government culling programs (Wiig, 1987) and in some areas have been extirpated (Haug et al., 1994). A crude estimate of the population of grey seals inhabiting northern Norway and the Murman coast of Russia is 4500 (Haug et al., 1994).

Two additional ice-breeding seals that occur in the Bering Sea are the spotted seal (*Phoca largha*) and the ribbon seal (*Phoca fasciata*). The spotted seal breeds in eight largely discrete birthing areas (Rice, 1998). They have a coastal distribution during the summer and early autumn, but migrate offshore to the edge of the ice pack for the rest of the year (Lowry et al., 1998). Spotted seals eat a wide variety of prey, including fish, crustaceans, and cephalopods (Bukhtiyarov et al., 1984; Lowry and Frost, 1981; Lowry et al., 1982). There are no recent, reliable population estimates for this species (Burns J., 2002). Ribbon seals are poorly known, packice breeders that congregate loosely in suitable areas of thick pack ice in the North Pacific during the breeding season (Rice, 1998). They do not haul out on land and are assumed to be either pelagic or northern pack-ice dwellers in summer (Burns J., 1981b). They are reported to eat crustaceans, fish, and cephalopods (Frost K.

and Lowry, 1980; Shustov, 1965). Current data on population size are not available, but counts in the 1970s revealed 100000 to 200000 animals (Burns J., 1981b).

Northern fur seals (*Callorhinus ursinus*), Steller sea lions (*Eumetopias jubatus*), and sea otters all breed terrestrially on the Pribilof, Aleutian, Commander, and Kurile Islands in the North Pacific. The latter two species breed as far south as the Californian coast.

Whales

White whales, narwhal (*Monodon monoceros*), and bowhead whales live only in the high Arctic (see Perrin et al., 2002) and are commonly found in ice-covered waters where they use edges, leads, and polynyas to surface for breathing. Narwhal mainly occur within the Atlantic region, while the others have patchy circumpolar ranges (Rice, 1998). All three migrate seasonally, largely in relation to the northward retraction and southward expansion of the seasonal sea ice. They prey on small fishes, especially polar cod, although narwhal also eat large quantities of cephalopods, and bowhead whales consume a greater proportion of planktonic crustaceans than either of the other two species.

Other cetaceans also frequent arctic waters in summer, but these remain in relatively ice-free waters and spend most of the year elsewhere. These include white-beaked dolphin (*Lagenorhynchus albirostris*) in the North Atlantic/Barents/Greenland Sea and Dahl's porpoise (*Phocoenoides dalli*), right whales (*Eubalaena glacialis*), and grey whales (*Eschrichtius robustus*) in the North Pacific/Bering Sea. Harbour porpoise (*Phocoena phocoena*) and killer whales (*Orcinus orca*) are among the toothed whales, and blue whales (*Balaenoptera musculus*), fin whales (*B. physalus*), minke whales (*B. acutorostrata*), humpback whales (*Megaptera novaeangliae*), and sei whales (*B. borealis*) are some of the baleen whales that are regular summer residents in arctic waters. Many of the great whales inhabit the Bering Sea in summer.

Seabirds

Some of the largest seabird populations in the world occur in the Arctic (e.g., Anker-Nilssen et al., 2000; Boertmann et al., 1996; Gaston and Jones, 1998; Norderhaug et al., 1977). Over 60 seabird species frequent the Arctic, and over 40 breed there (Murray, 1998). Many species take advantage of the summer peak in productivity and then overwinter elsewhere. In the extreme, the red phalarope (Phalaropus fulicarius), the northern phalarope (*P. lobatus*), and the Arctic tern (Sterna paradisaea) spend the summer in the high Arctic and overwinter in the southern hemisphere off Peru or West Africa. In contrast, the spectacled eider (Somateria fisheri), black guillemot (Cepphus grylle), ivory gull, and northern fulmar (Fulmaris glacialis) stay in the Arctic all year round, using the southern edges of the sea ice or open water areas for feeding in winter. Polynyas are extremely important winter habitats for these species

(Brown and Nettleship, 1981; Stirling, 1997). Most of the global population of the threatened spectacled eider overwinters in single-species flocks in a few polynyas in a restricted area of the Bering Sea (Petersen et al., 1999). In the rare instance that such polynyas freeze for longer than a few days, mass mortalities can occur, altering population growth and affecting the species for decades (Ainley and Tynan, 2003).

Most arctic seabird species nest in large colonies on cliffs, which offers some protection from terrestrial predators such as the Arctic fox (Alopex lagopus). Other species, such as Sabine's gull (Xema sabini), nest on the ground on isolated islands, while others use burrows either on sloping ground (e.g., little auk) or in rock crevices (e.g., black guillemot). Several of the auk species are among the most abundant nesting arctic seabirds, including the little auk, thick-billed murre, common murre (*Uria aalge*), and the Atlantic puffin (Fratercula arctica). The blacked-legged kittiwake (Rissa tridactyla) is the most numerous Arctic gull, but glaucous gulls (Larus hyperboreus) are also common. Arctic terns are abundant in some regions, as are common eider (Somateria mollissima). The Pribilof Islands, in the eastern Bering Sea, are breeding sites for large numbers of piscivorous seabirds including black-legged and red-legged kittiwake (R. brevirostris), and common and thick-billed murre.

The foraging ecology and energetics of seabirds have been studied quite extensively in many arctic areas (e.g., Barrett et al., 2002; Bogstad et al., 2000; Croxall, 1987; Montevecchi, 1993) and despite species differences, some basic patterns are evident. Most arctic seabirds forage on small fish and large copepods, primarily in the upper and mid-water column (e.g., Garthe, 1997; Montevecchi and Myers, 1996). Foraging is often concentrated in frontal areas or at ice edges, where convergences can concentrate marine zooplankton (Hunt et al., 1999). Eiders are the exception, foraging in shallow water for benthic animals, particularly echinoderms and mollusks. Polar cod is an extremely important prey item for most arctic seabirds, but other small school-forming species (such as capelin and herring in the Barents Sea) are extremely important regionally. Surface feeders (e.g., kittiwakes and fulmars) forage onthe-wing, dipping into the water to capture prey, or feed while sitting on the water surface when prey concentrations are high and available within the top few centimeters. The alcids and related species dive to considerable depths (Schreer and Kovacs, 1997) in search of prey. They also travel considerable distances and can stay underwater for relatively extended periods, allowing them to take advantage of fish and invertebrates that reside under the sea ice, e.g., euphausiids, amphipods, and polar cod (Bradstreet, 1980). As foragers, most seabird species are generalists responding to changing spatial and temporal prey availability (e.g., Montevecchi and Myers, 1995, 1996). However, the little auk and the Bering Sea least auklet (Aethia pusilla), which specialize on calanoid copepods, have a narrow foraging

niche (Karnovsky et al., 2003). Ivory gulls are one of the most specialized of the arctic seabirds, living in association with pack ice for most of their lives and breeding on exposed mountain peaks in glaciated areas of the high Arctic. One of their favorite foods is the blubber of marine mammals, acquired by scavenging on carcasses. Yet, similar to many arctic seabirds, a large part of their diet comprises polar cod and other small fish and invertebrates. The small fish and invertebrates are usually taken after being washed onto the surface of ice floes and edges (Haney and MacDonald, 1995; Hunt et al., 2002). Ross' gulls (*Rhodostethia rosea*) also perform this type of foraging behavior.

In addition to seabirds that are strictly marine feeders, skuas, a host of arctic shorebirds, and some ducks (beside the marine feeding eiders), geese, and divers also spend time at sea.

9.3.2. Physical factors mediating ecological change

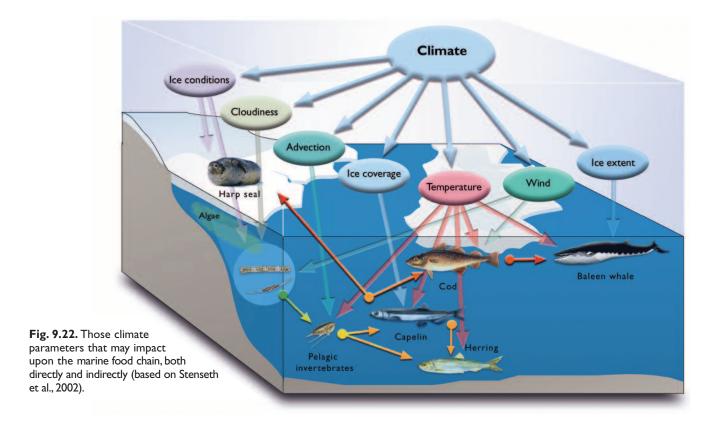
There are a variety of means by which climate can affect marine biota. These can be direct or indirect. Examples of the former include temperature, which affects the metabolism and distribution of organisms; wind-driven currents, which transport planktonic organisms; sea ice, which provides higher predators with a platform for birthing or foraging; and snow, which allows for the construction of overwintering lairs. An indirect means by which climate can affect biota is through those climate processes that affect nutrient levels and surface mixed layer depth, which in turn influence primary and secondary productivity, and ultimately food availability to the upper trophic levels. Figure 9.22 illustrates those

climatic factors that can influence the Barents Sea ecosystem, both directly and indirectly. Similar interactions are also valid for other marine areas. The timing of sea-ice formation and melt-back, as well as temperature, can influence the timing, location, and intensity of biological production.

Of the main factors mediating ecological change in the Arctic, the distribution of sea ice is most important. Sea ice, together with its snow cover, can reduce light levels at the water surface to those observed at 40 m or more in an ice-free water column. Primary production in the water column below the sea ice is thus severely light-limited. However, the sea ice is of major importance as a habitat for marine mammals and the location of ice edges is extremely important to seabirds. Moreover, the melting of sea ice in spring results in a stratification of the upper water column that promotes primary production.

The flow of warm water into the Arctic and the mixing and stratification of the water column are also important. The flow of warm water into the Arctic is important for the northward transport of zooplankton populations, such as the transport of *Calanus finmarchicus* from the Norwegian Sea to the Barents Sea. The mixing and stratification of the water column is determined by the opposing forces of wind and freshwater supply (Sakshaug and Slagstad, 1992).

Generally, sea surface temperatures in the Arctic are low, but true ectotherms (previously called "cold-blooded organisms", i.e., their body temperatures vary with the temperature of their surroundings) can grow at the freezing point of seawater. In principle, organisms



grow faster the higher the temperature up to an optimum range, which can be from 8 to 15 $^{\circ}$ C for species living in the Arctic. A temperature increase of 10 $^{\circ}$ C would roughly double the biochemical rates, and thus the growth rate.

9.3.2.1. Primary production

The effect of temperature on primary production is largely indirect, through its effect on sea-ice cover and the mixing characteristics of the water column. The direct effect of rising temperature, through its effect on growth rate, would primarily shorten the spring bloom by two to five days, and perhaps slightly increase regenerative production. New production would be likely to increase because it is primarily regulated by the vertical nutrient supply.

Limiting factors

Potentially limiting nutrients in the Arctic are nitrogen or phosphorus, and for diatoms, also silicate. Iron controls primary production by retarding nitrate uptake in the Northeast Pacific and the deep regions of the eastern Bering Sea (Frost and Kishi, 1999). It has also been observed to limit temporarily spring bloom production in the Trondheimsfjord (Õzturk et al., 2002). Silicate, which like nitrogen is also affected by iron control, limits diatom growth in some areas of the Barents Sea (Nielsen and Hansen, 1995; Wassmann et al., 1999). Because arctic rivers are rich in nitrogen and silicate but poor in phosphate, phosphorus limitation is likely in and around some estuaries.

Most microalgae are probably not limited by CO_2 because they contain the enzyme carbonic acid anhydrase, which can furnish CO_2 from bicarbonate (Anning et al., 1996; Goldman, 1999; Reinfelder et al., 2000; Sültemeyer, 1998). Production of the coccoliths that cover coccolithophorids also furnishes CO_2 .

In nature, an increase in the supply of the limiting nutrient typically causes a predominance of largecelled species. A sufficient supply of iron and silicate favors large bloom-forming diatoms that enhance the sedimentation rate.

Nutrient status in winter differs strongly between arctic regions, reflecting the nutrient concentration of the deep or intermediate waters that supply nutrients to the upper layers. This is related to the increasing age of

the intermediate and deep waters along their THC route. Thus, Atlantic water (which is relatively young) exhibits the lowest concentrations and the deep Bering Sea water (which is older) the highest (Table 9.7). However, because mixing between surface and intermediate water in the Bering Sea is low owing to the high stability of the water column, surface water concentrations in the Bering Sea are actually lower than in the Southern Ocean.

Owing to the high winter nutrient concentrations on the Bering Shelf and in the southern Chukchi Sea, productivity in these regions can be two to four times higher than in the Barents Sea (Coachman et al., 1999; Grahl et al., 1999; Olsen et al., 2003; Schlosser et al., 2001; Shiomoto, 1999; Walsh J.J. and Dieterle, 1994). Because of its distance from shelf-break upwelling, however, the northeast coastal Alaskan Shelf exhibits low nutrient levels, on a par with those of the Atlantic sector (Coachman and Walsh, 1981).

North of 85° N, severe light limitation restricts primary production in the water column to a six-week growth season, which is initiated by the melting of the snow on top of the sea ice in July (English, 1961; Kawamura, 1967; Usachev, 1961). In multi-year ice, the dense biomass on the underside of the sea ice is also strongly light-limited, but in melt ponds, intense small-scale production can occur (Booth and Horner, 1997; Gosselin et al., 1997; Sherr et al., 1997). Productivity in the multi-year ice in the shelf seas is an order of magnitude greater than in first-year ice, presumably because of a greater nutrient supply, however, the latter generally has very low levels of primary production (Andersen O., 1989; Gradinger, 1996; Juterzenka and Knickmeier (1999). In polynyas, early melting of sea ice can prolong the growth season by three months (Smith et al., 1997; Suzuki et al., 1997).

Timing

In seasonally ice-covered areas, the onset of the phytoplankton bloom is usually determined by the timing of the breakup of the sea ice (Alexander and Niebauer, 1981; Braarud, 1935; Gran, 1931; Head et al., 2000; Stabeno et al., 2001; Wassmann et al., 1999). Typically, an ice-edge bloom unfolds in a 20 to 100 km wide belt south of the northward-retreating ice edge. The bloom develops rapidly because water from the melting sea ice establishes a shallow wind-mixed layer of 15 to 35 m depth. The ice-edge bloom generally begins in mid-

Table 9.7. Winter nutrient levels (mmol/m³) in the Barents Sea, the Bering Sea (surface and at depths >300 m), and the Southern Ocean (the Ross and Scotia Seas) (Sakshaug, 2003).

	Barents Sea (Atlantic Water)	Bering Sea (surface water)	Bering Sea (deep water)	Ross Sea (surface water)	Scotia Sea (surface water)
Nitrate	10–12	10–30	45	25	30
Phosphate	0.85	1.0-2.0	3.5	2	2
Silicate	6–8	25–60	100-300	50–60	100

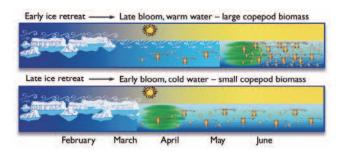


Fig. 9.23. The relative timing of the sea-ice retreat and the spring bloom in the Bering Sea (Hunt et al., 2002).

April to early May at the southernmost fringes of the first-year ice, both in the Barents and Bering Seas and in the Labrador/Newfoundland region (Alexander and Niebauer, 1981). In the Bering Sea, years with early sea-ice retreat (i.e., starting in winter) have delayed blooms as the blooms cannot begin until light levels and stratification are sufficient to support them. Thus, in the Bering Sea, early ice retreat implies a late bloom, while late ice retreat implies an early bloom (Fig. 9.23). In the Barents Sea, however, very cold winters that result in a more southern distribution of the ice edge (with sea ice forming over Atlantic water to the south of the Polar Front) can have very early blooms because once melting starts the sea ice melts rapidly from below. Near multiyear ice in the Arctic Ocean, melting is delayed until July, resulting in a short growing season (Strass and Nöthig, 1996), and in the ice-filled regions of the Greenland Sea, late melting can delay the ice-edge bloom until late May as far south as the Denmark Strait (Braarud, 1935).

Impact of physical and chemical forcing

After the ice-edge bloom, primary production becomes very low in the strongly stratified waters, with nutrients near the limit of detection (Fujishima et al., 2001; Taniguchi, 1999; Whitledge and Luchin, 1999). In iron-controlled waters, however, there are still high nitrate concentrations in the water column. Near the pycnocline (i.e., the region of strongest vertical density gradient) in arctic waters, a restricted vertical supply of nutrients enables the development of a 3 to 10 m thick chlorophyll maximum layer that is strongly light-limited (Heiskanen and Keck, 1996; Luchetta et al., 2000; Nielsen and Hansen, 1995).

In ice-free waters, it is the onset of thermally-derived stratification that determines the timing of the spring bloom. The blooms deplete the upper layer nutrient concentrations. In the Norwegian Sea and the Atlantic (southwest) part of the Barents Sea, thermally-derived water-column stability is established in late May to early June (Halldal, 1953; Olsen et al., 2003; Paasche, 1960; Steemann-Nielsen, 1935). In ice-free estuaries and fjords, and waters surrounding Iceland, freshwater-induced stability triggers a bloom in late March to late April (Gislason and Astthórsson, 1998; Braarud 1935; Sakshaug, 1972). On continental shelves, nutrient sup-

plies from upwelling or strong tidal mixing can maintain high levels of production, as observed in both the Barents and Bering Seas.

Pulsed (wind-driven) nutrient supplies associated with passing atmospheric low pressure systems often result in small blooms, however, in arctic waters, the pycnocline is usually too strong to allow a temporary deepening of the surface mixed layer and so bring in nutrients from sub-pycnocline waters (Overland et al., 1999b; Sakshaug and Slagstad, 1992). In the Bering Sea, storms, especially those in mid- to late May, lead to a large nutrient supply and prolonged primary production, whereas a weakening of the summer winds lowers the nutrient supply for continuing summer blooms (Stabeno et al., 2001).

Wind-driven nutrient supply supports about 50% of the annual primary production in the southern Barents Sea influenced by the Atlantic inflow and this supply exhibits no clear temporal trend. In the northern Barents Sea, however, primary production clearly follows variations in the NAO index, being high following NAO⁺ years — which correspond to years with relatively warm winters and little sea ice (Slagstad and Støle Hansen, 1991). The higher production is a result of the reduced sea-ice cover allowing a larger area of the northern Barents Sea exposure to the strong light levels.

For the outer and mid-shelf domains of the Bering Shelf, the wind-driven nutrient supply supports 30 to 50% of the annual primary production, depending on the frequency and intensity of summer storms. Interdecadal trends in chlorophyll-a (Chl-a) concentration were observed by Sugimoto and Tadokoro (1997) in eastern Bering Sea regions deeper than 150 m but it is not known if these resulted in changes in either the spring or overall annual primary production levels. The few available data suggest that the summer contribution to annual new production may have decreased in recent years with the advent of calmer, sunnier summers. Coastal domain production is not thought to vary much between years. On the northern shelf, variability in phytoplankton biomass and production has been linked to variability in the transport of the Bering Slope Current that leads to the Anadyr Stream (Springer et al., 1996).

Distribution of primary production

The distribution of primary production in the Arctic provides a good illustration of the effects of physical and chemical forcing (Table 9.8). Annual primary production in the deep Arctic Ocean, the lowest known for any sea, reflects the high incidence of multi-year sea ice with snow, and thus the short growing season (Cota et al., 1996; Gosselin et al., 1997). Nevertheless, present estimates are far higher than the pre-1990 estimates, which ignored production within the multi-year ice.

Due to the inflow of Atlantic and Bering Sea water, the Barents Sea and a patch of the Chukchi Sea, respectively,

have enhanced annual production (Hegseth, 1998; Noji et al., 2000; Sakshaug and Slagstad, 1992; Smith et al., 1997; Walsh J.J. and Dieterle, 1994). In the other Siberian shelf areas, annual production is low due to multi-year ice hindering wind-driven upwelling of nutrient-rich deep water along the shelf break, leaving re-mixing of nutrient-poor shelf water and phosphorus-poor river water as the main nutrient sources.

In Atlantic water, annual primary production is high, in part due to wind-driven episodic upwelling in summer (Fig. 9.24) (Olsen et al., 2003; Sakshaug and Slagstad, 1992). The most productive area is the Bering Shelf where a highly productive "greenbelt" is associated with the

upwelling of extremely nutrient-rich water along the shelf break and the Anadyr Current (Hansell et al., 1993; Nihoul et al., 1993; Springer et al.1996; Walsh J.J. et al., 1989). In the deep eastern Bering Sea, annual primary productivity is similar to, or slightly higher than that in the Barents Sea (Maita et al., 1999; Springer et al., 1996).

9.3.2.2. Secondary production

Although the zooplankton database is small, it suggests that growth rates of calanoid copepods and other crustaceans are dependent on temperature such that the time from hatching to the next adult generation is shorter in warmer water. The growth rate, however, is also very

Table 9.8. Estimated levels of primary production, defined as the integrated net photosynthesis (corrected for respiration) over at least 24 hours, plus the grazing rate of mesozooplankton (compiled by Sakshaug (2003) on the basis of data from several authors).

	Area (10³ km²)	Total primary production (g C/m²)	New primary production (g C/m²)	Grazing rate of zooplankton (g C/m²)	Total primary production (Tg C)
Central Deep Arctic	4489	>	<	-	>50
Arctic shelves	5052	32	8	10	279
Barents Sea	1512	<20-200a	<8-100	15 –50	136
Barents north slope	-	35	16	-	-
White Sea	90	25	6	-	2
Kara Sea	926	30-50	7–12	-	37
Laptev Sea	498	25-40	6-10	-	16
East Siberian Sea	987	25-40	6-10	-	30
Chukchi Sea	620	20->400	5->160	7->90	42
Beaufort Sea	178	30-70	7–17	-	8
Lincoln Sea	64	20-40	5-10	-	3
Other (Canadian Arctic)	182	20-40	5-10	-	5
Northeast Water Polynya	<50	20-50	13-32	-	-
North Water Polynya	-	150	70	-	-
Total Arctic Ocean	9541	>26	<5	-	>329
Atlantic sector	5000	97	50	-	483
Baffin Bay	690	60-120	25-50	-	62
Hudson Bay	820	50-70	25-35	-	49
Greenland Sea	600	70	40	-	42
Labrador Sea	1090	100	45	-	110
Norwegian Sea	1400	80-150	35–65	-	160
Icelandic Sea	400	100-200 ^b	45-90	-	60
West Spitsbergen	-	120	55	-	-
Bering Shelf	1300	>230	-	-	>300
Alaskan coastal	-	50-75	<20	32-50	-
Siberian coastal	-	>400	>160	>90	-
Middle, outer shelf	-	150-175	30-50	35 –70	-
Shelf Break	-	450 – 900	170-360	-	-
Bering oceanic	1000	60-180	-	-	155
Okhotsk Sea	1600	100-200	-	-	240
Global, ocean	362000	110	-	-	40 000°
Global, land	148000	405			60 000

^aHighest values occur where topography and currents cause continuous nutrient supply in Atlantic sector, lowest values in northernmost part; ^bproduction to the south and east of Iceland (i.e., in Atlantic water) is four times that to the north and east; ^cplus 5000 Tg benthic (seaweed) carbon production and 4000 to 7000 Tg of dissolved organic carbon.

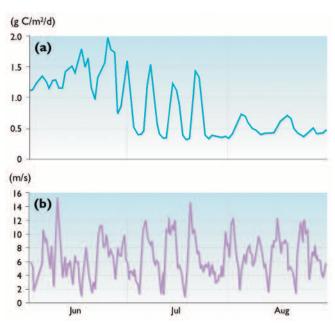


Fig. 9.24. Estimated (a) primary production and (b) wind speed for the Atlantic water of the Barents Sea in summer 1998 (wind data and hind-cast model data from the Norwegian Meteorological Institute; production model by D. Slagstad, Norwegian University of Science and Technology).

dependent on food supply. More specifically, the growth rate depends on the extent to which the fat-storage organs of the zooplankton are filled to capacity, which in turn is highly dependent on phytoplankton availability (Hygum et al., 2000). Nauplii (early-stage larvae) and early-stage copepodite stages can be food-limited at <0.5 to 0.7 mg Chl-a/m³ (Campbell et al., 2001). This level of concentration is common in waters which receive a low supply of new nutrients due to strong stratification and are therefore dominated by low levels of regenerative primary production (Båmstedt et al., 1991; Booth et al., 1993; Hirche and Kwasniewski, 1997; Irigoien et al., 1998).

Match versus mismatch

The concept of match and mismatch is very important in food-web energy transfer. A match implies that the predators are located in the same space and time as their prey and a mismatch when they are not. In principle, grazing by zooplankton is efficient when a large and growing population of zooplankton coincides with a phytoplankton bloom. Production of mesozooplankton is small in areas characterized by a mismatch. This is a highly nonlinear event because phytoplankton blooms and zooplankton swarms are episodic. To ensure a match higher in the food web, fish and zooplankton populations also need to coincide in time and space. Physical oceanographic conditions, such as temperature, salinity, stratification, mixing, and currents can influence the timing and location of the plankton production and biomass as well as the eggs and larvae of fish and invertebrates. In this sense, oceanographic conditions play a large role in determining the extent of a match or mismatch between trophic levels.

Non-grazed phytoplankton sink except for most of the (nanoplankton) fraction that is based on regenerated

nutrients. Thus, sedimentation rates are lower when there is a match between phytoplankton and zooplankton. Grazing and sedimentation are thus competing processes and both are strongly dependent on largecelled new production.

In Atlantic water, late development of copepodite stages of Calanus finmarchicus is a good match with the late and relatively long-lasting phytoplankton blooms that occur in mid-May to June (Dalpadado and Skjoldal, 1991; Skjoldal et al., 1987). But it is mismatched with the timing of the initial blooms, which is presumably one of the main reasons why C. finmarchicus is allochthonous in the Barents Sea (Melle and Skjoldal, 1998). The mismatch is greatest in very cold winters when sea ice covers Atlantic water and the blooms are typically four to six weeks earlier than usual (Olsen et al., 2003). The reason that the blooms are earlier than usual in such winters is because once melting starts the sea ice over the Atlantic water melts rapidly from below. This can result in the phytoplankton bloom being too early for the zooplankton, thus causing a mismatch in timing with the peak in zooplankton (Olsen et al., 2003; Skjoldal and Rey, 1989). Such years can have very low levels of secondary production. Although not strongly correlated, a match seems likely to occur in Atlantic water with mixing depths greater than 40 m, while a mismatch seems likely with mixing depths less than 40 m.

In the generally ice-free Norwegian fjords, the major phytoplankton blooms occur from February to early April, depending on latitude and the extent of freshwater-induced stability. As the major zooplankton peak does not occur until April or May, the zooplankton must feed on the secondary summer and autumn blooms (Wassmann, 1991). Owing to the extreme mismatch, almost all of the early spring bloom sinks to the bottom of the fjord.

9.3.2.3. Fish

Climate fluctuations affect fish directly, as well as by causing changes in their biological environment (i.e., in relation to predators, prey, species interactions, and disease). Direct physiological effects include changes in metabolic and reproductive processes. Climate variability may influence fish population abundance, principally through effects on recruitment. Variability in the physical environment may also affect feeding rates and competition by favoring one species relative to another, as well as by causing changes in the abundance, quality, size, timing, spatial distribution, and concentration of prey. Variability in the physical environment also affects predation through influences on the abundance and distribution of predators. Fish diseases leading to a weakened state or even death may also be environmentally triggered. Particular temperature ranges may, for instance, be more conducive to allowing disease outbreaks. While water temperature is typically the main source of environmental impact on fish, salinity and oxygen conditions, and ocean mixing and transport processes are also important.

Reproduction, recruitment, and growth

The physical environment affects the reproductive cycle of fish. For example, ambient temperatures may determine the age at sexual maturity. Atlantic cod off Labrador and the northern Grand Banks mature at 7 yr, while in the warmer waters off southwest Nova Scotia and on Georges Bank they mature at 3.5 and 2 yr, respectively (Drinkwater, 1999). Reproduction is typically temperature-dependent with gonad development occurring more quickly under warm conditions. Thus, temperature determines the time of spawning. Examples of low temperatures resulting in delayed spawning have been observed off Newfoundland, both in capelin (Nakashima, 1996) and Atlantic cod (Hutchings and Myers, 1994).

Understanding variability in recruitment (the number of young surviving long enough to potentially enter the fishery) has long been a prime issue in fisheries science. Evidence of changes in fish abundance in the absence of fishing suggests environmental causes. Following spawning, cod eggs and later young stages are generally distributed within the upper water column before they settle toward the bottom as half-year olds. The strength of a year-class is to a large degree determined during the first six months of life (Helle et al., 2000; Hjort, 1914; Myers and Cadigan, 1993; Sundby et al., 1989); life stages during which ocean climate may have a decisive effect (Cushing, 1966; De Young and Rose, 1993; Dickson and Brander, 1993; Ellertsen et al., 1989; Ottersen and Sundby, 1995; Sætersdal and Loeng, 1987). The effects of temperature on recruitment of Atlantic cod across its entire distribution range were examined by Ottersen (1996) and Planque and Fredou (1999). Populations inhabiting areas at the lower end of the overall temperature range of the species (i.e., West Greenland, Labrador, Newfoundland, and the Barents Sea) had higher than average recruitment when temperature anomalies were positive, while recruitment to populations occupying the warmer areas (e.g., the Irish and North Seas) seemed better with negative temperature anomalies. For populations inhabiting regions with midrange temperatures the results were inconclusive. The recruitment of Norwegian spring-spawning herring is also linked to variability in water temperature (Toresen and Østvedt, 2000; see section 9.3.3.3).

The pelagic ecosystem in the southeastern Bering Sea may, according to the recently published Oscillating Control Hypothesis, alternate between primarily bottom-up control in cold regimes and primarily top-down control in warm regimes (Hunt and Stabeno, 2002; Hunt et al., 2002). The timing of spring primary production in the southeastern Bering Sea is determined predominately by the timing of sea-ice retreat. Late retreat leads to an early, ice-associated bloom in cold water, whereas no ice, or early retreat, leads to an openwater bloom in warm water. In years when the spring bloom occurs in cold water, low temperatures limit the production of zooplankton, and the survival of larval and

juvenile fish, and their recruitment into the populations of large piscivorous fish, such as walleye pollock, Pacific cod, and arrowtooth flounder. Continued over decadal scales, this will lead to bottom-up limitation and a decreased biomass of piscivorous fish. Alternatively, in periods when the bloom occurs in warm water, zoo-plankton populations should grow rapidly, providing plentiful prey for larval and juvenile fish. Abundant zoo-plankton will support strong recruitment of fish and will lead to abundant predatory fish that control forage fish, including in the case of walleye pollock, their own juveniles (Hunt and Stabeno, 2002; Hunt et al., 2002).

Because fish are ectothermic, temperature is the key environmental factor. Individual growth is the result of a series of physiological processes (i.e., feeding, assimilation, metabolism, transformation, and excretion) whose rates are all controlled by temperature (Brett, 1979; Michalsen et al., 1998). Brander (1994, 1995) examined 17 North Atlantic cod populations and showed that mean bottom temperature accounted for 90% of the observed (ten-fold) difference in growth rates between populations. Higher temperatures led to faster growth rates over the temperature range experienced by these populations. Growth rate decreases at higher temperatures and the temperature for maximum growth decreases as a function of size (Björnsson, 2001).

The biomass of zooplankton, the main food for larval and juvenile fish, is generally greater when temperature is high in the Norwegian and Barents Seas (Nesterova, 1990). High food availability for the young fish results in higher growth rates and greater survival through the vulnerable stages that determine year-class strength. Temperature also affects the development rate of fish larvae directly and, thus, the duration of the highmortality and vulnerable stages decreases with higher temperature (Blood, 2002; Coyle and Pinchuk, 2002; Ottersen and Loeng, 2000; Ottersen and Sundby, 1995). Also, in the Barents Sea, mean body size as halfyear olds fluctuates in synchrony for herring, haddock, and Northeast Arctic cod and the length of all three is positively correlated with water temperature. This indicates that these species, having similar spawning and nursery grounds, respond in a similar manner to largescale climate fluctuations (Loeng et al., 1995; Ottersen and Loeng, 2000). For Barents Sea cod, mean lengthsat-age for ages 1 to 7 are greater in warm periods (Dementyeva and Mankevich, 1965; Michalsen et al., 1998; Nakken and Raknes, 1987).

For 2- and 3-year old Barents Sea capelin, Gjøsæter and Loeng (1987) found positive correlations between temperature and growth for different geographical regions and for different years. Changes in water temperature through altered climate patterns may also affect predator—prey interactions. In the Barents Sea, the increase in basic metabolic rates of Northeast Arctic cod, associated with higher temperatures, can result in a rise in the consumption of capelin by 100 000 tonnes per degree centigrade (Bogstad and Gjøsæter, 1994).

Distribution and migration

Temperature is one of the main factors, together with food availability and suitable spawning grounds, which determines the large-scale distribution pattern of fish. Because most fish species (and stocks) tend to prefer a specific temperature range (Coutant, 1977; Scott J., 1982), long-term changes in temperature can lead to expansion or contraction of the distribution range of a species. These changes are generally most evident near the northern or southern boundaries of the species range; warming results in a northward shift and cooling draws species southward. For example, in the Barents Sea, temperature-related displacement of Northeast Arctic cod has been reported on interannual time scales as well as at both small and large spatial scales. In warm periods, cod distribution is extended eastward and northward compared to colder periods when the fish tend to concentrate in the southwestern part of the Barents Sea (Ottersen et al., 1998). Capelin distribution also responds to changes in water temperature both in the Barents Sea (Sakshaug et al., 1992) and off Newfoundland and Labrador.

The relatively high interannual stability of residual currents, which prevail in most regions, maintains the main features of larval drift patterns from spawning area to bottom settlement area for each population, and consolidates differences between populations. Interannual variation is introduced through changes in largeand regional-scale atmospheric pressure conditions. These affect winds and upper ocean currents, which in turn modify drift patterns of fish larvae and introduce variability in water temperature and the availability of prey items. While a long and unrestricted larval drift is important for some cod populations, such as those in the Barents Sea and the Icelandic component at West Greenland, recruitment to populations residing in small and open systems depends on larval retainment and the avoidance of massive advective losses (Ottersen, 1996; Sinclair M., 1988).

Many species that undertake seasonal migrations appear to use environmental conditions as cues. For example, April sea surface temperatures and sea-ice conditions in the southern Gulf of St. Lawrence determine the average arrival time of Atlantic herring on their spawning grounds (Lauzier and Tibbo, 1965; Messieh, 1986). Sea-ice conditions also appear to control the arrival time in spring of Atlantic cod onto the Magdalen Shallows into the Gulf of St. Lawrence (Sinclair A. and Currie, 1994). Atlantic salmon arrive earlier along the Newfoundland and Labrador coasts during warmer years (Narayanan et al., 1995).

The Norwegian spring-spawning herring stock, inhabiting the Norwegian and Icelandic Seas, is highly migratory. Larvae and fry drift into the Barents Sea, while adults undergo substantial feeding and spawning migrations (Holst J. et al., 2002). Since around 1950, biomass and migration patterns have fluctuated dramatically. While

these shifting migration patterns may be dominated by density-dependence, environmental conditions are also likely to have been important (Holst J. et al., 2002).

In the Bering Sea, warmer bottom temperatures lead to the distribution of adult walleye pollock, Greenland turbot, yellow Irish lord (*Hemilepidotus jordani*), and thorny sculpin (*Icelus spiniger*) being more widespread on the shelf, while Arctic cod are restricted to the cold pool (Wyllie-Echeverria and Wooster, 1998).

The combination of environmentally influenced distribution patterns and politically restricted fisheries patterns can have pronounced impacts on the availability of fish to fishers. For instance, most of the Barents Sea is under either Norwegian or Russian jurisdiction, but there is a small, disputed region of international waters in the center. This area is aptly named the "Loophole" and at times it is the site of extensive fishing activity by the international fishing fleets. Most fishing occurs in the southern part of the Loophole, where in warmer years several species of all sizes are found throughout the year. However, in colder years there may be hardly any fish in the area for prolonged periods. The reason for this pattern is that the southern part of the Loophole lies to the south of the Polar Front so that even relatively small east-west movements of the water masses may result in large temperature changes. In cold years, the Polar Front is displaced farther south and west than the Loophole. The fish move in order to remain within the warmer water, thereby making them unavailable to the international fishing fleets (Aure, 1998). The movement of the Polar Front is most pronounced between warm and cold years in the Barents Sea as a whole, but movements may also occur on time scales of weeks.

9.3.2.4. Marine mammals and seabirds

Some important predator—prey match—mismatch issues also occur with higher predators. The timing of reproduction in many seal species is thought to match the availability of large zooplankton and small fishes at the time when pups are weaned and when polar bear den emergence occurs during the peak reproductive period of their favorite prey, ringed seal. Likewise, invertebrate or fish species must be available in the upper parts of the water column when seabird young commence self-feeding. Higher predators might not easily track shifts in the production of zooplankton and fish, which are more directly influenced by temperature.

Factors that influence the distribution and annual duration of sea ice or snow availability in the spring can potentially have profound influences on the population ecology of some arctic marine mammals. Sea ice is the breeding habitat for all pagophilic (i.e., ice-loving) seal species and it is the primary hunting platform for polar bear. Changes in the time of formation or disappearance of seasonal sea ice, in the quality of the sea ice, and in the extent of total coverage of both seasonal and multi-year ice could all affect ice-dependent species. Snow

cover is very important for polar bears and ringed seals and changes in average snow depth or duration of the snow season could affect their breeding success.

Walruses appear to follow an annual migratory pattern, moving with the advance and retreat of the sea ice in most parts of their range (Fay, 1981, 1982; Wiig et al., 1996). However, this may be due to the sea ice blocking access to shallow-water feeding areas, rather than to it serving as an essential habitat element.

The primary requirement for seabirds in the Arctic is suitable breeding cliffs near abundant prey sources. If ice edges or frontal regions shift such that the distance between these highly productive areas and the nesting areas becomes too great, the mismatch would have serious consequences for seabirds.

9.3.3. Past variability – interannual to decadal

Previous data collections combined with present-day models shows that climate variability is very likely to have influenced population parameters of marine organisms, especially fish (section 9.3.2.3). Water temperature undoubtedly affects species composition in different areas, as well as the recruitment, growth, distribution, and migration of different fish species. However, most of the relationships between water temperature and population variables are qualitative and few of those discussed here can be quantified.

9.3.3.1. Plankton

There are few long time series for phytoplankton in the Arctic. Exceptions include (1) datasets covering 20 years or more for Icelandic waters (Thordardóttir, 1984) and Norway (Oslofjord, Trondheimsfjord; Johnsen et al., 1997); (2) a program undertaken during the 1990s to monitor harmful algae along the Norwegian coast (Dahl E. et al., 1998, 2001); and (3) zooplankton data provided by the Continuous Plankton Recorder, which has been used in much of the North Atlantic between 50° and 65° N for over fifty years (Johns et al., 2001). This has generated one of the most detailed records of seasonal, interannual, and decadal variability in zooplankton to date. Sampling in the Northwest Atlantic is less complete but extends across the Labrador Sea to the Grand Banks, the Scotia Shelf, and the Gulf of Maine.

The copepod *Calanus finmarchicus* contributes >50% of the biomass of sampled plankton in the North Atlantic. Its population has declined substantially in the Northeast Atlantic since the early 1960s (Fig. 9.25), apparently as a function of variation in the NAO (Planque and Batten, 2000). Also, recent and persistent declines seem to be related to a low-frequency change in the volume of Norwegian Sea Deep Water, where *Calanus finmarchicus* overwinters (Heath et al., 1999). Figure 9.26 shows that, in contrast, the arctic species *Calanus glacialis* extended its range in the Northwest Atlantic during the

1990s as a consequence of the extension of cold Labrador Slope Water (Johns et al., 2001).

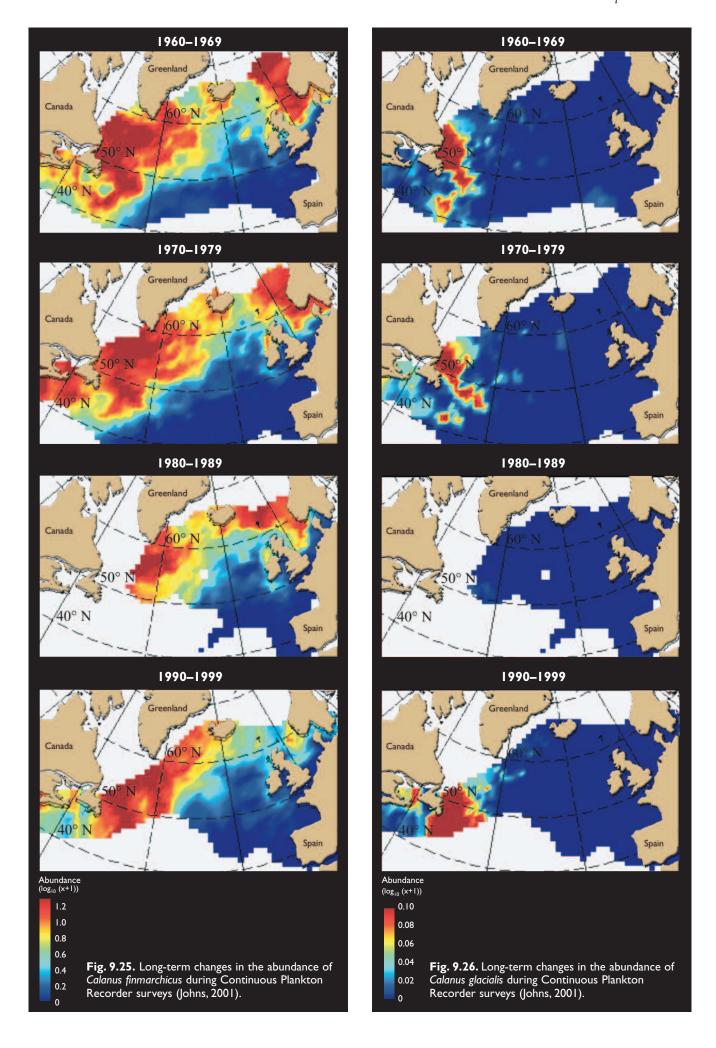
Historical time series of zooplankton biomass suggest a decrease in biomass between 1954 and 1995 in the oceanic and outer shelf regions of the eastern Bering Sea (Sugimoto and Tadokoro, 1998). However, when the data are separated by shelf region, such a trend is not apparent (Napp et al., 2002). Inshore sampling of Calanus marshallae indicates a much higher biomass in the late 1990s compared to the early 1980s. Water temperature is the most important factor influencing zooplankton growth rates and may be responsible for the observed interannual variability in mid-shelf zooplankton biomass (Coyle and Pinchuk, 2002; Napp et al., 2000). During cold springs when the spring bloom is dominated by ice-edge blooms, reduced coupling between the mesozooplankton and phytoplankton means more phytoplankton will be ungrazed and sink to the bottom, so enhancing the benthic food web. Stronger coupling between mesozooplankton and phytoplankton in warmer springs may result in a stronger pelagic production.

The population of the jellyfish *Chrysaora melamaster* increased at least ten-fold during the 1990s (Brodeur et al., 1999b). These large jellyfish compete for food with young walleye pollock (consuming an estimated 5% of the annual crop of zooplankton) and also feed upon them (consuming an estimated 3% of newborn walleye pollock). Jellyfish have very low energy requirements compared with fish (20 times less) and mammals (200 times less than whales) on a per unit weight basis. Their increased abundance may be due to reduced nutrients and a lower-energy plankton regime.

9.3.3.2. Benthos

Data are available for sedentary and long-lived macrozoobenthos, which are relevant indicators of multi-year environmental fluctuations between the late 1700s and the present. Biogeographical boundaries in the Barents Sea have shifted as a result of temperature fluctuations (Blacker, 1965). Based on analyses using temperature paleo-reconstructions, it appears that high arctic species tend to survive only when temperatures remain between -1.8 and 6 °C, whereas adults of boreal species can survive temperatures of -1 to 25 °C. Also, biogeographical changes in the bottom fauna appear to occur faster and are more easily detected during warm periods than cold periods.

The zoobenthos of the Russian Arctic seas has been most intensively studied in the Barents Sea. Deryugin (1924) detected several unusual species in Kola Bay in 1908 and 1909 and related this to fluctuations in water temperature. Some boreal species in the Barents Sea have responded to environmental change by shifting their biogeographical borders (Fig. 9.27; Chemerisina, 1948; Nesis, 1960). This reflects variations in population size at habitat boundaries, not changes in the size and shape of the habitats themselves (Galkin, 1998).



In years following warming, the polychaete *Spiochaetopterus typicus* predominates along the Kola Section in the Barents Sea. Following cold years, the polychaete *Maldane sarsi* predominates. *Spiochaetopterus typicus* is thus an indicator of warming or warm conditions.

Estimating natural fluctuations in zoobenthos biomass in the Barents Sea is difficult owing to the impact of commercial bottom trawling (Denisenko, 2001). In the Pechora Sea, where there is no traditional demersal fishery, changes in zoobenthos biomass in 1924, 1958 to 1959, 1968 to 1970, and 1992 to 1995 show a negative correlation between zoobenthos biomass and temperature (Denisenko, pers. comm., Zoological Institute RAS, St. Petersburg, 2003).

In the Bering Sea, long-term change in zoobenthos communities is known for the eastern regions as a result of Soviet and American investigations in 1958 to 1959 and 1975 to 1976. In the 1950s, maximum biomass occurred in the northwestern part of the eastern Bering Sea in the mid-shelf region at bottom depths between 50 and 150 m. In the early 1970s, the highest biomasses occurred in the mid-shelf area, southeast of the Pribilof Islands. Because the early 1970s were cold compared to the late 1950s, it may be that the difference in zoobenthos biomass related to changes in the southern limit of the ice edge and thus to the amount of ice-edge primary production that fell to the benthos, ungrazed by pelagic zooplankton.

Recent studies indicate ongoing change in the benthic communities of the Bering and Chukchi Seas (Francis et al., 1998; Grebmeier and Cooper, 1995; Sirenko and Koltun, 1992). The region just north of the Bering Strait is a settling basin for organic carbon, which results in a high benthic standing stock and high oxygen uptake rates (Grebmeier, 1993; Grebmeier et al., 1988, 1989).



Fig. 9.27. Biogeographical boundaries in the Barents Sea during the 20th century. I maximal western extent of arctic species in cold periods; Il line of 50% average relation between boreal and arctic species; III maximal eastern extent of boreal species in warm periods; IV transition zone.

Benthic productivity in this region near 67°30′ N, 169° W has historically maintained the highest benthic faunal biomass of the entire Bering/Chukchi system (Grebmeier, 1993; Grebmeier and Cooper, 1994; Grebmeier et al., 1995; Stoker, 1978, 1981). Although benthic biomass remains high in the area, regional changes in the dominant benthic species have occurred. This is likely to indicate changing hydrographic conditions (Grebmeier, 1993; Grebmeier et al., 1995).

In the St. Lawrence Island polynya region, changes in regional oceanography due to the position or size of the Gulf of Anadyr gyre are ultimately related to the northward transport of water through the Bering Strait, and to the geostrophic balance within the Arctic Ocean basin. The latter, which is related to variations in the NAO/AO index, drives the northward current system in the northern Bering Sea (Walsh et al., 1989). Roach et al. (1995) found little flow through the Bering Strait into the Arctic Ocean during the NAO-positive period of the early 1990s, and a large increase in flow when the NAO became negative in 1996. Small flow into the Arctic Ocean is coincident with reduced northward transport of water south of St. Lawrence Island.

The Gulf of Anadyr "cold pool" is maintained by sea-ice production and brine formation in the St. Lawrence Island polynya. Reduced sea-ice production to the south of the polynya resulting in a decreased supply of nutrients for early-season primary production would limit benthic populations (Grebmeier and Cooper, 1995). However, it is possible that an enhanced and more energetic polynya could result from warming. This could maintain a chemostat-type bloom system, as to the north of St. Lawrence Island (Walsh J.J. et al., 1989), allowing a longer growing season and greater production and thus transport.

The three species of crab that inhabit the eastern Bering Sea shelf (red king crab, Tanner crab, and snow crab) exhibit highly periodic patterns in abundance. Rosenkranz et al. (2001) found that anomalously cold bottom temperatures in Bristol Bay may adversely affect the reproductive cycle of Tanner crab and that northeasterly winds may promote coastal upwelling, which advects larvae to regions of fine sediments favorable for survival upon settling. Incze and Paul (1983) linked low densities of copepods within the 70 m isobath in Bristol Bay with low abundance of Tanner crab larvae. Recruitment patterns for red king crab in Bristol Bay show the populations to be negatively correlated with the deepening of the Aleutian Low and warmer water temperatures (Zheng and Kruse, 2000). Red king crabs were commercially exploited during the late 1970s, which has also contributed to the population decline.

9.3.3.3. Fish

There are few records of marine biota showing interannual and longer-term variability in the Arctic Ocean, but records of the abundance of commercial fish species for the Labrador, Greenland, Iceland, Norwegian, and Barents Sea go back to the start of the twentieth century and even earlier in some cases. Within these areas capelin, cod, and herring populations have undergone very large fluctuations in biomass and distribution.

The period of warming from the mid-1920s to the mid-1960s, which affected Greenland and Iceland in particular (see section 9.2.4.2), had a profound effect on the major commercial fish species and also on most other marine life. A number of species, which had been rare in offshore areas west of Greenland, became abundant at this time and population biomass increased by several orders of magnitude. These changes were not related to fishing and are clearly due to climate variability.

Boreal species such as cod are likely to respond strongly to temperature variability and so show greater variability in recruitment at the extremes of their range (Brander, 2000; Ottersen and Stenseth, 2001). However, for the period over which records are available most populations have been reduced to low levels as a result of fishing pressure and may therefore show high variability throughout their distribution.

The warming period of the 1920s

The warming period of the 1920s caused a poleward extension in the range of distribution for many fish and other marine and terrestrial species from Greenland to Iceland and eastward to the Kara Sea. Records of changes in species distribution during the 1920s provide some of the most convincing evidence of the pervasive effects of a change in climate on the marine ecosystem as a whole. Jensen (1939) published a comprehensive review of the effects of the climate change in the Arctic and subarctic regions during this period, which presents much of this information. Some of the salient points concerning fish species are summarized in Table 9.9.

The marine shelf ecosystem off West Greenland is affected by cold polar water masses and temperate Atlantic water. Changes in the distribution of these water masses, under the influence of the NAO, affect the distribution and abundance of fish species and hence fisheries yields (Pedersen and Rice, 2002; Pedersen and Smidt, 2000; Schopka, 1994).

The distribution of cod extended poleward by about 1000 km between 1920 and 1930 and can be followed in some detail, because fishing stations were established progressively further north as directed coastal fisheries were established by the Greenland Administration.

The international offshore fishery for cod off West Greenland reached a peak of over 400 000 tonnes in the early 1960s before collapsing. The decline was due to a combination of fishing pressure and reduced water temperature, and probably to a lack of recruitment from Iceland. The relationship between water temperature and recruitment level is clear for this area (Brander, 2000; Buch et al., 1994), with poor recruitment occurring at temperatures below about 1.5 °C (measured on Fylla Bank, 64° N, in June). The warming of the North Atlantic that has taken place since about the early 1990s has also affected Greenland but temperatures remained below 1.5 °C until 1996. Thus it is too early to expect a recovery of the cod population; cod take about seven years to reach maturity and may be adversely affected by the trawl fishery for shrimps which is now the mainstay of the Greenland fisheries.

One of the principal changes which took place off Iceland during the 1920s warming period occurred within the major pelagic populations — those of herring and capelin (Table 9.9). Prior to 1920, the capelin spawned regularly on the south and southwest coasts of Iceland, but from 1928 to 1935 very few capelin were taken in these areas. In contrast, herring extended their spawning areas from the south and southwest coast to the east, northwest, and north coasts in this period (Saemundsson, 1937).

Similar changes are also recorded for Jan Mayen, the Barents Sea, the Murman Coast, the White Sea, Novaya Zemlya, and the Kara Sea, where cod and herring extended their ranges and became more abundant.

Table 9.9. Changes in the distribution and abundance of fish species off West Greenland and Iceland during the period of warming from 1920 onwards. Prepared by Brander (2003) based on Saemundsson (1937) and Jensen (1939).

	West Greenland	Iceland
Species previously absent, but which appeared from 1920 onwards	Haddock (Melanogrammus aeglefinus),tusk (Brosme brosme), ling (Molva molva)	Bluntnose sixgill shark (<i>Notidanus griseus</i>), swordfish (<i>Xiphias gladius</i>), horse mackerel (<i>Trachurus trachurus</i>)
Rare species which became more common and extended their ranges	Coal fish (Pollachius virens; new records of spawning fish), Atlantic salmon (Salmo salar), spurdog (Squalus acanthias)	Witch (Glyptocephalus cynoglossus), turbot (Psetta maxima), basking shark (Cetorhinus maximus), northern bluefin tuna (Thunnus thynnus), mackerel (Scomber scombrus), Atlantic saury (Scomberesox saurus), ocean sunfish (Mola mola)
Species which became abundant and extended their ranges poleward	Atlantic cod, Atlantic herring (new records of spawning fish)	Atlantic cod, Atlantic herring (both extended their spawning distribution)
Arctic species which no longer occurred in southern areas, and extended their northern limits	Capelin, Greenland cod, Greenland halibut (became much less common)	Capelin

Climate effects on fish in the Barents Sea

Understanding of the processes underlying major fluctuations in the fish ecosystem of the Barents Sea is considerably better than for most other areas of the northern North Atlantic (Rødseth, 1998). The main species involved are Atlantic cod, capelin, and Atlantic herring. These species are closely linked through the food web. Cod is highly dependent on capelin as its main prey. One- to two-year old herring prey heavily on the larvae of capelin, whose mortality increases greatly in years with a large biomass of young herring. Interactions between these species are strongly affected by the highly variable oceanographic conditions of the Barents Sea (Hamre, 1994).

The early years of the twentieth century, particularly 1902, were extremely cold in the Barents Sea, with extensive sea-ice cover. This resulted in a crisis for the Norwegian fisheries, with low catches of small Northeast Arctic cod in very poor condition. Large numbers of seals, primarily harp seals, moved down the Norwegian coast from the Barents Sea. A similar sequence of events occurred during the cold period in the 1980s, when the capelin population collapsed; the cod were small and in poor condition and harp seals again invaded the northern coast of Norway.

For cod in particular, the consequences of variability in water temperature, transport, and food during early life stages have been studied closely (Michalsen et al., 1998; Ottersen and Loeng, 2000; Ottersen et al., 1998; Sætersdal and Loeng, 1987). Growth and survival rates of larvae and juveniles are higher in warm years and the large year-classes of cod spread further east into the Barents Sea, where they encounter cooler water and their growth rate slows as a result (Ottersen et al., 2002).

Norwegian spring-spawning herring

The biomass of Norwegian spring-spawning herring increased almost ten-fold between 1920 and 1930, when the Norwegian Sea and much of the North Atlantic went

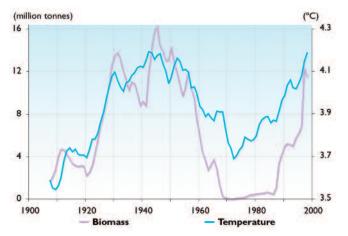


Fig. 9.28. Relationship between water temperature and the biomass of the Norwegian spring-spawning herring stock (Toresen and Østvedt, 2000).

through a period of rapid warming (Toresen and Østvedt, 2000). The herring population declined rapidly from the late 1950s and by 1970 had decreased by more than four orders of magnitude. The decline was coincident with a period of cooling (Fig. 9.28). Although this cooling may have been a contributing factor, it is likely that heavy fishing pressure was the primary cause of the collapse of the population.

The collapse of the Norwegian spring-spawning herring population coincided with a retraction of the summer feeding distribution due to the southward and eastward shift in the location of the Polar Front. The Polar Front was to the north of Iceland prior to 1965 but has since stayed west of Iceland (see Box 9.8). Despite a complete recovery of the herring spawning stock and a rise in water temperature north of Iceland in 2000 to levels similar to those of the mid-1960s (Malmberg and Valdimarsson, 2003), the herring have not returned to their earlier feeding areas.

The rapid cooling during the mid- and late 1960s also resulted in reduced growth and recruitment of the Norwegian spring-spawning herring (Toresen and Østvedt, 2000). The same happened with the Icelandic summer spawning herring (Jakobsson et al., 1993).

Temperature-mediated habitat changes in Canadian capelin

Capelin off Newfoundland and Labrador spread southward as far as the Bay of Fundy when water temperatures declined south of Newfoundland in the mid-1960s and retracted northward as water temperatures rose in the 1970s (Colton, 1972; Frank et al., 1996; Tibbo and Humphreys, 1966). During cooling in the latter half of the 1980s and into the 1990s, capelin again extended their range, eastward to Flemish Cap and southward onto the northeastern Scotia Shelf off Nova Scotia (Frank et al., 1996; Nakashima, 1996). For example, small quantities of capelin began to appear in the groundfish trawl surveys on the Scotia Shelf in the mid-1980s and since then numbers have increased dramatically (Frank et al., 1996). Initially, only adult capelin were caught, but juveniles later appeared, suggesting capelin were successfully spawning.

This shift appears to have been part of a larger-scale ecosystem change. While capelin were spreading onto the Scotia Shelf, polar cod, whose primary grounds have traditionally been the Labrador Shelf stretching southward to northern Newfoundland, were moving southward. In the late 1980s and early 1990s, as water temperatures decreased, polar cod pushed southward onto the Grand Banks and into the Gulf of St. Lawrence in large numbers (Gomes et al., 1995; Lilly et al., 1994).

Historical climate and fish in the Bering Sea

The direct effects of atmospheric forcing resulting from climate variations are very important to the physical

oceanographic conditions of the Bering Sea. Since the eastern Bering Sea shelf has a characteristically sluggish mean flow and is separated from any direct oceanographic connection to the North Pacific Ocean by the Alaska Peninsula, linkages between the eastern Bering Sea and the climate system are primarily a result of the ocean-atmosphere interaction (Stabeno et al., 2001). Climate variations in this region are directly linked to the location and intensity of the Aleutian Low pressure center, which affects winds, surface heat fluxes, and the formation of sea ice (Hollowed and Wooster, 1995). The pressure index has experienced eight statistically significant shifts on roughly decadal time scales that alternated between cool and warm periods (Overland et al., 1999a). A well-documented shift (Trenberth, 1990 among others) from a cool to a warm period occurred between 1977 and 1989, which coincided with the start of fishery-independent sampling programs and fishery catch monitoring of major groundfish species. Information from the contrast between this period and the previous and subsequent cool periods (1960 to 1976 and 1989 to 2000) forms the basis of the following discussion.

Changes in atmospheric climate are primarily transmitted through the Bering Sea to the biota via the mechanisms of wind stress (Francis et al., 1998) and the annual variation in sea ice extent (Stabeno et al., 2001). These mechanisms directly alter the timing and abundance of primary and secondary production by changing the salinity, mixed-layer depth, nutrient supply, and vertical mixing in the ocean system.

The extent and timing of the sea ice also determines the area where cold bottom water temperatures will persist throughout the following spring and summer. This eastern Bering Sea area of cold water, known as the cold pool, varies with the annual extent and dura-

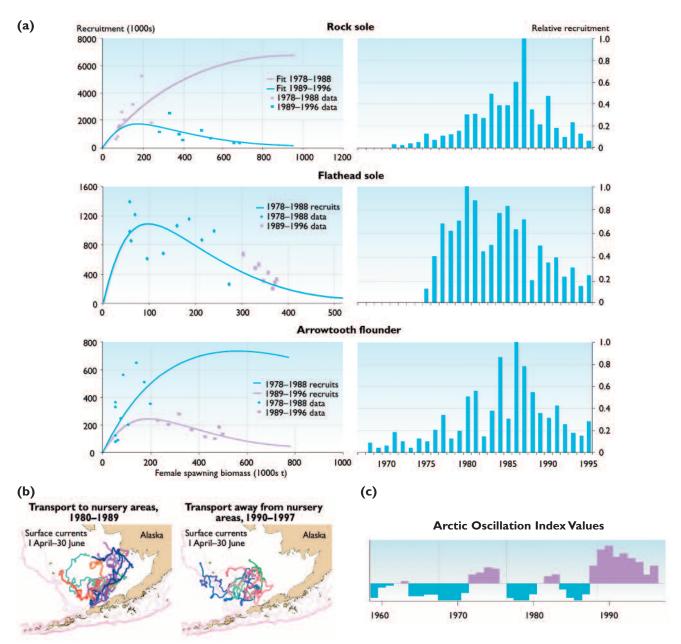


Fig. 9.29. Winter spawning flatfish (a) recruitment and (b) predicted wind-driven larval drift patterns relative to (c) decadal-scale atmospheric forcing in the eastern Bering Sea (Wilderbuer et al., 2002).

Box 9.9. Effect of atmospheric forcing in the Bering Sea

Recruitment responses of many Bering Sea fish and crab species are linked to decadal scale patterns of climate variability (Francis et al., 1998; Hare and Mantua, 2000; Hollowed et al., 2001; Wilderbuer et al., 2002; Zheng and Kruse, 2000). Decadal changes in the recruitment of some flatfish species in the eastern Bering Sea appear to be related to patterns in atmospheric forcing (see Fig. 9.29). The AO index, which tracks the variability in atmospheric pressure at polar and mid-latitudes, tends to vary between negative and positive phases on a decadal scale. The negative phase brings higher-than-normal pressure over the polar region and the positive phase does the opposite, steering ocean storms farther north. These patterns in atmospheric forcing in winter may influence surface wind patterns that advect fish larvae onto or off the shelf. When the index was in its negative phase in the 1980s, southwesterly winds tended to dominate, which is likely to have resulted in the transport of flatfish larvae to favorable nursery grounds. The positive phase in the 1990s showed winds to be more southeasterly, which would tend to advect larvae off the shelf. The relative recruitment of three species of winter spawning flatfish in the Bering Sea – arrowtooth flounder, rock sole, and flathead sole – was high in 1977 to 1988 and low in 1988 to 1998, indicating a link between surface wind advection patterns during the larval stage and flatfish survival.

However, periods of strong Aleutian Lows are associated with weak recruitment for some Bering Sea crab species and are unrelated to others (Zheng and Kruse, 2000) depending on species-specific life history traits. Winds from the northeast favor retention of crab larvae in offshore mud habitats that serve as suitable nursery areas for young Tanner crabs since they bury themselves for protection (Rosenkranz et al., 2001). However, southwesterly winds promote inshore advection of crab larvae to coarse, shallow water habitats in inner Bristol Bay that serve as nursery areas for red king crabs who find refuge among biogenic structures (Tyler and Kruse, 1998). Timing and composition of the plankton blooms may also be important, as red king crab larvae prefer to consume Thalassiosira spp. diatoms, whereas Tanner crab larvae prefer copepod nauplii. Some species, such as Bering Sea herring, walleye pollock, and Pacific cod, show interannual variability in recruitment that appears more related to ENSO-driven climate variability (Hollowed et al., 2001; Williams and Quinn, 2000). Years of strong onshore transport, typical of warm years in the Bering Sea, correspond to strong recruitment of walleye pollock, possibly due to separation of young fish from cannibalistic adults (Wespestad et al., 2000). Alaskan salmon also exhibit decadal scale patterns of production, which are inversely related to the pattern of west coast salmon production (Hare and Mantua, 2000). Including environmental variables such as sea surface temperature and air temperature significantly improved the results of productivity models for Bristol Bay sockeye salmon (Oncorhynchus nerka) compared to models containing density-dependent effects only (Adkison et al., 1996).

tion of the ice pack and can influence fish distributions. Pollock have shown a preference for warmer water, and exhibit an avoidance of the cold pool (Wyllie-Echeverria, 1995). In cold years they utilize a smaller portion of the shelf waters, in contrast to warm years when they have been observed as far north as the Bering Strait and the Chukchi Sea. Strong year-classes of pollock have been found to occur synchronously throughout the Bering Sea (Bulatov, 1995) and to coincide with above-normal air and bottom water temperatures and reduced sea-ice cover (Decker et al., 1995; Quinn and Niebauer, 1995). These favorable years of production are the result of good juvenile survival and are related to how much cold water habitat is present (Ohtani and Azumaya, 1995), the distribution of juveniles relative to the adult population which influences the level of predation (Wespestad et al., 2000), and enhanced rates of embryonic development in warmer water (Blood, 2002; Haynes and Ignell, 1983).

The distributions of forage fishes including Pacific herring, capelin, eulachon (*Thaleichthys pacificus*), and juvenile Pacific cod and pollock indicate temperature-related differences (Brodeur et al., 1999a). Capelin exhibits an expanded range in years with a larger cold pool and contracts in years of reduced sea-ice cover. Although the

productivity of capelin populations in relation to water temperature is not known, Bering Sea herring populations exhibited improved recruitment during warm years (Williams and Quinn, 2000), similar to other herring populations where the timing of spawning is also temperature-related (Zebdi and Collie, 1995).

Recruitment and stock biomass have been examined for evidence that climatic shifts induce responses in the production of groundfish species in the Bering Sea and North Pacific Ocean (Hollowed and Wooster, 1995; Hollowed et al., 2001). Even though results from these studies are highly variable, strong autocorrelation in recruitment associated with the significant change in climate in 1977 was observed for many salmonids and some winterspawning flatfish species such as eastern Bering Sea arrowtooth flounder and Greenland halibut. The two latter species showed opposite changes post-1977 (increasing biomass for arrowtooth flounder and decreasing biomass for Greenland halibut). Substantial increases in the abundance of Pacific cod, skates, flatfish such as rock sole, and non-crab benthic invertebrates also took place on the Bering Shelf in the 1980s (Conners et al., 2002).

The decadal-scale patterns in recruitment success for winter-spawning flatfish (Fig. 9.29) may be associated with

decadal shifts in the Aleutian low pressure system that affects cross-shelf advection patterns of larvae to favorable nursery areas rather than with water temperature (Wilderbuer et al., 2002). Box 9.9 describes the effects of atmospheric forcing in the Bering Sea in more detail.

9.3.3.4. Marine mammals and seabirds

Although fragmented, there is a lot of evidence to suggest that climate variations have profound effects on marine mammals and seabirds. The capelin collapse in the Barents Sea in 1987 had a devastating effect on seabirds breeding on Bjørnøya. Repeated years (1967, 1981, 2000, 2001, and 2002) with little or no sea ice in the Gulf of St. Lawrence resulted in years with almost zero production of seal pups, compared to hundreds of thousands in good sea-ice years.

Vibe (1967) explored the relationship between climate fluctuations and the abundance and distribution of animals, including marine mammals and seabirds, in Greenland. During the cold, dry, and stable "drift-ice stagnation" phase in West Greenland (approximately 1810 to 1860), marine mammals and seabirds concentrated at central West Greenland because the sea ice did not advance far north into Davis Strait. During the "drift-ice pulsation stage" (1860 to 1910), when the sea ice of the Arctic Ocean drifted into the Atlantic Ocean

in larger amounts than before, marine mammal and seabird populations decreased in the unstable and wet climate of West Greenland because the East Greenland Current and the East Greenland sea ice advanced far north into Davis Strait in summer. In the same period, the Greenland right whale (*Balaena mysticetus*) population "stagnated" in the Atlantic region. During the "drift-ice melting stage" (1910 to 1960) the East Greenland sea ice decreased in Davis Strait and populations of marine mammals and seabirds increased in northern West Greenland. Cod were abundant along the coast of West Greenland and multiplied in Greenland waters.

The condition of adult male and female polar bears has declined in Hudson Bay since the early 1980s, as have birth rates and the proportion of first-year cubs in the population. Stirling et al. (1999) suggest that the proximate cause of these changes in physical and reproductive parameters is a trend toward earlier breakup of the sea ice, which has resulted in the bears coming ashore in poorer condition.

9.3.4. Future change – processes and impacts on biota

Table 9.4 summarizes the potential physical oceanographic changes in the Arctic based on the projected changes in the atmospheric forcing functions (Table 9.1)

Table 9.10. Potential long-term ecological trends due to climate warming. Unless otherwise specified these projected changes are very likely to happen.

	Phytoplankton	Zooplankton	Benthos	Fish	Marine mammals and seabirds
Distribution	Increased spatial extent of areas of high primary production in the central Arctic Ocean.	Southern limit of distribution for colder water species to move northward. Distribution of more southerly species to move northward.	Southern limit of distribution for colder water species to move northward. Distribution of more southerly species to move northward.	Southern limit of distribution for colder water species to move northward. Distribution of more southerly species to move northward. Timing and location of spawning and feeding migrations to alter.	
Production	Increased production in central Arctic Ocean, and Barents and Bering Sea shelves.	Difficult to predict, will depend on the timing of phytoplankton production and seawater temperatures.	Difficult to predict, will partly depend on the degree of match/mismatch between phytoplankton/zooplankton production and on water temperature. Production by shrimp and crab species may decline.	Wind-driven advection patterns of larvae may be critical as well as a match/mismatch in the timing of zooplankton production and fish larval production.	Dramatic declines in production by ice-associated marine mammals and increases by more temperate species. Seabird production likely to be mediated through forage availability, which is unpredictable.
Species composition/ diversity	Dependent on mixing depth: shallow mixing favors diatoms, intermediate depth mixing favors <i>Phaeocystis</i> , deep mixing may favor nanoflagellates.	Adaptable arctic copepods, such as <i>Calanus</i> glacialis, may be favored.	Cold-water species may decline in abundance along with some clams and crustaceans, while warm water polychaetes, blue mussel (Mytilus edulis), and other types of benthos may increase.	Cod, herring, walleye pollock, and some flatfish are likely to move northward and become more abundant, while capelin, polar cod, and Greenland halibut will have a restricted range and decline in abundance.	Declines in polar bear, and in ringed, harp, hooded, spotted, ribbon, and possibly bearded seals. Increased distribution of harbour seals and grey seals. Possible declines in bowhead, narwhal, grey, and beluga whales. Ivory gulls and several small auk species are likely to decline while other changes in bird populations are unpredictable.

and potential future sea-ice conditions discussed in Chapter 6. Table 9.10 summarizes the potential long-term ecological changes in the marine system that are considered likely to arise as a result of these physical changes. The time frames for these changes to the biological system are addressed in this section by trophic level and by region where appropriate. The most pronounced physical changes are likely to include a substantial loss of sea ice, an increase in air and sea surface temperature, and changes in the patterns of wind and moisture transport.

Changes in the distribution of many species, ranging from phytoplankton to whales, are very likely to occur. The main habitat changes affecting marine mammals and seabirds include a reduction in sea ice, changes in snow cover, and a rise in sea level. Phenological changes, species replacements, and changes at lower trophic levels are also likely to have a strong influence on upper trophic level species.

9.3.4.1. Primary production

Changes in sea ice, water temperature, freshwater input, and wind stress will affect the rate of nutrient supply through their effect on vertical mixing and upwelling. Changes in vertical mixing and upwelling will affect the timing, location, and species composition of phytoplankton blooms, which will in turn affect the zooplankton community and the productivity of fish.

Changes in the timing of the primary production will determine whether this production is utilized by the pelagic community or is exported and utilized by the benthos (Box 9.10). The retention to export ratio also depends upon the advection and temperature preferences of grazing zooplankton, which together determine the

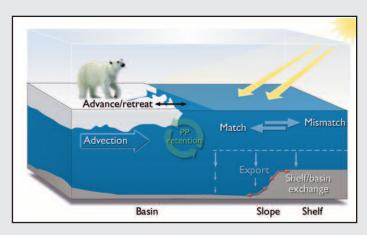
degree of match or mismatch between primary and secondary production. The projected disappearance of seasonal sea ice from the Barents and Bering Seas (and thus elimination of ice-edge blooms) implies that these areas would have blooms resembling those of more southerly seas. The timing of these open ocean blooms in the Barents and Bering Seas will then be determined by the onset of seasonal stratification, again with consequences for a match/mismatch in timing with zooplankton.

Removal of light limitation in areas presently covered by multi-year sea ice is likely to result in a two- to fivefold increase in primary production, provided wind mixing is sufficient to ensure adequate nutrient supply. Moreover, earlier melting in the seasonal sea-ice zone is likely to enhance annual primary production by extending the growing season. The actual outcome in terms of annual production, however, is highly dependent upon regional and local changes in upwelling, wind-driven vertical mixing, and freshwater supply from sea ice and rivers. Note, for example, that it takes only a small increase in salt stratification (i.e., a decrease in surface salinity) to offset the effect of increased winds on vertical mixing. Regional cooling, as projected by some of the ACIA-designated models, would result in the opposite effects to those of the warming scenarios described in the rest of this section.

The disappearance of sea ice from the Barents Sea is likely to result in a more than doubling of the present levels of primary production, especially in the northernmost part. This is a consequence of a deeper wind-mixed layer and an increased vertical supply of nutrients from the underlying Atlantic water. Predicting changes in the timing of the spring bloom requires a better understanding of, and capability of modeling, the combined effects of

Box 9.10. Effects of a variable ice edge on key biological processes affecting carbon flux on an arctic shelf

Primary production (PP) occurs in the euphotic zone when light and nutrient conditions allow. This primary production may be retained by recycling within the euphotic zone or exported to deeper waters and be available for the benthos. The efficiency of retention is strongly determined by the occurrence of a match (where zoo-plankton are available to graze and recycle the primary production) or mismatch (where zooplankton are not present in sufficient numbers and primary production sinks out of the euphotic zone to be grazed by the ben-



thos). Zooplankton densities may be affected by advection in certain shelf locations such as the Barents and Chukchi Seas. Additional concerns involve sequestration of carbon in shelf, slope, and basin sediments, and exchange processes that act to move carbon from one regime to another (red arrows). The location of the ice edge, where much primary production occurs, relative to topography (e.g., the shelf break and slope) strongly impact upon all of these processes. Under climate change scenarios, the ice edge will retreat further and faster into the basin, thus increasing the export of PP first to the slope and then to the abyssal ocean (E.C. Carmack, pers. comm. 2004).

ice-edge retreat and stability in the position of the Polar Front. To the south of the Polar Front, the absence of sea ice will reduce stratification thereby delaying the spring bloom until the onset of thermal stratification and the development of the seasonal surface mixed layer. North of the Polar Front, however, the timing of the spring bloom is strictly tied to light availability. At present, the spring bloom in the northern Barents Sea must await the retreat of the marginal ice zone for adequate light levels. In the absence of sea ice, the spring bloom is likely to occur earlier, and is very likely to occur earlier than in the region to the south of the Polar Front.

Primary production on the Bering Shelf is also likely to be enhanced if it becomes permanently ice-free, primarily due to an extended growing season and continuous upwelling of nutrient-rich water along the highly productive zone associated with the Bering Shelf break. More intense wind and more arid conditions at and near the Gobi and Takla Makan deserts in northeast Asia will possibly lessen the impact of iron control in the Northeast Pacific and the eastern Bering Sea.

In the shelf seas of the Arctic Ocean (e.g., the Kara, Laptev, East Siberian, and Beaufort Seas), a significant increase in nutrient supply is very likely to happen when the edge of the permanent ice pack retreats beyond the shelf break. This is very likely to trigger the onset of shelf-break upwelling and the delivery of nutrient-rich offshore waters to shallow shelf regions, perhaps more than doubling present levels of productivity.

In the central Arctic Ocean, two additional conditions of sea-ice retreat are important to primary production: the disappearance of sea-ice cover in summer and the regional appearance of open water areas in winter (e.g., north of Svalbard and northeast of the Chukchi Sea). In open water areas during summer, productivity is likely to increase due to increased wind mixing and nutrient re-supply. Within areas regionally open in winter, additional nutrients are likely to be supplied through the combined effects of wind stress and convective mixed layer deepening. It is possible that these two types of area will be as productive as is currently the case in their southern counterparts (the Greenland and deep Bering Seas, respectively). Before the development of these two distinctive conditions, areal primary production is likely to increase as the number and size of leads in the multi-year ice increase.

Surface mixed-layer depth is likely to have a strong impact on phytoplankton community structure, particularly in the Nordic Seas. Regions where the seabed or the depth of mixing (due to ice melt or river inflow) is less than about 40 m are likely to favor diatom blooms. Deeper mixing, to about 80 m, is likely to favor *Phaeocystis*. Thus, unless there is an increase in freshwater input, stronger winds are likely to result in *Phaeocystis* becoming more common than at present. This is possible in Atlantic water to the south of the Polar Front. If the surface mixed layer in the Atlantic water extends beyond

about 80 m, it is possible that a low-productive community dominated by nanoflagellates would be favored, as currently occurs in the off-shelf parts of the Southern Ocean (Hewes et al., 1990). This implies little transfer of carbon to herbivores and sediments because the grazers would be largely ciliates (Sakshaug and Walsh, 2000).

9.3.4.2. Zooplankton production

Any northward extension of warm water inflows is likely to carry with it temperate zooplankton, for instance into the Siberian Shelf Seas and the Bering Shelf (Brodeur and Ware, 1992; Overland et al., 1994; Skjoldal et al., 1987). Such inflows are likely to include gelatinous plankton in summer and autumn (Brodeur et al., 2002). Ice fauna such as the large amphipods will suffer massive loss of habitat if multi-year ice disappears. The possibility of increased transport of cold water on the western side of the North Atlantic could bring cold-loving zooplankton species farther south. Correspondingly, the southern limit of distribution of northern species may shift northward on the eastern side of the North Atlantic and southward on the western side, as indicated by zooplankton studies over the last 40 years (Beaugrand et al., 2002).

If the Siberian Shelf Seas become warmer in the future, it is possible that *Calanus finmarchicus* will thrive and multiply throughout the area as a whole, rather than being restricted to the Siberian Shelf water as currently occurs. There is, however, risk of a mismatch with phytoplankton blooms in that earlier melting will cause earlier stratification and, thus, an earlier bloom. However, if sea ice is absent during summer and autumn, there will be deeper vertical mixing, making the system more like that of the southern Barents Sea, with later blooms, albeit dependent on stratification caused by freshwater inputs from rivers. If water temperatures in the Siberian Shelf Seas stay lower than presently occur in the southern Barents Sea, the development of *C. finmarchicus* is likely to be retarded.

Grazing versus sedimentation

If a mismatch occurs in the timing of phytoplankton and zooplankton production due to early phytoplankton blooms, the food web will be highly inefficient in terms of food supply to fish and export production (Hansen et al., 1996). Export production and protozoan biomass are likely to increase.

A match with phytoplankton blooms can be achieved by arctic copepods, such as *C. glacialis*, which can adjust its egg production to the development of the phytoplankton bloom whether early or late in the season. This may also pertain to other important copepods in arctic waters. If so, actively grazing zooplankton "for all seasons" are very likely to exist for any realistic climate change and thus future ratios of grazed to exported phytoplankton biomass in the Arctic Ocean are unlikely to be much different to those at present.

Fish versus zooplankton

The crucial issue concerning the effects of climate change on zooplankton production is likely to be related to the match versus mismatch between herbivorous zooplankton and fish. The extent to which commercially valuable fish will migrate northward and the extent to which they will be able to utilize early developing populations of *C. glacialis* along the Siberian Shelf are unknown. A worst-case scenario would be a mismatch resulting in starving and, ultimately, dying fish in a summer ecosystem characterized by protozoans and unsuccessful, inflexible copepods such as *C. finmarchicus*.

9.3.4.3. Benthos

Future fluctuations in zoobenthic communities are very likely to be related to the temperature tolerance of the animals and to future water temperatures. While the majority of boreal forms have planktonic larvae that require a fairly long period to develop to maturity, arctic species do not (Thorson, 1950). Thus, boreal species should be quick to spread in warm currents in periods of warming, while the more stenothermal arctic species (i.e., those able to live within a narrow temperature range only) will perish quickly. In periods of cooling, the arctic species, with their absence of pelagic stages are very likely to slowly follow the warmer waters as they recede. Boreal species that can survive in near-freezing water could remain within the cooler areas.

From the prevailing direction of warm currents in the Barents Sea, shifts in the geographical distribution of the fauna should be quicker and more noticeable during periods of warming than periods of cooling. Any change in the abundance or biomass of benthic communities is most likely to result from the impact of temperature on the life cycle and growth rate of the various species. If warming occurs within the Barents Sea over the next hundred years, thermophilic species (i.e., those capable of living within a wide temperature range) will become more frequent. This is likely to force changes in the zoobenthic community structure and, to a lesser extent, in its functional characteristics, especially in coastal areas.

The highly productive region to the north of the Bering Strait is likely to undergo changing hydrographic conditions, which in turn are likely to result in changes to the dominant species (Grebmeier, 1993; Grebmeier et al., 1995). The hydrography of the St. Lawrence Island polynya region and the Anadyr region is ultimately related to the northward transport of water through the Bering Strait. Because the latter is related to variations in the AO, the future of the northern Bering Shelf is very likely to be closely related to variations in these oscillations (Walsh J.J. et al., 1989). If AO⁺ conditions predominate in the future, it is likely that the flow of Bering Water into the Arctic Ocean will be small, resulting in a reduction in northward transport of water south of St Lawrence Island.

Because the Gulf of Anadyr "cold pool" is maintained by sea-ice production/brine formation in the St Lawrence Island polynya, an enhanced and more energetic polynya resulting from warming is likely to maintain a chemostattype bloom system (Walsh J.J. et al., 1989), allowing a longer growing season and higher levels of production.

9.3.4.4. Fish production

Understanding how climate variability affects individual fish populations and fisheries and how the effects differ between species is extremely important when projecting the potential impacts of climate change. Projections of the response of local marine organisms to climate change scenarios have a high level of uncertainty. However, by using observations of changes in fish populations due to past climate variability it is possible to predict some general responses.

Climate change can affect fish production through a variety of means. Direct effects of temperature on the metabolism, growth, and distribution of fish could occur. Food web effects could also occur, through changes in lower trophic level production or in the abundance of top-level predators, but such effects are difficult to predict. However, it is expected that generalist predators are more adaptable to change than specialists. Fish recruitment patterns are strongly influenced by oceanographic processes such as local wind patterns and mixing and by prey availability during early life stages, which are also difficult to predict. Recruitment success could be affected by changes in the time of spawning, fecundity rates, survival rate of larvae, and food availability.

General trends in distribution and production

Poleward extensions of the distribution range for many fish species are very likely under the projected climate change scenarios (see Fig. 9.30 and Box 9.11). Some of the more abundant fish species that would be very likely to move northward under the projected warming include Atlantic and Pacific herring and cod, walleye pollock in the Bering Sea, and some of the flatfishes that might presently be limited by bottom temperatures in the northern areas of the marginal arctic seas. The southern limit of colder-water fishes such as polar cod and capelin would be very likely to move northward. The Greenland halibut is also likely either to shift its southern boundary northward or restrict its distribution more to continental slope regions. Salmon, which show high fidelity of return to natal streams, might possibly be affected in unknown ways that relate more to conditions in natal streams, early marine life, or feeding areas that might be outside the Arctic.

Fish production patterns are also very likely to be affected, although there are large uncertainties regarding the timing and location of zooplankton and benthic production that serve as prey resources for fish growth, and the wind advection patterns and direction that favor

Box 9.11. Climate impact on the distribution of fish in the Norwegian and Barents Seas

An increase in water temperature of I to 2 °C in the Atlantic part of the Norwegian and Barents Sea is very likely to result in a change in distribution for several species of fish. However, in both seas there are fronts between the warm Atlantic water and the cold arctic water masses, whose position is partly determined by bottom topography. How these fronts may move in future is addressed in section 9.2.5.4.

Previous experience of how fish react to changes in water temperature in the Barents Sea may be used to speculate about future changes. The most likely impact of an increase in water temperature on some commercial fish species in shown in Fig. 9.30. Capelin is very likely to extend its feeding area north and northeastward. During summer it might feed in the Arctic Basin and migrate to the Kara Sea. Whether the capelin maintain their spawning ground along the coast of northern Norway and the Kola Peninsula is unknown. They may possibly move eastward, and may even spawn along the west coast of Novaya Zemlya. Cod is also likely to expand its feeding area eastward, especially as capelin is its main food source. As cod is demersal (i.e., a near-bottom fish), it is not likely to migrate north of the Barents Sea and into the deep Arctic Basin. Haddock will probably follow the same track as cod, but as at present is likely to remain further south than cod.

In the Norwegian Sea, herring is likely to return to the feeding and overwintering area used before 1964 (see Box 9.8), but is likely to maintain the same spawning areas along the Norwegian coast. Mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*) are likely to migrate northeast to the Barents Sea. The mackerel and blue whiting will then compete with the other pelagic species in the Barents Sea for a limited supply of food. It is also likely that new species may enter the Norwegian Sea.

survival of some fish species relative to others. This is an active area of research, presently being addressed by GLOBEC (Global Ocean Ecosystem Dynamics) research programs around the world. Given historical recruitment patterns, it seems likely that herring, cod, and walleye pollock recruitment would be increased under future climate warming scenarios. Benthic-feeding flatfish, such as rock sole in the eastern Bering Sea, would be likely to have higher average recruitment in a warmer Bering Sea. Greenland halibut, capelin, and polar cod would be likely to decline in abundance. The

Herring

Mackerel

Mackerel,
Bluefin Tuna

North Sea

Herring

Anchoyy, Sardine

Fig. 9.30. Likely extension of the feeding area for some of the main fish populations if sea temperature increases. For herring, see also Box 9.8 (modified after Blindheim et al., 2001).

greatest variability in recruitment would occur for all species at the extremes of their ranges.

Migration patterns are very likely to shift, causing changes in arrival times along the migration route. The timing of the spring migration of cod into the Gulf of St. Lawrence appears to be related to the timing of ice melt. In winter, cod appear to congregate at the edge of the sea ice but do not pass beneath it (Fréchet, 1990). The spring migration appeared to be delayed by as much as 20 days in 1992, when ice melt was particularly late in the southern region of the Gulf. Change in sea ice distribution is one of the expected effects of climate change that is likely to have pronounced impacts on many fish species. Growth rates are very likely to vary, with the amplitude and direction being species dependent. While cod growth rates in the southern areas of the Arctic are very likely to increase with a rise in water temperature (Brander, 1995; Michalsen et al., 1998), this may not be the case for Arctic Ocean species.

Qualitative predictions of the consequences of climate change on fish resources require good regional atmospheric and oceanic models of the response of the ocean to climate change. Dynamically or statistically downscaled output from global circulation models, which are only recently becoming available, could be very useful. Greater understanding is needed concerning the life histories for those species for which predictions are required, and concerning the role of the environment, species interactions, and fishing in determining the variability of growth, reproduction, distribution, and abundance of fish populations. The multi-forcing and numerous past examples of "failed" predictions of environment—fish relationships indicate the difficulties faced by fisheries scientists in providing reliable predictions of the response to climate change.

9.3.4.5. Marine mammals and seabirds

The impacts of climate change scenarios on marine mammals and seabirds in the Arctic are likely to be profound, but the precise form these impacts will take is not easy to determine (Jarvis, 1993; Shugart, 1990). Patterns of change are non-uniform (Parkinson, 1992) and highly complex. Oscillations occurring at a variety of scales (e.g., Mysak et al., 1990) complicate regional predictions of long-term trends. Also, species responses will vary dramatically (e.g., Kitaysky and Golubova, 2000). Mesoscale environmental features, e.g., frontal zones and eddies, that are associated with enhanced productivity are important to apex predators, but future changes in these features are not represented well at the present spatial resolution of circulation models (Tynan and DeMaster, 1997). Regional, small-scale coupled air—sea—ice models are needed in order to make reliable projections of change in mesoscale environmental features.

Given the most likely scenarios for changes in oceanographic conditions within the ACIA region by 2020 (Table 9.4), changes in seabird and marine mammal communities are very likely to be within the range(s) observed over the last 100 years. If, however, the increase in water temperature and the sea-ice retreat continue as projected until 2050 and 2080, marine ecosystems will change in ways not seen in recent history. One of the first changes expected is a poleward shift in species (and broader assemblages). However, there is a limit to how far north arctic species can shift following the sea ice. Once seasonal sea-ice cover retreats beyond the shelf regions, the oceanographic conditions will change dramatically and become unsuitable for many species. If the loss of sea ice is as dramatic temporally and spatially as has been projected by the ACIAdesignated models, negative consequences are very likely within the next few decades for arctic animals that depend on sea ice for breeding or foraging (Brown, 1991; Burns, 2001; Stirling and Derocher, 1993; Tynan and DeMaster, 1997). The worst-case scenarios in terms of reduced sea-ice extent, duration, thickness, and concentration by 2080 are very likely to threaten the existence of whole populations and, depending on their ability to adapt to change, are very likely to result in the extinction of some species. Prospects for long-term abundance projections for populations of large marine predators are not good (e.g., Jenkins, 2003).

Climate change also poses risks to marine mammals and seabirds in the Arctic in terms of increased risk of disease for arctic-adapted vertebrates owing to improved growing conditions for the disease vectors and from introductions via contact with non-indigenous species (Harvell et al., 1999); increased pollution loads via increased precipitation bringing more river borne pollution northward (Macdonald et al., 2003b); increased competition from northward temperate species expansion; and impacts via increased human traffic and development in previously inaccessible, ice-covered areas. Alterations to the density, distribution, or abundance of

keystone species at various trophic levels, such as polar bears and polar cod, are very likely to have significant and rapid effects on the structure of the ecosystems they currently occupy.

Although many climate change scenarios focus on negative consequences for ecosystems, climate change will provide opportunities for some species. The ability to adapt to new climate regimes is often vast, and this potential should not be underestimated; many higher marine vertebrates in the Arctic are adapted to dealing with patchy food resources and high variability in the abundance of food resources.

Marine mammals

Changes in the extent and type of sea ice will affect the distribution and foraging success of polar bears. The earliest impact of warming had been considered most likely to occur at the southern limits of their distribution, such as James and Hudson Bays (Stirling and Derocher, 1993), and this has now been documented (Stirling et al., 1999). Late sea-ice formation and early breakup means a longer period of annual fasting for polar bears. Reproductive success is strongly linked to their fat stores; females in poor condition have smaller litters and smaller cubs, which are less likely to survive, than females in good condition. There are also concerns that direct mortality rates are likely to increase with the climate change scenarios projected by the ACIA-designated models. For example, increased frequency or intensity of spring rain could cause dens to collapse resulting in the death of the female as well as the cubs. Earlier spring breakup of ice could separate traditional den sites from spring feeding areas, and young cubs forced to swim long distances from breeding areas to feeding areas would probably have a lower survival rate. It is difficult to envisage the survival of polar bears as a species given a zero summer sea-ice scenario. Their only option would be a terrestrial summer lifestyle similar to that of brown bears, from which they evolved. In such a case, competition, risk of hybridization with brown bears and grizzly bears, and increased interactions with people would then number among the threats to polar bears.

Ice-living seals are particularly vulnerable to the changes in the extent and character of arctic sea ice projected by the ACIA-designated models because they depend on the sea ice as a pupping, molting, and resting platform, and some species forage on many iceassociated prey species (DeMaster and Davis, 1995). Of the high arctic pinnipeds ringed seals are likely to be most affected because many aspects of their life history and distribution are linked to sea ice (Finley et al., 1983; Smith T. et al., 1991; Wiig et al., 1999). They are the only arctic seal species that can create and maintain holes in thick sea ice and hence their distribution extends further north than that of all other pinnipeds. Ringed seals require sufficient snow cover to construct their lairs and the sea ice must be sufficiently stable in spring to rear young successfully (Fig. 9.31) (Lydersen



Fig. 9.31. A ringed seal pup outfitted with a radio-transmitter that was deployed as part of a haul-out behavior study in Svalbard, spring 2003 (photo by Kit Kovacs & Christian Lydersen, Norwegian Polar Institute).

and Kovacs, 1999). Premature breakup of the sea ice could result in premature separation of mother—pup pairs and hence high neonatal mortality. Ringed seals do not normally haul out on land and to do this would represent a dramatic change in behavior. Land breeding would expose the pups to much higher predation rates, even in a best-case scenario.

Bearded seals use regions of thin, broken sea ice over shallow areas with appropriate benthic prey communities (Burns J., 1981a). Their distribution, density, and reproductive success are dependent on the maintenance of suitable sea-ice conditions in these shallow, often coastal, areas. Walruses, another predominantly benthic feeder, also have quite specific sea-ice requirements. They overwinter in areas of pack ice where the ice is sufficiently thin that they can break through and maintain breathing holes (Stirling et al., 1981), but is sufficiently thick to support the weight of groups of these highly gregarious animals. Ice retreat may result in much of the remaining arctic sea ice being located over water that is too deep for these benthic foragers. Also, there is a more general concern that the likely decline in the community of plants, invertebrates, and fishes that live in close association with the underside of sea ice are very likely to result in a dramatic decrease in the flux of carbon to the benthic community, upon which bearded seals, walruses, and other animals such as grey whales depend (Tynan and DeMaster, 1997).

Harp seals are flexible about the nature of their summer sea-ice habitat, but during breeding travel to traditional sites in southern waters where they form large herds on extensive areas of pack ice. Massive pup mortality occurs during poor ice years. Hooded seals also breed in traditional areas, but select thicker sea ice than harp seals, and prefer areas where individual floes are large. Females move away from ice edges, presumably to reduce harassment from males (Kovacs, 1990). Pup mortality is also high for hooded seals during poor ice years. The situation which occurred during three years

in the last two decades when ice did not form in the Canadian Gulf of St. Lawrence breeding area implies severe consequences for harp and hooded seals if spring sea-ice conditions continue to follow current and projected trends. The range and relative abundance of these species is linked to sea-ice cover and climatic conditions (Vibe, 1967) and it is not known whether natal site fidelity is maintained for life, regardless of reproductive outcome. Thus, it is difficult to predict whether harp and hooded seals will adjust the location of their breeding and molting activities if spring sea-ice distribution changes dramatically over a relatively short period.

Spotted seals require sea ice over waters of specific depth and so, like bearded seals in the Atlantic, are very likely to be strongly affected by reduced sea-ice extent. The ecological requirements of ribbon seals are so poorly known that the effects of changes in sea-ice conditions are impossible to predict. Their flexibility in shifting from traditional breeding and foraging sites is unknown. Poor seasonal sea-ice conditions will result in a decimation of year-classes in the short term, but in the longer term, herds may form at more northerly sites that meet their needs. Those species that haul out on land when sea ice is not available, such as walrus and spotted seal, may be less affected by changes in sea-ice conditions than the other ice-associated seals.

In contrast, harbour seals and grey seals are likely to expand their distribution in an Arctic with less sea ice. They are for the most part temperate species that have a broad enough niche that they can occupy warm spots in the current Arctic. Other pinnipeds that breed on land in the Arctic are otariid seals. These are likely to be profoundly affected by changes in their food base, as is thought to be happening in the present regime shift in the North Pacific. They could also be affected by heat stress, but Steller sea lions have a present distribution that includes the Californian coast, implying a considerable tolerance for warm conditions given access to the ocean. Sea otters, like Steller sea lion, have a broad distribution at present and are likely to be most affected by changes at lower trophic levels which affect their food availability.

The impact of climate-induced perturbations on cetaceans is less certain than for ice-breeding pinnipeds and polar bears (Tynan and DeMaster, 1997), although Burns (2001) suggests grave implications for cetaceans in the Arctic. The uncertainty arises because the link between arctic cetaceans and sea ice is largely via prey availability rather than the sea ice itself (Moore, 2000; Moore et al., 2000). All the northern whales exhibit habitat selection, with sea-ice cover, depth, bathymetric structure, for example, of varying importance (Moore, 2000; Moore et al., 2000). Bowhead whales, beluga whales (Delphinapterus leucas), narwhals, and minke whales can all break young sea ice with their backs in order to breathe in ice-covered areas, but their distribution is generally restricted to areas containing leads or polynyas and open-water areas at the periphery of the pack-ice zone. Bowhead whales are considered the most

ice-adapted cetacean. They feed largely on high arctic copepods and euphausiids (Lowry, 1993), and the distribution of these prey species determines their movements and distribution. Bowhead whales have evolved as ice whales, with elevated rostrums (i.e., beaks) and blow holes that allow them to breathe more easily in sea ice; it is not known whether they could adjust to ice-free waters (Tynan and DeMaster, 1997). Bowhead whales are presently an endangered species despite decades of protection from commercial hunting. They consume *Calanus* spp. and euphausiids and changes in sea-ice conditions are likely to have a major impact on their foraging (Finley, 2001).

Narwhal and beluga are known to forage at ice edges and cracks (Bradstreet, 1982; Crawford and Jorgenson, 1990), but are highly migratory and range well south of summer edges in the arctic pack ice (Rice, 1998), foraging along the fronts of glaciers (Lydersen et al., 2001) or even in areas of open water (Reeves, 1990). A small, threatened, population of belugas is resident in the Canadian Gulf of St. Lawrence, well south of the Arctic Circle, which has been affected by industrial pollution and habitat disturbance. Tynan and DeMaster (1997) predicted that arctic belugas might alter the timing and spatial patterns of seasonal migration given a retreat of the southern ice edge, particularly in the Canadian Archipelago. Vibe (1967) reported that the historical beluga distributions are linked to sea ice, wind, and current conditions along the Greenland coast (see section 9.3.3.4). The changes projected for arctic sea ice over the coming decades may promote genetic exchange between populations that are currently isolated due to the barrier formed by the southern ice edge. Narwhal utilize coastal habitats in summer, but in winter move offshore to deepwater areas with complex bathymetry. These areas are completely ice-covered except for shifting leads and cracks. Narwhal are thought to feed on cephalopods at this time (Dietz et al., 2001), thus the effects of climate change on narwhal are likely to be via sea-ice distribution patterns and effects on key prey species.

All other cetacean species that frequent the Arctic avoid ice-covered areas. Their distributions are predominantly determined by prey availability (Ridgway and Harrison, 1981-1999) and so the impact of climate change will occur indirectly via changes to their potential prey base. Grey whales are unusual in that they are benthic feeders, and so are very likely to be affected by climate change in ways more similar to walruses and bearded seals than other cetaceans.

Seabirds

The effects of climate change on seabird populations, both direct and indirect through effects on the oceans, are likely to be detected first near the limits of the species range and near the margins of their oceanographic range (Barrett and Krasnov, 1996; Montevecchi and Myers, 1997). Brown (1991) suggests that the southern limits for many arctic seabird species will move north-

ward, as will their breeding ranges. Changes in patterns of distribution, breeding phenology, and periods of residency in the Arctic are likely to be some of the first responses to climate change observed in arctic seabird populations. This is partly because these are more easily detected than subtle or complex changes such as changes in population size and ecosystem function (Furness et al., 1993; Montevecchi, 1993). Because arctic seabirds are long-lived, have generally low fertility, and live in a highly variable environment, effects of climate change on population size, even if quite significant, may take several years to show (Thompson and Ollason, 2001).

Seabirds are likely to be influenced most by indirect changes in prey availability (Brown, 1991; IPCC, 1998; Schreiber E., 2001). Seabirds respond to anything that affects food availability and so are often good indicators of a system's productivity (Bailey et al., 1991; Hunt et al., 1991; Montevecchi, 1993). Several studies have shown that climate-induced changes in oceanographic conditions can have large-scale and pervasive effects on vertebrate trophic interactions, affecting seabird population size and reproductive success (Duffy, 1990; Montevecchi and Myers, 1997; Schreiber R. and Schreiber, 1984). Species with narrow food or habitat requirements are likely to be the most sensitive (Jarvis, 1993; Vader et al., 1990). As warmer (or colder) water would affect the distribution of prey, the distribution of individual seabird species is likely to change in accordance with changes in the distribution of macrozooplankton and fish populations. Brown (1991) suggests that improved foraging conditions will result in range expansions northward for many species. This is because the retreating pack ice will open up more feeding areas in spring and will provide phytoplankton with earlier exposure to daylight, thereby increasing productivity throughout the Arctic. However, from analyses of probable changes in food availability in subantarctic waters, Croxall (1992) concluded that it was not possible to be certain whether a change in the amount of sea ice would mean more or less prey for seabirds. Many of these uncertainties are also relevant to arctic areas.

Changes in water temperature are very likely to have significant consequences for pelagic fish species (see section 9.3.4.4 and Chapter 13). Most fish species are sensitive to changes in water temperature (e.g., Gjøsæter, 1998), and only slight changes in the thermal regime can induce changes in their temporal and spatial (both vertical and horizontal) distributions (Blindheim et al., 2001; Loeng, 2001; Methven and Piatt, 1991; Shackell et al., 1994). For example, increases in air temperature will probably lead to a greater inflow of warm Atlantic water into the Barents Sea, caused by complex interactions between different water masses, ocean currents, and wind systems in the north Atlantic. This inflow is very likely to displace the Polar Front north- and eastward, especially in the eastern Barents Sea. The ice edge would then be located further north in winter, with a consequent reduction in the phytoplankton bloom which normally follows the receding ice edge during

spring and summer. It is likely that the distribution of the Barents Sea capelin would be displaced northeastward, from the central to the northeastern Barents Sea. Important life-cycle changes are likely to include changes in the timing of spawning, with a consequent shift in the timing of migration and a displacement of migration routes (Loeng, 2001). Such changes to capelin alone could have profound consequences for many arctic seabirds in the Barents Sea.

Extreme changes in the spatial and temporal availability of food can have dramatic effects on the survival of adult seabirds (Baduini et al., 2001; Piatt and van Pelt, 1997). However, seabirds are able to travel great distances and so are insulated to some extent from environmental variability. They are able to exploit locally and ephemerally favorable conditions during much of the year quite freely. However, during the breeding season when they are constrained to return to a land-based breeding site but are dependant on marine resources for foraging, less extreme reductions in prey availability can affect reproductive success. Most Northern Hemisphere seabirds forage within 200 km of their colonies (Hunt et al., 1999). Because seabirds generally lay only one egg they cannot alter clutch size to compensate for low food availability in a given season. Instead, they reduce the extent of their parental care contribution when resources are in short supply in order to protect their own long-term survival (Øyan and Anker-Nilssen, 1996; Weimerskirch, 2001). Because they are long-lived, have delayed sexual maturity, and have conservative reproductive output, even dramatic reductions in fledgling survival may not be apparent in terms of overall population size for several years.

If climate change induces long-term shifts in the spatial distribution of macrozooplankton (predominantly crustaceans) and small schooling pelagic fish, seabird breeding distribution patterns are likely to alter. These prey species are usually concentrated in frontal or upwelling areas, which provide a spatially and temporally predictable food supply for seabirds (Hunt, 1990; Hunt et al., 1999; Mehlum et al., 1998a,b; Schneider, 1990; Watanuki et al., 2001). If changing environmental conditions cause these oceanographic features to relocate, then prey distributions are very likely to change. If new breeding sites become available in close proximity to the new feeding areas, little change is likely. However, if suitable breeding areas are not available near the relocated fronts or upwelling, the seabirds may not be able to take advantage of available food at its new location during the reproductive season, resulting in reproductive failure. The impacts of future climate change on seabirds are likely to be extremely variable in a spatial context.

Temporal changes in prey availability can also change the timing of breeding in seabirds (Schreiber E., 2001), and potentially result in a mismatch between the timing of reproduction and the time of food abundance (Visser et al., 1998). Such a mismatch may have profound impacts on reproductive success (Brinkhof et al., 1997). The timing of breeding is especially critical for birds breeding in

arctic areas; low temperatures and a restricted period of prey availability create a narrow temporal window in which the nesting period sits (Hamer et al., 2001).

The ivory gull is an exception to many of these general patterns. This species is closely associated with sea ice throughout most of its life cycle. Changes in sea-ice extent and concomitant changes in the distribution of ice-associated seals and polar bears are very likely to result in changes in ivory gull distribution and potentially negative effects on abundance. There is concern that major reductions in ivory gull populations have already occurred (Krajick, 2001; Mallory et al., 2003). There is also concern that little auks, specialist feeders on arctic copepods during the summer, would be negatively affected by the changes predicted in the "Calanus complex" in the Barents Sea and other parts of the North Atlantic.

Changes in sea level may restrict breeding at existing sites, but may increase the suitability of other sites that are not currently usable owing to, for example, predator access.

Direct evidence of negative effects of environmental conditions (weather) for seabirds is rare, although wind is thought to be important for foraging energetics. Healthy arctic seabirds have little difficulty coping with extreme cold; they are insulated by feathers and subcutaneous fat. However, owing to these adaptations they may have difficulty keeping cool. Warmer temperatures in the Arctic are very likely therefore to set southern limits to seabird distributions that are unrelated to the availability of prey or breeding sites (Brown, 1991). Extreme weather can result in direct mortality of chicks or even adults, but it is most likely that the greatest effect of inclement weather would be to restrict the opportunity for seabirds to forage (Harris and Wanless, 1984). Heavy rain could flood the nests of burrowing species such as little auks or puffins (Rodway et al., 1998; Schreiber E., 2001) and freezing rain could affect the thermal balance of exposed chicks leading to mortality (Burger and Gochfeld, 1990). Changes to the normal patterns of wind speed and direction could alter the cost of flight, particularly during migration (Furness and Bryant, 1996; Gabrielsen et al., 1987), but it is the nature and extent of the change that determine whether the consequences are negative (or positive) for individual seabird species.

9.4. Effects of changes in ultraviolet radiation

This section assesses the potential impacts of ozone depletion-related increases in solar ultraviolet-B radiation (280–315 nm = UV-B) on arctic marine ecosystems. For a comprehensive review of the extensive and rapidly growing technical literature on this subject, readers are referred to several recent books (DeMora et al., 2000; Häder, 1997; Helbling and Zagarese, 2003), and particularly to Hessen (2001) with its focus on the Arctic. UV-B optics in marine waters and ozone layer depletion and solar ultraviolet radiation are described in Chapter 5.

The exponential relationship between the capacity of ozone to filter ultraviolet light – lower wavelengths are much more strongly filtered – means that small reductions in stratospheric ozone levels result in large increases in UV-B radiation at the earth's surface (e.g., Kerr and McElroy, 1993; Madronich et al., 1995). Since ozone layer depletion is expected to continue for many more years, albeit at a slower rate (Shindell et al., 1998; Staehelin et al., 2001; Taalas et al., 2000), the possible impacts of solar UV-B radiation on marine organisms and ecosystems are currently being investigated (Browman, 2003; Browman et al., 2000; De Mora et al., 2000; Häder, 1997; Häder et al., 2003; Helbling and Zagarese, 2003; Hessen, 2001). A growing number of studies have found that current levels of UV-B radiation are harmful to aquatic organisms and may, in some extreme instances, reduce the productivity of marine ecosystems (De Mora et al., 2000; Häder, 1997; Häder et al., 2003; Helbling and Zagarese, 2003; Hessen, 2001). Reductions in productivity induced by UV-B radiation have been reported for phytoplankton, heterotrophic organisms, and zooplankton; the key intermediary levels of marine food chains (De Mora et al., 2000; Häder, 1997; Häder et al., 2003; Helbling and Zagarese, 2003; Hessen, 2001). Similar studies on planktonic fish eggs and larvae indicated that exposure to levels of UV-B radiation currently incident at the earth's surface results in higher mortality and may lead to reduced recruitment success (Hunter et al., 1981, 1982; Lesser et al., 2001; Pommeranz, 1974; Walters C. and Ward, 1998; Williamson et al., 1997; Zagarese and Williamson, 2000, 2001).

Ultraviolet radiation also appears to affect biogeochemical cycling within the marine environment and in a manner that could affect overall ecosystem productivity and dynamics (Zepp et al., 2003).

9.4.1. Direct effects on marine organisms

The majority of UV-B radiation research examines direct effects on specific organisms. Some marine copepods are negatively affected by current levels of UV-B radiation (Häder et al., 2003). UV-B-induced mortality in the early life stages, reduced survival and fecundity in females, and changes in sex ratios have all been reported (Chalker-Scott, 1995; Karanas et al., 1979, 1981; Lacuna and Uye, 2001; Naganuma et al., 1997; Tartarotti et al., 2000). UV-B-induced damage to the DNA of crustacean zooplankton has also been detected in samples collected up to 20 m deep (Malloy et al., 1997). Eggs of Calanus finmarchicus — a prominent member of the mesozooplankton community throughout the North Atlantic - incubated under UV-B radiation exhibited a lower percentage hatch rate than those protected from UV-B radiation (Alonso Rodriguez et al., 2000). This indicates that Calanus finmarchicus may be sensitive to variation in incident UV-B radiation. Results for the few other species that have been studied are highly variable with some showing strong negative impacts, while others are resistant (Damkaer, 1982; Dey et al., 1988;

Thomson, 1986; Zagarese and Williamson, 2000). The factors determining this susceptibility are many and complex, but include seasonality and location of spawning, vertical distribution, presence of UV-B-screening compounds, and the ability to repair UV-B-induced damage to tissues and DNA (Williamson et al., 2001).

The work of Marinaro and Bernard (1966), Pommeranz (1974), and Hunter et al. (1979, 1981, 1982) provided clear evidence of the detrimental effect of UV-B radiation on the planktonic early life stages of marine fish. Hunter et al. (1979), working with northern anchovy (Engraulis mordax) and Pacific mackerel (Scomber japonicus) embryos and larvae, reported that exposure to surface levels of UV-B radiation could be lethal. Significant sub-lethal effects were also reported: lesions in the brain and retina, and reduced growth rate. The study concluded that, under some conditions, 13% of the annual production of northern anchovy larvae could be lost as a result of UV-B-related mortality (Hunter et al., 1981, 1982). Atlantic cod eggs were negatively affected by exposure to UV-B radiation in very shallow water; 50 cm deep or less (Béland et al., 1999; Browman and Vetter, 2001). With the exception of a small (but rapidly growing) number of recent studies, little additional information is available on the effects of UV-B radiation on the early life stages of fish. However, as for copepods, the early life stages of fish will vary in their susceptibility to UV-B radiation and for the same reasons. Thus, some studies conclude that the effects of UV-B radiation will be significant (e.g., Battini et al., 2000; Lesser et al., 2001; Williamson et al., 1997), while others conclude that they will not (e.g., Dethlefsen et al., 2001; Kuhn et al., 2000; Steeger et al., 2001).

9.4.2. Indirect effects on marine organisms

Exposure to UV radiation, especially UV-B radiation, has many harmful effects on health. These may result in poorer performance, or even death, despite not being directly induced by exposure to UV-B radiation. UV-B radiation suppresses systemic and local immune responses to a variety of antigens, including microorganisms (Garssen et al., 1998; Hurks et al., 1994). In addition to suppressing T-cell-mediated immune reactions, UV-B radiation also affects nonspecific cellular immune defenses. Recent studies demonstrate disturbed immunological responses in UV-B-irradiated roach (Rutilus rutilus): the function of isolated head kidney neutrophils and macrophages (immuno-responsive cells) were significantly altered after a single dose of UV-B radiation (Salo et al., 1998). Natural cytotoxicity, assumed to be an important defense mechanism in viral, neoplastic, and parasitic diseases, was also reduced. A single dose of UV-B radiation exposure decreased the ability of fish lymphocytes to respond to activators, and this was still apparent 14 days later (Jokinen et al., 2001). This indicates altered regulation of lymphocyte-dependent immune functions. Finally, exposure to UV-B radiation induces a strong systemic stress response which is manifested in fish blood by an

increased number of circulating phagocytes and elevated plasma cortisol levels (Salo et al., 2000a). Exposure to UV-A (315-400 nm) radiation induced some of the same negative effects on the immune system (Salo et al., 2000b). Since high cortisol levels induce immunosuppression in fish (Bonga, 1997) the effect of exposure to UV-B radiation on the immune system clearly has both direct and indirect components. Taken together, these findings indicate that the immune system of fish is significantly affected by exposure to a single, moderatelevel dose of UV-B radiation. At the population level, a reduction in immune response might be manifested as lowered resistance to pathogens and increased susceptibility to disease. The ability of the fish immune system to accommodate increases in solar UV-B radiation is not known. Also, the immune system of young fish is likely to be highly vulnerable to UV-B radiation because lymphoid organs are rapidly developing and because critical phases of cell proliferation, differentiation, and maturation are occurring (Botham and Manning, 1981; Chilmonczyk, 1992; Grace and Manning, 1980). It is also possible that exposure to ambient UV-B radiation impedes the development of the thymus or other lymphoid organs resulting in compromised immune defense later in life. The effect of UV-B radiation on the immune function of fish embryos and larvae, and on the development of the immune system, is unknown.

Other indirect effects of UV-B radiation are also possible. For example, UV-B radiation may affect sperm quality for species that spawn in the surface layer (Don and Avtalion, 1993; Valcarcel et al., 1994) and so affect fertilization rate and/or genome transfer.

Studies on the impact of UV-B radiation have almost all examined the effects of short-term exposure on biological end-points such as skin injury (sunburn), DNA damage, development and growth rates, immune function, or outright mortality. Few have examined the potential effects of longer-term (low-level) exposure (but see Fidhiany and Winckler, 1999). All these indirect (and/or longer-term) effects of UV-B radiation have yet to be investigated.

9.4.3. Ecosystem effects

9.4.3.1. Food chains

Although the effects of UV-B radiation are strongly species-specific, marine bacterioplankton and phytoplankton can be negatively affected (De Mora et al., 2000; Hessen, 2001). Severe exposure to UV-B radiation can, therefore, decrease productivity at the base of marine food chains. The importance of this decrease is highly speculative, but decreases in carbon fixation of 20 to 30% have been proposed (Helbling and Villafañe, 2001). Arctic phytoplankton appear more susceptible than antarctic species, possibly owing to deeper surface mixed layers in the Arctic (Helbling and Villafañe, 2001). Also, if UV-B radiation reduces the productivity of protozoans and crustacean zooplankton there will be less prey available for fish larvae and other organisms that feed upon them.

The few studies that have investigated the indirect effects of UV-B radiation on specific organisms conclude that UV-B-induced changes in food-chain interactions can be far more significant than direct effects on individual organisms at any single trophic level (Bothwell et al., 1994; Hessen et al., 1997; Williamson et al., 1999). Recent investigations indicate the possibility of food-chain effects in both the marine and freshwater environment: exposure to UV-B radiation (even at low dose rates) reduces the total lipid content of some microalgae (Arts and Rai, 1997; Arts et al., 2000; Plante and Arts, 1998) and this includes the polyunsaturated fatty acids (PUFAs) (Goes et al., 1994; Hessen et al., 1997; Wang K. and Chai, 1994). For zooplankton and fish larvae, the only source of PUFAs is the diet - they cannot be synthesized and so must be obtained from prey organisms (Goulden and Place, 1990; Rainuzzo et al., 1997; Reitan et al., 1997; Sargent et al., 1997). Dietary deficiencies are manifested in many ways. For example, in the freshwater cladoceran Daphnia spp., growth rates are correlated with the concentration of eicosapentaenoic acid in the water column (De Lange and Van Donk, 1997; Müller-Navarra, 1995a,b; Scott C. et al., 1999). In Atlantic herring, dietary deficiencies of essential fatty acids, in particular docosahexaenoic acid, reduce the number of rods in the eyes (Bell M. and Dick, 1993) and negatively affect feeding at low light levels (Bell M. et al., 1995; Masuda et al., 1998). Other negative consequences of essential fatty acid deficits have also been reported (Bell J. et al., 1998; Kanazawa, 1997; Rainuzzo et al., 1997). A UV-B-induced reduction in the PUFA content of microalgae will be transferred to the herbivorous zooplankton that graze on them, thereby decreasing the availability of this essential fatty acid to fish larvae. Since fish larvae (and their prey) require these essential fatty acids for proper development and growth, a reduction in the nutritional quality of the food base has potentially widespread and significant implications for the overall productivity and health of aquatic ecosystems.

9.4.3.2. Quantitative assessments

Quantitative assessments of the effects of UV-B radiation on marine organisms at the population level are scarce. However, several studies are currently underway using mathematical simulation models. Neale et al. (1998, 2001) estimated that a 50% seasonal reduction in stratospheric ozone levels could reduce total levels of primary production – integrated throughout the water column – by up to 8.5%. Kuhn et al. (2000) developed a model that incorporates physical and biological information and were able to generate an absolute estimate of mortality under different meteorological and hydrographic conditions. As a result, they were able to evaluate the relative impacts of different combinations of environmental conditions – for example, a typical clear sky versus a typical overcast sky; a typical clear water column versus a typical opaque coastal water column; current ambient ozone levels versus a realistically

thinned ozone layer. For Calanus finmarchicus eggs in the estuary and Gulf of St. Lawrence, UV-B-induced mortality for all model scenarios ranged from <1% to 51%, with a mean of 10.05% and an uncertainty of $\pm 11.9\%$ (based on 1 standard deviation and 48 modeled scenarios). For Atlantic cod, none of the scenarios gave a UV-B-induced mortality greater than 1.2%, and the mean was $1.0\pm 0.63\%$ (72 modeled scenarios).

In both assessments (Kuhn et al., 2000; Neale et al., 1998, 2001), the most important determinant of UV-B-related effects was water column transparency (see Fig. 9.32): even when ozone layer depletions of 50% were modeled, the effect on mortality remained far lower than that resulting from either thick cloud cover or opacity of the water column. This demonstrates that variability in cloud cover, water quality, and vertical distribution and displacement within the surface mixed layer have a greater effect on the flux of UV-B radiation to which planktonic marine organisms are exposed than ozone layer depletion. In contrast, Huot et al. (2000) showed that ozone thickness could in some instances be the single most important determinant of DNA damage in bacterioplankton.

Since the concentrations of dissolved organic carbon (DOC) and Chl-a are strongly correlated with the transparency of the water column to UV-B radiation, it follows that their concentrations are an overriding factor affecting UV-B-induced mortality. The Kuhn et al. (2000) model supports this contention. DOC levels in eutrophic coastal zones are often greater than 3 to 4 mg/L; the diffuse attenuation coefficients for UV-B radiation at such levels essentially protect Calanus finmarchicus and cod eggs from UV-B-induced mortality (Fig. 9.33). Thus, DOC can be considered as a sunscreen for organisms inhabiting eutrophic coastal zone waters. DOC concentrations in arctic waters are typically <1 mg/L (Aas et al., 2001). At these levels, DOC is not as effective at protecting planktonic marine organisms from UV-B-related damage (Fig. 9.33).

Although these model-based predictions are useful, there are limited data to parameterize the models, and it will be some time before similar predictions can be made for the many species inhabiting the full range of conditions within the world's ocean, including those of the Arctic.

9.4.4. General perspectives

Although UV-B radiation can have negative impacts (direct effects) on marine organisms and populations, it is only one of many environmental factors (e.g., bacterial and/or viral pathogens, predation, toxic algae) that result in the mortality typically observed in these organisms. Recent assessments indicate that UV-B radiation is generally only a minor source of direct mortality (or decreases in productivity) for populations, particularly in "DOC-protected" coastal zones. However, for those species whose early life stages occur near the surface, there may be circumstances (albeit rare) —

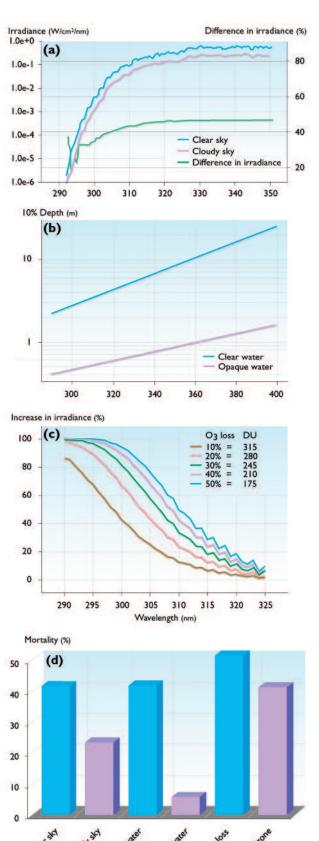


Fig. 9.32. Output of a mathematical simulation model (Kuhn et al., 2000) illustrating the relative effects of selected variables on UV-induced mortality in *Calanus finmarchicus* embryos (modified from Browman et al., 2000). The plots illustrate the effects on irradiance of (a) clear versus cloudy sky, (b) clear versus an opaque water column, (c) 50% thinning of ozone versus ambient ozone, while (d) compares the relative impacts of all three on mortality. This graphic illustrates that water column transparency is the single most important determinant of UV exposure – of considerably more importance than ozone layer depletion.

such as a cloudless sky, thin ozone layer, lack of wind, calm seas, low nutrient loading — under which the contribution of UV-B radiation to the productivity and/or mortality of a population could be far more significant. The impact of indirect effects has not as yet been adequately evaluated.

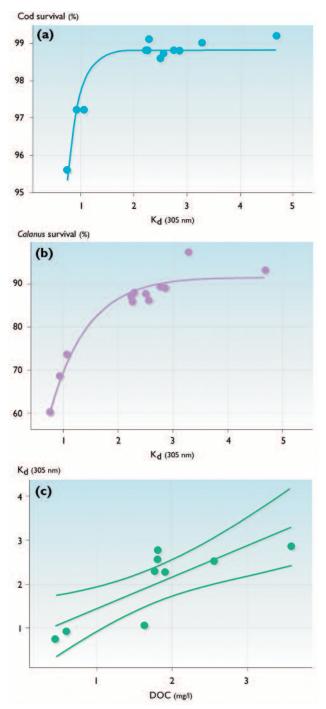


Fig. 9.33. Level of protection from UV damage afforded by the organic matter content of the water column. (a) diffuse attenuation coefficient (K_d) at 305 nm versus modeled survival of Atlantic cod embryos exposed to UV radiation in a mixed water column; (b) K_d at 305 nm versus modeled survival of *Calanus finmarchicus* embryos exposed to UV radiation in a mixed water column; (c) dissolved organic carbon (DOC) versus K_d at 305 nm from field measurements in temperate marine coastal waters (the estuary and Gulf of St. Lawrence, Canada). The straight line is the regression; the curved lines the 95% confidence intervals (modified from Browman, 2002).

9.5. The carbon cycle and climate change

The Arctic Ocean has not been considered a significant carbon sink; first, because extensive sea-ice cover constrains atmosphere—ocean exchange, and second, because levels of biological production under perennial sea ice were considered low (English, 1961). Under warmer conditions, however, the amount of carbon sequestered by the Arctic Ocean is very likely to increase significantly. The role of the Arctic as a potential carbon source, in the form of CH₄ and CO₂, is unclear owing to limited information on the likely impact of climate change on the substantial frozen reserves in permafrost and gas hydrate layers.

The ocean carbon cycle comprises a physical pump, a biological pump, and an alkalinity or anion pump. The physical pump is driven by physical and chemical processes, which affect the solubility of CO₂ and the transport of water from the surface mixed layer to depth. The biological pump is driven by primary production, consuming dissolved CO₂ through photosynthesis and producing particulate organic carbon (POC) and DOC. The alkalinity pump concerns the removal of carbon by calcification in the upper waters and the release of carbon when calcium carbonate is dissolved at depth. The alkalinity pump is not affected by temperature itself, but is affected indirectly through shifts in biological speciation.

9.5.1. Physical pump

The presence of sea ice strongly affects the physical pump, which regulates the exchange of ${\rm CO_2}$ between the atmosphere and the ocean. This exchange is primarily determined by the difference in partial pressure of ${\rm CO_2}$ ($p{\rm CO_2}$) over the air—sea interface. Physical factors, such as wind mixing, temperature, and salinity, are also important in this exchange. Dissolved inorganic carbon (DIC) is the largest component of the marine carbon pool.

Multi-year ice restricts air—sea exchange over the central Arctic Ocean and seasonal sea ice restricts air-sea exchange over shelf regions to ice-free periods. Because the solubility of CO, in seawater increases with decreasing temperature, the largest uptake of atmospheric CO, occurs primarily in the ice-free Nordic Seas ($\sim 86 \times 10^{12}$ g C/yr; Anderson L. and Katlin, 2001) where northward flowing Atlantic waters are rapidly cooled. Similarly, the Barents and Bering/Chukchi Seas, where inflowing Atlantic and Pacific waters undergo cooling, are also important uptake regions: uptake in the Barents Sea is \sim 9 x 10¹² g C/yr (Fransson et al., 2001) and in the Bering/Chukchi Seas is ~22 x 10¹² g C/yr (Katlin and Anderson, 2005). Uptake in the Bering/Chukchi Seas is higher than in the Barents Sea for reasons discussed in greater detail in section 9.5.2; namely, a higher potential for new production owing to a greater supply of nutrients, and a larger area of retreating ice edge along which much of the primary production occurs. Carbon uptake in the ice-covered Arctic Ocean and interior shelf seas is \sim 31 x 10¹² g C/yr (Katlin and Anderson, 2005).

Although these fluxes are not large on a global scale ($\sim 2000 \times 10^{12} \text{ g C/yr}$), the air—sea CO₂ flux is very likely to increase regionally under scenarios of climate warming. For example, the ACIA-designated models project the Barents Sea and the northern Bering Sea to be totally ice-free by 2050 (see section 9.2.5.2). Such changes in ice cover and longer periods of open water will result in more regions that resemble the Greenland Sea, where the physical pump is strong due to low surface water temperatures and high wind speeds (Johannessen T. et al., 2002). Atmospheric exchange will also increase as the areal coverage of the permanent ice pack is reduced and more leads and polynyas are formed. Here, the combination of increased atmospheric exchange (driven by winds) and ventilation (driven by sea-ice formation and convection) transport CO₂ from the atmosphere into the halocline and potentially deeper, eventually entering the deep North Atlantic Ocean and the THC. Ventilation of Arctic Ocean intermediate waters has been estimated to sequester ~0.026 Gt C/yr, nearly an order of magnitude more than the sink due to convection in the Greenland Sea (Anderson L. et al., 1998) and this is very likely to increase, possibly significantly.

Seasonally ice-covered shelf regions are also important dense water formation areas. Brine release during seaice formation increases the density of surface waters which then sink and are advected from the shelf to basin interiors, transporting CO_2 into the halocline and deeper waters. Under warming conditions, ice formation on shelves will occur later and ice melt will occur earlier, thereby increasing the time available for air—sea

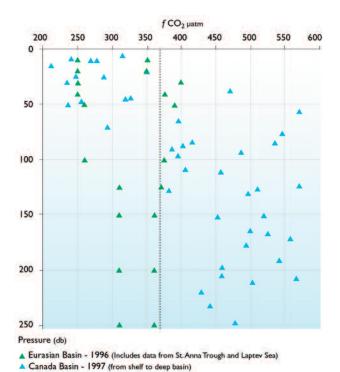


Fig. 9.34. Profiles of the fugacity (partial pressure corrected for the fact that the gas is not ideal) of CO₂ in Canada Basin and the Eurasian Basin. Data to the left of the dotted line are undersaturated and to the right are over-saturated.

interaction/equilibration and CO_2 uptake. The coincidence of open water with late summer storms will also increase air—sea exchange and CO_2 uptake.

Changes in dense water production and the THC will affect the ocean carbon reservoir (Hopkins, 2001). The global ocean stores approximately fifty times more carbon than the atmosphere, mostly in the deep waters of the Pacific Ocean owing to their volume and long residence time. Slowing or stopping the THC would make the Atlantic circulation more like that of the Pacific, increasing its carbon storage and thus weakening the greenhouse effect and cooling the atmosphere — a negative feedback. In contrast however, if sites of deep ventilation were to move northward into the Arctic Basin (Aagaard and Carmack, 1994), the resulting overturn may result in a positive feedback due to CO₂ release to the atmosphere.

Changes in ice cover extent also affect the uptake of atmospheric CO2 by altering the equilibrium concentrations in the water column. Anderson L. and Katlin (2001), using the Roy et al. (1993) solubility equations, calculated that melting 2 to 3 m of sea ice and mixing the resulting freshwater into the top 100 m of the water column would increase CO, uptake and could remove ~3 g C/m². But, where warming is sufficient to increase surface water temperatures by 1 °C, ~8 g C/m² could be released due to the decrease in solubility. At high latitudes, surface waters are often undersaturated because heat is lost to the atmosphere more quickly than CO2 can dissolve. If ice cover retreated and the contact period with the atmosphere increased, this undersaturation would result in atmospheric CO₂ uptake. Anderson L. and Katlin (2001), using data for the Eurasian Basin where Atlantic waters dominate the upper water column, calculated that surface waters in the St. Anna Trough, the Eurasian Basin, and the Makarov Shelf slope have a potential carbon uptake of 35, 48, and 7 g C/m², respectively, when ice cover conditions allow saturation.

Regionally, the effects of upwelling of halocline waters onto the shelf must also be considered. For example, a profile of the fugacity (partial pressure corrected for the fact that the gas is not ideal) of CO_2 (fCO_2) shows that Pacific-origin waters below 50 m in Canada Basin are oversaturated due to their origin in the productive Bering/Chukchi Seas (see Fig. 9.34). If upwelling brought these oversaturated waters onto the shelf and they mixed with surface waters CO, would be released. Upwelling of waters with salinity ~33 (near 150 m in the Canada Basin) has been observed on the Alaskan and Beaufort shelves (Aagaard et al., 1981; Melling, 1993; Melling and Moore, 1995). Upwelling is also expected to increase when the ice edge retreats beyond the shelf break (Carmack and Chapman, 2003). In contrast, the f CO₂ profile of Atlantic-origin waters shows that waters below 50 m in the Eurasian Basin are undersaturated and will take up atmospheric CO, if moved onto the shelf by upwelling (Anderson L. and Katlin, 2001). Hence, the recent shift in the Makarov Basin from a

Pacific- to an Atlantic-origin halocline has modified shelves on the perimeter from a potential source to a potential sink of atmospheric CO_2 .

9.5.2. Biological pump

The DOC concentrations in the deep arctic regions are comparable to those in the rest of the world's oceans (Agatova et al., 1999; Borsheim et al., 1999; Bussmann and Kattner, 2000; Gradinger, 1999; Wheeler et al., 1997). Within the Arctic Ocean, shelves are regions of high biological production, especially those within the Bering, Chukchi, and Barents Seas. Here, CO₂ uptake is increased because CO₂ fixation during photosynthesis affects the physical pump by reducing pCO₂.

Levels of primary production are high on shelves due to increased light levels during ice-free periods and the supply of new nutrients by advection or vertical mixing. Although phytoplankton blooms are patchy, they are strongly associated with the retreating ice edge and the position of the ice edge in relation to the shelf break. In the northern Bering and southern Chukchi Seas, primary production occurs over a shallow shelf (50 to 200 m) and as the zooplankton and bacterioplankton cannot fully deplete this carbon source, it is either transferred to the benthos or advected downstream (Shuert and Walsh, 1993). On the southeast Bering Sea shelf, which is deeper at ~200 m, there is potential for a match/mismatch of primary production and zooplankton grazing due to water temperature (Box 9.10). An early bloom in cold melt water means most of the primary production goes to the benthos. A shift from an ice-associated bloom to a water-column bloom in the central and northern Bering Sea shelf as a result of ice retreat provides the potential for development of the plankton community at the expense of the benthic community (Hunt et al., 2002). Under climate warming, the benthic community is very likely to be most affected if this carbon is transferred to the deep basin instead of the shelf. Under these circumstances, carbon is disconnected from the food web and can be buried. In contrast, the Barents Sea shelf is much deeper (300 m) and primary production supports a large pelagic community that is unlikely to be affected. Nevertheless, a larger quantity of carbon is likely to be buried in future as deposition shifts from the shelf region to the deeper slope and basin region due to the northward movement of the ice edge.

Projections that the Arctic Ocean will be ice-free in summer (see section 9.2.5.2) imply that production will increase in waters where it was previously limited by ice cover. Based on nutrient availability, Anderson L. et al. (2003) estimated that the biological carbon sink would increase by 20 x 10^{12} g C/yr under ice-free conditions. However, mesocosm studies on the effect of high initial ambient CO $_2$ (750 μatm) on coccolithophore assemblages have shown an increase in POC production (Zondervan et al., 2002). This would be a negative response to atmospheric CO $_2$ increase.

9.5.3. Alkalinity pump

Removal of carbonate ions during the formation of calcareous shells and the subsequent sinking of these shells is important in the transfer of inorganic carbon to deeper waters and eventually the sediments. Carbonate shell sinking is also an efficient means of removing organic carbon from the euphotic zone (see section 9.5.2). Together, these processes will provide a negative feedback. However, calcification results in an increase in oceanic $p\mathrm{CO}_2$ through the redistribution of carbonate species, which represents a positive feedback. Partial equilibrium with the atmospheric CO_2 will result in an increase in pH that may reduce calcification (Riebesell et al., 2000).

9.5.4. Terrestrial and coastal sources

The Arctic Ocean accounts for 20% of the world's continental shelves and these receive, transport, and store terrestrial organic carbon (primarily from rivers and coastal erosion sources) to an extent significant at the global scale (Rachold et al., 2004). Olsson and Anderson (1997) estimated that 33 to 39 x 10^{12} g of inorganic carbon are delivered to the Arctic Ocean each year by rivers. Although the amount of total organic carbon is more difficult to estimate because more than 90% is deposited in deltas (Rachold et al., 1996), it may be similar. An increase in precipitation due to climate warming will not necessarily increase carbon burial, however, as the geological composition of the drainage basin and the amount of flow are both controlling factors. For example, the Mackenzie and Yukon are both erosional rivers, while the Siberian rivers are depositional, especially the Ob for which the drainage basin includes marsh lowlands (Pocklington, 1987). Thus, increased precipitation is likely to lead to increased DIC delivery in the first case but not the second, and depends on the timing and intensity of the freshwater flow into the sea. Burial will occur on the shelf, and in adjacent ocean basins if transported offshore by sea ice, ocean currents, or turbidity currents.

Regional transport of terrestrial organic carbon to the marine system also results from coastal erosion. For example, the near-shore zone of the Laptev and East Siberian Seas is the most climatically sensitive area in the Arctic and has the highest rates of coastal retreat (Are, 1999; Grigoriev and Kunitsky, 2000). Biodegradation of this coastal material is a regional source of high pCO_2 in surface waters of the Laptev and East Siberian Seas (Semiletov, 1999a). Longer ice-free conditions and latesummer storms may accelerate the release of terrestrial carbon frozen during the last glaciation. Pleistocene permafrost soils contain huge ice wedges (up to 60 to 70% by volume) and are enriched by organic carbon (~1 to 20% by weight; Are, 1999, Romanovsky et al., 2000). The amount of organic carbon stored in permafrost is large (~450 Gt C), similar to the quantity of dissolved carbon stored in the Arctic Ocean (Semiletov, 1999b), and its release to the atmosphere depends on sediment burial rates and competing consumption by biota.

The rate of coastal erosion in the Arctic appears to have increased from a few meters per year to tens of meters per year (Are, 1999; Tomirdiaro, 1990). The highest rates of coastal retreat have been observed at capes; regions important as hunting locations. Bottom erosion is also evident. The bottom depth in the near-shore zone of the Northern Sea Route has increased by ~0.8 m over the past 14 years (Tomirdiaro, 1990). Many climaterelated factors affect coastal retreat in the Arctic: permafrost ice content, air temperature, wind speed and direction, duration of open water, hydrology, and sea-ice conditions. In addition to the direct effects of climate change, rates of coastal retreat might also increase indirectly due to wave fetch and storm surge activity. Sea-level rise (~15 cm per 100 years, Proshutinsky et al., 2001) will further accelerate coastal erosion.

9.5.5. Gas hydrates

The release of $\mathrm{CH_4}$ and $\mathrm{CO_2}$ trapped in vast gas-hydrate reservoirs in permafrost is very likely to play a key but largely overlooked role in global climate, particularly as $\mathrm{CH_4}$ is 60 times more efficient as a GHG (on a molar basis) than $\mathrm{CO_2}$. For example, Semiletov (1999a) estimated that the upper 100 m layer of permafrost contains at least 100 000 Gt of organic carbon in the form of $\mathrm{CH_4}$ and $\mathrm{CO_2}$. Although $\mathrm{CH_4}$ is one of the most important GHGs, there are currently only ~4 Gt of $\mathrm{CH_4}$ carbon in the atmosphere. If a small percentage of $\mathrm{CH_4}$ from the gas-hydrate reservoir were released to the atmosphere, it could result in an abrupt and significant increase in global temperature through positive feedback effects (Bell P., 1982; Nisbet, 1990; Paull et al., 1991; Revelle, 1983).

The marine Arctic is a particularly important source region for CH₄. Following glacial melting and sea-level rise during the Holocene, relatively warm (0 °C) Arctic Ocean waters flooded the relatively cold (-12 °C) Arctic permafrost domain (Denton and Hughes, 1981). As a result, permafrost sediments underlying the arctic shelf regions are still undergoing a dramatic thermal regime change as this heat is conducted downward as a thermal pulse. Subsurface temperatures within the sediment may have risen to the point that both gas hydrate and permafrost may have begun to thaw. In this case CH₄ would undergo a phase change, from a stable gas hydrate to a gas, and therefore rise through the sediment. Little is known about the fate of CH4 released in this manner. Depending on the structure and ice matrix of surrounding sediments, CH_4 can be either consumed by anaerobic CH₄ oxidation or released upward through conduits into the overlying seawater. Evidence of elevated CH₄ concentrations in seawater has been observed in the Beaufort Sea (Macdonald, 1976) and along the North Slope of Alaska (Kvenvolden, 1991; Kvenvolden et al., 1981). Kvenvolden et al. (1993) noted that CH₄ concentrations under sea ice in the Beaufort Sea were 3 to 28 times higher in winter than summer, suggesting that CH₄ accumulates under the sea ice in winter and is rapidly released into the atmosphere when the sea ice

retreats. The timing and release of these under-ice accumulations will change with changes in ice cover.

9.6. Key findings

This section summarizes the conclusions from sections 9.2.5, 9.3.4, 9.4, and 9.5.

The Arctic is a major component of the global climate system; it both impacts and is impacted upon by the larger global system. This interaction is illustrated in the bulleted list of key findings, respectively labeled A>G and G>A. There are also forcing mechanisms and responses that remain internal to the Arctic (A>A). Any change in atmospheric forcing (wind, temperature, and precipitation) is of great importance for the ocean circulation and ocean processes (G>A).

- Large uncertainties in the response of the arctic climate system to climate change arise through poorly quantified feedbacks and thresholds associated with the albedo, the THC, and the uptake of GHGs by the ocean. Since climate models differ in their projections of future change in the pressure fields and hence their associated winds, much uncertainty remains in terms of potential changes in stratification, mixing, and ocean circulation.
- The Arctic THC is a critical component of the Atlantic THC. The latest assessment by the Intergovernmental Panel on Climate Change (IPCC, 2001) considered a reduction in the Atlantic THC likely, while a complete shutdown is considered unlikely but not impossible. If the Arctic THC is reduced, it will affect the global THC and thus the long-term development of the global climate system (A>G). Reduction in the global THC may also result in a lower oceanic heat flux to the Arctic (G>A). If the THC is reduced, local regions of the Arctic are likely to undergo cooling rather than warming, and the location of ocean fronts may change (A>A). The five ACIAdesignated models cannot assess the likelihood of these occurrences.
- Most of the present ice-covered arctic areas are very likely to experience reductions in sea-ice extent and thickness, especially in summer.
 Equally important, it is very likely that there will be earlier sea-ice melt and later freeze-up (G>A).
 This is likely to lead to an opening of navigation routes through the Northwest and Northeast Passages for greater periods of the year and thus to increased exploration for reserves of oil and gas, and minerals.
- Decreased sea-ice cover will reduce the overall albedo of the region, which is very likely to result in a positive feedback for global warming (A>G).
- Upper water column temperatures are very likely to increase, especially in areas with reduced sea-
- The amount of carbon that can be sequestered in the Arctic Ocean is likely to increase significantly under

- scenarios of decreased sea-ice cover, through surface uptake and increased biological production (A>G).
- Greenhouse gases (CO₂ and CH₄) stored in permafrost may be released from marine sediments to the atmosphere subsequent to warming, thus initiating a strong positive feedback (A>G).
- In areas of reduced sea-ice cover, primary production is very likely to increase, which in turn is likely to increase zooplankton and possibly fish production. Increased cloud cover is likely to have the opposite effect on primary production in areas that are currently ice free (G>A).
- The area occupied by benthic communities of Atlantic and Pacific origin is very likely to increase, while areas occupied by colder-water species are very likely to decrease. Arctic species with a narrow range of temperature preferences, especially longlived species with late reproduction, are very likely to be the first to disappear. A northward retreat for the arctic benthic fauna may be delayed for the benthic brooders (the reproductive strategy for many dominant polar species), while species producing pelagic larvae are likely to be the first to colonize new areas in the Arctic (G>A).
- A reduction in sea-ice extent is very likely to decrease the natural habitat for polar bears, ringed seals, and other ice-dependent species, which is very likely to lead to reductions in the survival of these species. However, increased areas and periods of open water are likely to be favorable for some whale species and the distribution of these species is very likely to move northward (G>A).
- Some species of seabird such as little auk and ivory gull are very likely to be negatively affected by the changes predicted to occur within the arctic communities upon which they depend under climate warming, while it is possible that other species will prosper in a warmer Arctic, as long as the populations of small fish and large zooplankton are abundant (G>A).
- Increased water temperatures are very likely to lead to a northward shift in the distribution of many species of fish, to changes in the timing of their migration, to a possible extension of their feeding areas, and to increased growth rates. Increased water temperatures are also likely to lead to the introduction of new species to the Arctic but are unlikely to lead to the extinction of any of the present arctic fish species. Changes in the timing of biological processes are likely to affect the overlap of spawning for predators and their prey (match/mismatch; Box 9.10) (G>A).
- Stratification in the upper water column is likely to increase the extent of the present ice-free areas of the Arctic, assuming no marked increase in wind strength (G>A).
- There are strong correlations between DOC, Chl-a, and the attenuation of UV radiation in marine waters. This is particularly significant within the context of possible UV-B attenuation in marine coastal systems, since DOC and Chl-a are

- usually more highly concentrated in ice-free waters than ice-covered waters.
- Present assessments indicate that UV-B radiation generally represents only a minor source of direct mortality (or decreased productivity) for populations, particularly in DOC-protected coastal zones. However, for those species whose early life stages occur near the surface, it is possible that under some circumstances – a cloudless sky, thin ozone layer, lack of wind, calm seas, low nutrient loading – the contribution of UV-B radiation to the productivity and/or mortality of a population could be far more significant. Thus, it is likely that UV-B radiation can have negative impacts (direct and/or indirect effects) on marine organisms and populations. However, UV-B radiation is only one of many environmental factors responsible for the mortality typically observed in these organisms.

9.7. Gaps in knowledge and research needs

Many aspects of the interaction between the atmosphere and the ocean, and between climate and the marine ecosystem require a better understanding before the high levels of uncertainty associated with the predicted responses to climate change can be reduced. This can only be achieved through monitoring and research, some areas requiring long-term effort. For some processes, the ocean responds more or less passively to atmospheric change, while for others, changes in the ocean themselves drive atmospheric change. The ocean clearly has a very important role in climate change and variability. Large, longlived arctic species are generally conservative in their lifehistory strategies, so changes, even dramatic changes, in juvenile survival may not be detected for long periods. Zooplankton, on the other hand, can respond within a year, while microorganisms generally exhibit large and rapid (within days or weeks) variations in population size, which can make it difficult to detect long-term trends in abundance. Long data series are thus essential for monitoring climate-induced change in arctic populations.

Although the ACIA-designated models all project that global climate change will occur, they are highly variable in their projections. This illustrates the great uncertainty underlying attempts to predict the impact of climate change on ecosystems. The models do not agree in terms of changes projected to wind fields, upon which ocean circulation and mixing processes depend. Thus, conclusions drawn in this chapter regarding future changes to marine systems are to a large extent based on extrapolations from the response of the ocean to past changes in atmospheric circulation. This is also the case for predictions regarding the effects of climate change on marine ecosystems. The present assessment has been able to provide some qualitative answers to questions raised regarding climate change, but has rarely been able to account for non-linear effects or multi-species interactions. Consequentially, reliable quantitative information on the response of the marine ecosystem to climate change is lacking.

9.7.1. Gaps in knowledge

This section highlights some of the most important gaps in knowledge. These require urgent attention in order to make significant progress toward predicting and understanding the impacts of climate change on the marine environment. Each item includes an explanation as to why it is considered important.

Thermohaline circulation

Global circulation models provide an ambiguous assessment of potential changes to the THC. Most project a decrease in the strength of the THC; however, some recent models project little or no change. The THC is extremely important for the thermal budget of the Arctic Ocean and the North Atlantic.

Vertical stratification

Present climate models are unable to project future wind conditions, or to project how increased air temperatures, ice melt, and freshwater runoff will influence the vertical stability of the water column. The amount of vertical mixing that will occur is thus uncertain. Such information is required in order to project the effects of climate change on vertical heat and nutrient fluxes.

Ocean currents and transport pathways

It is necessary to understand the forces driving ocean circulation (wind, freshwater runoff, sea-ice freezing/melting) and their variability. Ocean circulation is fundamental to the distribution of water masses and thus the distribution and mixture of species within the marine ecosystem.

Fronts

Open ocean fronts act as barriers to many marine organisms and are important feeding areas for higher trophic organisms. The relative importance of production at frontal regions compared to that at non-frontal regions has not been assessed for the Arctic, nor has the importance of fronts in terms of recruitment success for fish. Few climate models provide information on fronts and their variability, and even less have an adequate spatial resolution with which to address this issue.

Release of greenhouse gases and sequestration of carbon

Changes in the balance of GHGs (i.e., sources relative to sinks) are known to impact upon climate yet little is known about the arctic reservoir. This is made all the more important through positive feedback mechanisms. Carbon can be sequestered by physical and biological processes, and can be released during ocean mixing events and the thawing of permafrost; estimates of the rates and reservoir sizes need refining before they can be used in global circulation models. Changes in the extent

and timing of sea-ice cover may affect trophic structure and thus the delivery of carbon to the sediment.

Species sensitivity to climate change

Little is known about the response times of species to climate change. For example, the rapid disappearance of sea ice may not allow for adaptive change by many arctic specialists and may possibly result in the disappearance of ice-dependent species. Microorganisms, zooplankton, and fish are all expected to exhibit shifts in distribution but the rates at which this will occur cannot be predicted at present.

Match/mismatch between predators and prey

The timing of reproduction for many species is related to that of their prey. How the timing and location of the production or spawning of most species might alter in response to climate change is unclear and so therefore is the extent of a potential match/mismatch between predators and their prey. Potentially, this could impact upon the whole arctic ecosystem.

Indirect and non-linear effects on biological processes

Biota are indirectly affected by atmospheric climate change through effects on their surrounding environment and on the food web. While the response of a species to change in one particular variable can often be surmised, although generally not quantified, its response to a collection of direct and indirect effects occurring simultaneously is considerably more difficult to address. This is further complicated by the non-linearity of many processes.

Competition when/if new species are introduced into the ecosystem

Many arctic specialists have relatively narrow habitat and other niche requirements. Their likely response to a possible increase in competition from more opportunistic/generalist species in a warmer Arctic is unclear.

Gelatinous zooplankton

The abundance and variability of gelatinous zooplankton such as jellyfish has not been determined for most arctic regions. Although gelatinous zooplankton are known to be important as both predators and prey, and that they can represent a significant component of the biomass at times, their actual role within the ecosystem is unclear.

UV-B radiation exposure

Almost all existing evaluations of the effects of UV radiation are based on short-term studies. Studies are lacking on longer-term sub-lethal exposure to UV radiation, on both individual species and the overall productivity of marine ecosystems. UV-induced reductions in the nutri-

tional quality of the food base could possibly pass through the food chain to fish, potentially reducing their growth rates as well as their nutritional condition.

9.7.2. Suggested research actions

This section lists possible actions that could be undertaken to improve the knowledge and understanding of important processes related to climate change. To reduce the uncertainties in the predicted responses to climate change it is necessary for work to proceed on several fronts simultaneously. Research actions that are considered to be of highest priority are identified by an **H**.

Observational technologies

- Increase the application of recently developed technologies. Recent developments range from current meters, to satellite sensors, to monitors for marine mammals.
- Develop Remote Underwater Vehicles (RUVs) capable of working reliably under the sea ice for extended periods.
 This will reduce sampling costs and enable data collection in regions difficult to access using conventional sampling methods. Instrumentation on the RUVs should include means to sample the biota.

Surveying and monitoring

- Undertake surveys in those areas of the marine Arctic
 that are poorly mapped and whose resident biota have
 not been surveyed (H). These include surveys under
 the permanent ice cap in winter (perhaps using
 RUVs), and surveys to quantify the CH₄ and
 carbon reserves in the arctic marine sediments.
- Continue and expand existing monitoring programs (H), both spatially and in breadth of measurement. New monitoring activities should be established in areas where they are presently lacking and these should be designed to address the effects of climate change. Issues to be addressed include the timing and amount of primary and secondary production, larval fish community composition, and reproductive success in marine mammals and seabirds. Key ecosystem components, including noncommercial species, must be included.
- Evaluate monitoring data through data analysis and modeling to determine their representativeness in space and time.

Data analysis and reconstruction

- Reconstruct the twentieth-century forcing fields over the arctic regions. Present reconstructions only extend back to around 1950. These reconstructions would help to model past climates.
- Establish an arctic database that contains all available physical and biological data. There should be open access to the database.
- Recover past physical and biological data from the Arctic.
 There are many data that are not presently available but could be recovered.

• Undertake analysis of past climate events to better understand the physical and biological responses to climate forcing. An example is the dramatic air temperature warming that took place from the 1920s to 1960 in the Arctic.

Field programs

• Undertake field studies to quantify climate-related processes (H). Examples of particular processes that require attention are: open ocean and shelf convection; forces driving the THC; physical and biological processes related to oceanic fronts; sequestrating of carbon in the ocean, including a quantification of air—ice—ocean exchange; long-term effects of UV-B radiation on biota; and, interactions between benthic, ice, and pelagic fauna.

Modelling

- Improved modeling of the ocean and sea ice in global circulation models (H). For example, how will the THC change? What are the consequences of change in the THC for the position and strength of ocean fronts, ocean current patterns, and vertical stratification?
- Development of reliable regional models for the Arctic
 (H). These are essential for determining impacts on the physics and biology of the marine Arctic.
- Strengthen the bio-physical modeling of the Arctic.
 Increased emphasis is required on coupling biological models with physical models in order to improve predictive capabilities.

Approaches

Prioritize ecosystem-based research (H). Previous biological research programs were often targeted on single species. While these data are essential for input to larger-scale programs, the approach must be complemented by a more holistic ecosystem-based approach. Alternative concepts, methods, and modeling approaches should be explored. More effort should be placed on integrating multiple ecosystem components into modeling efforts concerning climate effects. Research on microbial communities, which may play a future role in a warmer Arctic, must be included.

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