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ICES STATUS REPORT ON CLIMATE CHANGE IN THE NORTH ATLANTIC

EDITORS

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the Exploration of the Sea
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Foreword

The International Council for the Exploration of the Sea (ICES) was founded in 1902 and currently comprises an alliance of 20 countries, including all coastal states bordering the northern North Atlantic and the Baltic Sea.[1] Major national marine scientific institutes of the Member States are partners of ICES. The remit of the Council is to coordinate, plan, and promote marine research on oceanography, the marine environment, marine ecosystems, and living marine resources in the North Atlantic. Coordination and development of this role is delegated to a Scientific Committee (SCICOM), which is guided by a Science Plan (2009–2013) and operates through a number of steering groups and strategic initiatives. A key part of the mission is to plan and develop multidisciplinary research, especially on topics where collaboration between scientists working in different parts of the North Atlantic is required. In many cases, the outcome of this research provides a basis for international policy development.

One of the most real and important concerns of ICES is climate change. A continuing rise in the concentration of greenhouse gases in the atmosphere, mainly caused by the burning of fossil fuels, is driving changes in the oceans and in the climate of the Earth. In this context, the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2007) concluded that changes in global climate over the past 50 years were *very likely* caused by anthropogenic greenhouse gas emissions and not to known natural causes alone. They also concluded that a continuation of emissions at or above current rates would *very likely* induce further changes in the present century that would be larger than those observed so far. It is clear that the climate of the Earth has entered a period of rapid change, with potential negative consequences for the oceans, their ecosystems, and living marine resources. These changes may be compounded by ocean acidification, a second important and independent consequence of rising concentrations of atmospheric CO_2 caused by the direct exchange of the gas into seawater. What is not clear is whether these changes in the oceans, through feedbacks, may reinforce or reduce the effects of climate change.

Fortunately, the governments of most countries have recognized the importance of addressing this crisis and, in many recent declarations, have identified climate change as the most important priority to be tackled through common and concerted actions by societies throughout the world. A need to move to a low-carbon economy is recognized, as is the urgent need to reduce global greenhouse gas emissions. If the necessary reductions are not achieved, or are achieved too late, greater emphasis will need to be placed on adaptive measures in order to counteract the climatic consequences of greenhouse gas emissions and thereby ensure the welfare and safety of populations in coastal regions, and the maintenance of ecosystem services, trade, and goods. In 2006, the Stern Review estimated that the social and economic cost of climate change to the global economy would reach €5500 billion by 2050 and recommended that, if strong mitigation and adaptation action is taken now, there is still time to avoid the worst impacts of climate change (Stern, 2006).

As an ocean, the North Atlantic plays a major role in climate because it is a key node in the thermohaline circulation. The inflow of cold deep water into the northern

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[1] Belgium, Canada, Denmark (including Greenland and Faroe Islands), Estonia, Finland, France, Germany, Iceland, Ireland, Latvia, Lithuania, The Netherlands, Norway, Poland, Portugal, Russia, Spain, Sweden, the United Kingdom, and the United States of America.

North Atlantic and the consequent transport of warm surface water to the north ensure that Europe is much warmer than equivalent latitudes elsewhere in the world. By this route, heat is transferred to the Arctic and contributes to the melting of sea ice and to the potential release of methane hydrates. Despite its modest size (15% of the global ocean), the North Atlantic contains ~23% of the anthropogenic carbon stored in the oceans as a result of the inflow of deep water and the deep mixing that takes place here.

A challenge facing ICES is the need to integrate climate change research into the main themes identified in the recently published *ICES Science Plan* (2009). The plan calls for the establishment of a cross-cutting, integrated programme on climate change that will allow the Council to establish a solid scientific research base in order to (i) understand the functioning of marine ecosystems under the pressure of climate change and ocean acidification, (ii) determine the impacts of climate change on marine ecosystems, (iii) develop and evaluate options for mitigation and sustainable use of marine ecosystems, and (iv) provide information to the public that will also assist policy-makers and other stakeholders in their decisions.

Coordinated by ICES Strategic Initiative on Climate Change, this report is a synthesis of findings from published literature, reports, and the expertise of ICES working groups. It is presented as a summation of the scientific and technical knowledge of the ICES scientific community on the effects and impacts of climate change in the North Atlantic, and as a contribution to debates on climate policy. A synthesis of this nature is timely because it provides the information necessary to help the preparation of robust plans for ameliorating the expected impacts of climate change (i.e. loss of marine and coastal services and goods) on human well-being. The report aims to (i) deliver new insights into the ways in which climate change and variability are affecting marine ecosystems in the North Atlantic, (ii) reduce the scientific uncertainty behind environmental change, and (iii) provide a solid basis for future comparisons. The report also includes an overview of the future scientific challenges facing climate change research in both the North Atlantic and in other oceans and seas, as well as highlighting future research needs and priorities. Its conclusions support the development of an international coordinated research strategy that addresses these priorities, the maintenance of a sustained climate change monitoring network for the oceans that includes a biological component, improvements in modelling, and the development of indicators.

We thank all of the members of the Strategic Initiative on Climate Change and all who contributed to the drafting, reviewing, editing, and printing of this volume for their dedication and time; together they have produced a comprehensive assessment of current knowledge of climate variability and change, and of related impacts in the North Atlantic.

—**Philip C. Reid and Luis Valdés**

1 Introduction

Luis Valdés (corresponding author), Philip C. Reid, and Jürgen Alheit

Although the physical and chemical principles that explain the warming of the Earth's system resulting from emissions of CO_2 and other greenhouse gases were understood at the end of the 19th century (Tyndall, 1861; Arrhenius, 1896) and at the beginning of the 20th century (Callendar, 1938), it was almost 100 years later, in the mid-1980s, before it was realized that these processes were contributing to a rapid change in climate. The potential consequences of this global warming have still to be revealed and are difficult to anticipate.

1.1 Scientific literature addressing climate change

Since 1990, when the First Assessment Report (FAR) of the Intergovernmental Panel on Climate Change (IPCC, 1990) was published, literature on climate change has grown exponentially. Nowadays, climate change is a challenging scientific issue that has developed a body of observations, models, and hypotheses that is being used to assess possible consequences for critical processes involved in the functioning of the Earth. This progression has strongly influenced other disciplines, modifying approaches to topics such as risk analysis, socio-economics, ethics, politics, energy, natural resource management, geo-engineering, and even evolution. The scientific debate has moved rapidly from observations to impacts to discussions of potential mechanisms that may be used to mitigate and adapt to this new reality; a development that reflects an urgent need to minimize the impacts of global warming by taking action based on robust scientific knowledge.

In a succession of assessment reports, from the first to the fourth (FAR, SAR, TAR, AR4; IPCC 1990, 1996, 2001, 2007a, respectively), the IPCC has played an essential role in organizing data and synthesising results published in a vast scientific literature. Development of a comprehensive understanding of the ramifications and implications of climate change for human society, and for the ecology and sustainability of the entire planet, is only possible by adopting such an international, integrated approach. However, the information published in the scientific literature is often incomplete, local, and fragmented, and up to the most recent report (AR4) had given only modest coverage to the oceans (Richardson and Poloczanska, 2008).

Over the past two decades, a number of international scientific and political fora (e.g. the United Nations Conference on Environment and Development (UNCED), Rio de Janeiro, 1992; the three World Climate Conferences, Geneva, 1979, 1990, 2009; and the recent UN Climate Change Conference, including the 15th and 16th sessions of the Conference of the Parties (COP15 and COP 16) in Copenhagen, 2009, and Cancun, 2010, respectively) have encouraged national marine observatories and the oceanic scientific community to initiate coordinated studies at a regional scale on climate change in the oceans. These events also encouraged the development of new approaches to data management, including open access, so that data are made available to potential users in the shortest possible time. The recommendations are implemented by cooperative actions between two or more international scientific bodies (e.g. ICES and its counterpart, the North Pacific Marine Science Organization (PICES), the Intergovernmental Oceanographic Commission (IOC), World Meteorological Organization (WMO), United Nations Environment Programme (UNEP), International Council of Scientific Unions (ICSU), and the Scientific Committee on Oceanic Research (SCOR)) and other well-recognized international programmes (e.g. the International Geosphere–Biosphere Program (IGBP), Global Ocean Observation System (GOOS), World Climate Research Program (WCRP), and the Intergovernmental Panel on Climate Change (IPCC)).

Although new and relevant research is being produced and published every year, there is general agreement that climate-change science is still in its infancy, and that the number and intensity of the impacts currently observed are likely to be only a fraction of what will become apparent in coming years. Moreover, it is difficult to disentangle the impacts of climate change from impacts caused by other natural or anthropogenic stressors for both terrestrial and marine ecosystems. However, responses in the ocean are substantially more complex and difficult to monitor. Whereas, in other ecosystems, the impacts of climate change are primarily driven by changes in temperature, changes in the oceans are forced by an increase in both temperature and CO_2, which modifies not only the thermal characteristics of the environment but also the physical structure of the water column and ocean biogeochemistry. Both temperature and CO_2 may alter pivotal processes in the ecology and physiology of marine organisms to the extent that the sustainability of entire ecosystems (e.g. coral reefs) is jeopardized. As these changes in temperature and CO_2 are expected to continue, there is a risk that marine ecosystems will be seriously degraded, with long-term consequences for human health and welfare.

There is a perception in the marine scientific community that the IPCC's Fourth Assessment Report (IPCC, 2007a) did not adequately address marine issues. For example, only 30 marine dataseries (biological and physical) were used in Chapter 1 of the Working Group II contribution to the IPCC report (Rosenzweig *et al.*, 2007) compared with 622 series from the cryosphere and 527 series from terrestrial biological systems. Furthermore, only 85 biological changes in marine and freshwater systems were reported, whereas 28 586 were noted for terrestrial systems (Richardson and Poloczanska, 2008). To address this gap in information, marine organizations and scientific journals have promoted the publication of marine data and time-series as reports and monographs. These documents address the effects that climate change has on the oceans and the mitigating role that the oceans play by their responses to climate change (Hoepffner *et al.*, 2006; WBGU, 2006; Philippart *et al.*, 2007; Cicin-Sain, 2009; Reid *et al.*, 2009b; Philippart *et al.*, 2011). There is an increasing demand for new and updated data at a regional scale, and the need for scientific information in the North Atlantic is even more urgent. The North Atlantic occupies a strategic geographical position in the functioning of the Earth's system (e.g. the warm North Atlantic Current that influences the climate of Europe, the meridional overturning of the thermohaline circulation, and the sea ice of the Arctic that prevents surface communication between the North Atlantic and the North Pacific). In this respect, ICES is an authoritative voice that can help in the debate, offering expertise and data that is focused on the North Atlantic.

1.2 Role of ICES in climate-change research

ICES has maintained an interest and made important contributions to the study of climate change and its impacts in the North Atlantic region since its foundation in 1902 (see Rozwadowski, 2002; Brander, 2008). In particular, the Council has played a prominent role in developing an understanding of the effects of climate and environmental variability on the abundance and distribution of marine organisms, on the growth and survival of fish, and on hydrographic change in the North Atlantic and Arctic oceans. In addition, the Council has developed its own databases, where more than 255 million measurements of environmental data from the North Atlantic, dating back to 1877, are stored and made freely available to the international marine community. One of the first conferences on climate change in 1948 was organized by ICES as a response to the marked environmental and fishery changes associated with the warming of the North Atlantic region in the 1920s to 1940s; this event provides an important analogue for the prediction of future changes in the current period of rapid warming, Since 1975, decadal symposia with a climate theme and workshops (e.g. on ocean acidification) have been organized. Support has also been provided towards the formation of international programmes such as GLOBEC. ICES has sponsored its associated Cod and Climate Change (CCC) programme and publishes an annual ICES Report on Ocean Climate (IROC). In the 2009–2014 *ICES Science Plan* (ICES, 2009), climate change is identified as a priority issue for future work by the Council. It is hoped that this report will inform the world of the work done by ICES on climate change and help provide future direction on policy development on this issue within the Council.

1.3 Overview of this report

This document reviews the range of climate-change impacts that have been reported from the North Atlantic and discusses potential future changes to the ecological processes of marine systems. The data used to document and illustrate this report come not only from published literature, but also from ICES data and contributions from experts who are members of ICES expert groups. It is important to note that, since its foundation in 1902, ICES has promoted the establishment of monitoring programmes that have been collecting oceanographic data along the coast and in the open ocean, covering much of the North Atlantic. Consequently, the North Atlantic is the most sampled oceanic region in the world, with the best coverage and background of data. Routine long-term surveillance by ICES partners across a network of sampling sites makes this region unique in terms of observational facilities, moored instruments, and data collections.

Many trends and impacts of climate change and variability have been reported in the North Atlantic. These include direct linear and indirect non-linear climatic impacts, and synergies between climate change and anthropogenic factors, as well as ocean acidification (Figure 1.1). Together, they make any attempt to determine the priority and true causation of the impacts complex. In this report, a systematic approach to the review of recent advances in understanding of these issues has been adopted. Direct and localized effects of change in the marine environment, including impacts on individuals, populations, and communities, are addressed, as well as broader, indirect non-linear responses that may emerge from these localized impacts. Emerging responses include alterations to important biological and physico-chemical patterns and processes ranging from ocean circulation or primary productivity to biodiversity, biogeography, and evolution.

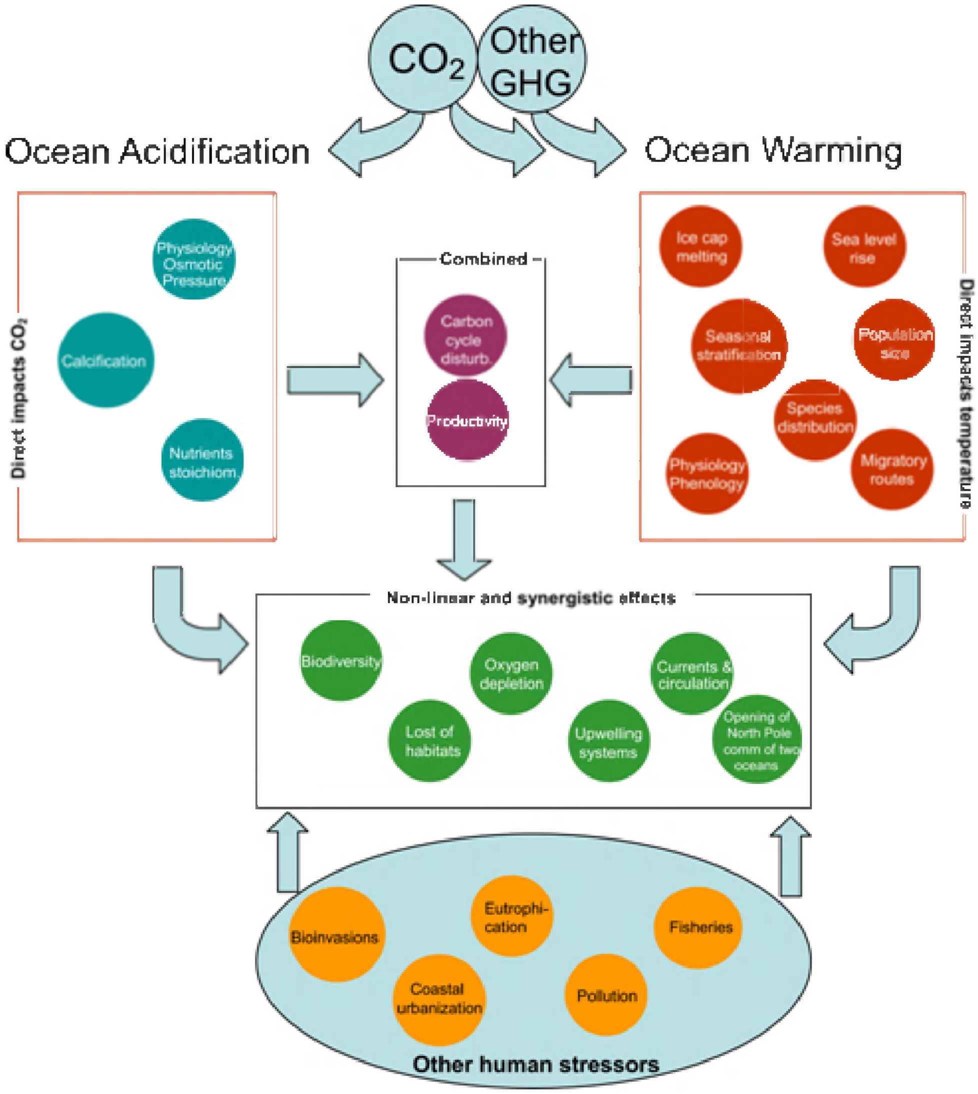

Figure 1.1. Examples of the effects of global warming and ocean acidification on coastal and ocean ecology. Synergistic effects caused by other anthropogenic stressors could alter our perception of climate-change impacts on marine ecosystems. GHG = greenhouse gases.

Synergisms between climate change and anthropogenic stressors are a special case of non-linear/non-independent effects; fishing pressure is a clear example that needs to be addressed with caution. The difficulty of disentangling multiple stressors within poorly sampled systems has hindered the investigation of marine climate-change impacts. At present, no part of the oceans remains unaffected by multiple, anthropogenic stressors, such as fishing, pollution, eutrophication, habitat destruction, hypoxia, litter, and species introductions (Halpern *et al.*, 2008). These multiple stressors may have masked more subtle impacts of climate change (Figure 1.1) and may even have misled researchers into attributing impacts caused by climate change to local environmental changes. Because the combined effects of multiple stressors may lead to changes in marine systems greater than those expected from studies that focus on a single stressor, future work must determine which variables are most likely to interact and why.

The determination of the potential effects of climate change at all levels of oceanic and ecological organization requires the use of predictive mathematical models that are based on quality-controlled data. For direct linear changes, predictions can be made with accuracy because future states will depend substantially on past history (prognosis is based in diagnosis). This embraces some physical and chemical processes, but biology and ecology are very often governed by non-linear changes (e.g. regime shifts), and prognosis is particularly difficult because past events provide limited information on future trends. The challenge of predicting the impacts and outcomes of climate change is made even more difficult when the combined effects of two or more variables cannot be predicted from the individual effects.

It is important to remember that non-linear changes are most important for Earth's ecology. Lovelock (1972) and Lovelock and Margulis (1974) noted the important role that biology plays in controlling the environment of the Earth, as well as the strong links between biological, physical, and chemical processes. They also suggested that the Earth's system is characterized by critical thresholds and that gradual changes in climate may provoke sudden, and perhaps unpredictable, biological responses from human activities as ecosystems shift from one state to another, inadvertently triggering abrupt changes.

Finally, knowledge gaps are highlighted in the hope that continuing research efforts will fill these gaps and thus improve the ability to predict, adapt to, and mitigate the effects of climate change. The immense area of the open ocean and the modest extent of our knowledge severely limit predictions of how ocean systems will respond to climate change. The successful management and conservation of marine species, habitats, living marine resources, and ecosystem services require a considerable improvement in observational capabilities and predictive power.

This report, coordinated by the ICES Strategic Initiative on Climate Change aims to (i) deliver new insights into the ways in which climate change and variability are affecting the North Atlantic, (ii) reduce scientific uncertainty regarding environmental change, and (iii) provide a baseline synthesis in the North Atlantic for future comparisons.

The report also features an overview of the research needs and future scientific challenges of climate change in both the North Atlantic and other oceans and seas. Its conclusions support the development of future research strategies and highlight the need for sustained climate-change monitoring, improvements in modelling, and the development of indicators.

2 North Atlantic circulation and atmospheric forcing

N. Penny Holliday (corresponding author), Markus Quante, Toby Sherwin, Glenn Nolan, Kjell-Arne Mork, Heather Cannaby, and Dave Berry

The climate of the North Atlantic region is intimately linked to the circulation of its oceanic currents in both the short and long term. The ocean has a great capacity to store and transport heat, water, and radiatively active gases around the world, and to exchange these with the atmosphere. In this way, the global oceans play a vital role in the climate system. Climate-driven changes to the circulation are major drivers of variability in ecosystems and fisheries, and there is an intimate relationship between atmospheric variability and oceanic circulation. As background for the rest of this volume, we first summarize the major patterns of surface, intermediate, and deep circulation in the North Atlantic, and then provide an introduction to some of the atmospheric processes that are important for the ocean and climate system.

2.1 Circulation of the North Atlantic

The Atlantic Ocean is one of only two oceans that straddle the equator and link Arctic and Antarctic waters (the other being the Pacific). The circulation is dominated by two systems. One is a wind-driven circulation that is mainly horizontal and includes the clockwise Subtropical Gyre in the southern part and the anticlockwise Subpolar Gyre in the northern part. The other is the Meridional Overturning Circulation (MOC), which draws warm, saline surface waters north towards the Arctic Ocean and transports cold, fresher deep water south. The MOC includes a thermohaline cell that cools the surface layers convectively at high latitudes and drives the North Atlantic Deep Water (NADW) south as part of the global thermohaline circulation. The MOC transports oceanic heat north and, if it ceased, the climate of northern Europe could cool considerably (Vellinga and Wood, 2002).

The principal surface feature of circulation in the mid-latitude North Atlantic is the Subtropical Gyre, the great circulating pool of warm water that stretches from 10° to 50°N. The western side of the gyre is dominated by the Gulf Stream system. In the Gulf of Mexico, recirculating waters from the eastern Atlantic and Equatorial Current systems are drawn into the narrow Florida Current, which carries between 30 and 35 Sv ($1\ \text{Sv} = 10^6\ \text{m}^3\ \text{s}^{-1}$) north along the coast of Florida (Baringer and Larsen, 2001). Farther north, with the addition of recirculating water from the Sargasso Sea, the current becomes the Gulf Stream, carrying up to 100 Sv by the time it reaches Cape Hatteras at 35°N, where it leaves the American coast (Hogg, 1992). Offshore, the Gulf Stream continues to grow so that it transports as much as 150 Sv at its maximum, south of Nova Scotia. At this stage, it loses its coherence, and meanders and eddies (Gulf Stream rings) are formed. Inshore of the Gulf Stream, the colder, fresher Labrador Current flows south over the outer shelf (Rossby, 1999).

At around 50°W, 30 Sv of Gulf Stream water is drawn northeastwards in the North Atlantic Current, whereas 15 Sv is deflected towards the Mediterranean Sea (1 Sv in the Azores Current) and the equator (14 Sv in the Canaries Current; Figure 2.1; Schmitz and McCartney, 1993). The remainder drifts south into the Sargasso Sea, partly in the form of cold-core eddies. On the eastern side of the Atlantic, the Mediterranean outflow (0.7 Sv) contributes a significant salinity signal at intermediate depths, where Mediterranean Water disperses, largely in the form of eddies (Potter and Lozier, 2004). Along the northwestern European shelf edge, a current of warm water propagates north through the Bay of Biscay and Rockall Trough into the Norwegian Sea (Holliday *et al.*, 2008).

The northeastward drift of the North Atlantic Current (NAC) is driven (i) by the local windstress (it lies directly beneath the North Atlantic storm track); (ii) by the meridional pressure gradient resulting from cooling in the north; and (iii) from entrainment overflows, particularly along the Greenland–Scotland Ridge. The Subpolar Front associated with the NAC marks the boundary between the cold Subpolar Gyre and the warm Subtropical Gyre. Cold, fresh Subarctic Intermediate Water is subducted (forced downwards) along this front, descending beneath the various branches of the Gulf Stream and NAC, and is distributed across the temperate Atlantic. The Subpolar Front becomes diffuse as it meanders through the Iceland Basin towards the Iceland–Faroe Ridge (where ~3.5 Sv crosses into the Norwegian Sea) and separates cooler, fresher Western North Atlantic Water (WNAW) from warmer, saltier Eastern North Atlantic Water (ENAW) in the Rockall Trough (Pollard *et al.*, 2004). Some surface waters in the Iceland Basin recirculate around the Reykjanes Ridge into the Irminger Basin. Of this, 1 Sv enters the Iceland Sea around the western side of Iceland in the Irminger Current (Hansen and Østerhus, 2000).

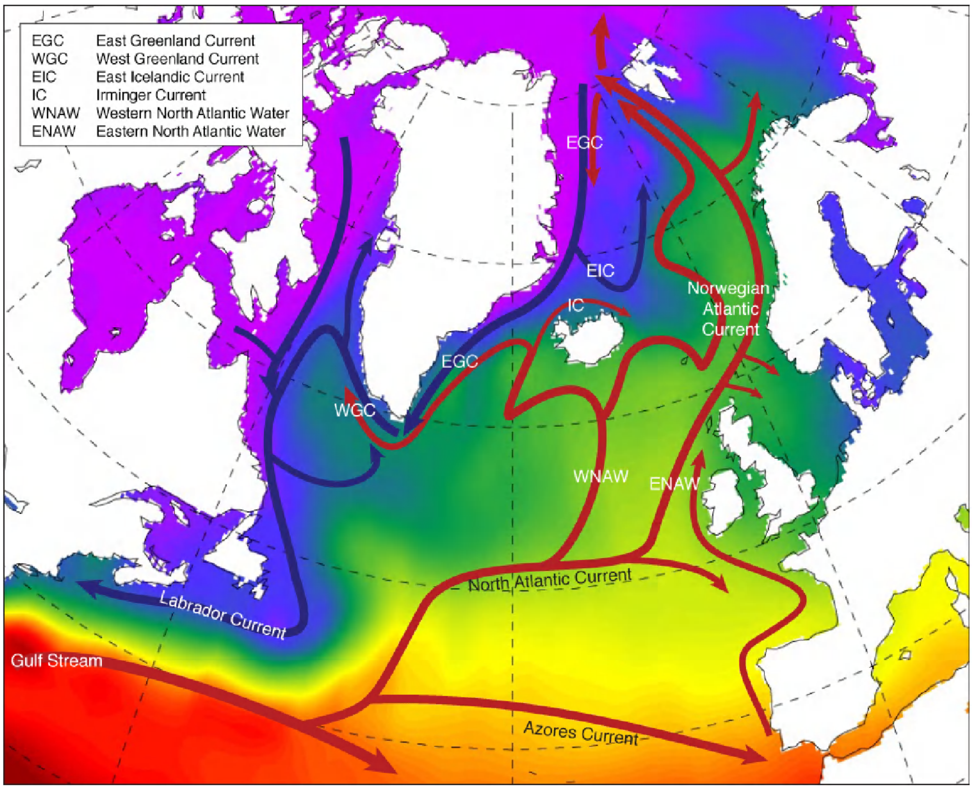

Figure 2.1. Schematic of the pathways of the major near-surface currents of the North Atlantic, superimposed on a map of sea surface temperature for February 2010. Red arrows = the warm, saline waters originating in the Gulf Stream/North Atlantic Current; blue arrows = cold, fresh waters originating in the Arctic Ocean; pink shading = ice-covered regions. (Data from www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html. Sea surface temperature image generated by Dave Berry, National Oceanography Centre, Southampton, UK.)

Water from the Irminger Current flows east along the northern side of the Iceland–Faroe Ridge, where it mixes with WNAW that has crossed the Ridge in the Iceland–Faroe Front. Approximately 2 Sv enters the Faroe–Shetland Channel and mixes with ENAW before flowing north in the Norwegian Atlantic Current (Hansen and

Østerhus, 2000). The eastern branch of the Norwegian Atlantic Current, which is trapped along the Norwegian shelf edge, is barotropic (i.e. it extends to the seabed) and has a pronounced seasonal variability (Skagseth and Orvik, 2002). Its yearly transport averages 4 Sv, although, being influenced by both local and large-scale windfields, the current is intensified during positive North Atlantic Oscillation (NAO) conditions (Orvik *et al.*, 2001). The western branch of the Norwegian Atlantic Current, a jet associated with the Arctic Front, has a mean transport of up to 5 Sv. There is significant exchange of water between the two branches (Mork and Skagseth, 2009; Rossby *et al.*, 2009).

Off northern Norway, the Norwegian Atlantic Current bifurcates: one branch of 2 Sv flows into the Barents Sea (Skagseth *et al.*, 2008), and one branch continues towards the Arctic Ocean. When it enters the Arctic Ocean through the Fram Strait, it submerges under the cold halocline, at ca. 200 m depth, and circulates around the Arctic Ocean. From the Barents Sea, in the northeast, ca. 2 Sv enters the Arctic Ocean, where approximately half is made up of cold, dense bottom water (Gammelsrød *et al.*, 2009).

The East Greenland Current carries cold water from the Arctic and modified, recirculating Atlantic Water south along the western margin of the Nordic seas. The transport in the East Greenland Current has large seasonal variability with an annual mean of 21 Sv at 75 °N (Woodgate *et al.*, 1999). Approximately 2.5 Sv is released from the East Greenland Current into the East Icelandic Current (Jonsson, 2007).

North Atlantic Water is greatly modified in the Nordic seas where it mixes with water from the Arctic and forms cold dense water that traverses the Greenland–Scotland Ridge and eventually flows into the Labrador Sea (Eldevik *et al.*, 2009; Figure 2.2). These dense waters pass through two main channels and seep over gaps in the Ridge. First, west of Iceland, approximately 3 Sv of Denmark Strait Overflow Water enters the Irminger Basin at the sill, descending rapidly as it flows south along the continental slope east of Greenland. Second, in the Faroe–Shetland Channel, approximately 4 Sv of Iceland–Scotland Overflow Water passes through the Faroe-Bank Channel, and then follows the slope of the Iceland shelf and Reykjanes Ridge en route to the Irminger Basin (Dickson and Brown, 1994; Yashayaev and Dickson, 2008).

The intermediate water mass that predominates in the North Atlantic is Labrador Sea Water. Cold and fresh, this water is formed by deep convection and can extend to 2400 m depth in severe winters, although at other times, it may not form at all or be much shallower (Yashayaev, 2007). It partly recirculates within the centre of the Subpolar Gyre, but also spreads northeast to the Iceland Basin and Rockall Trough (Yashayaev *et al.*, 2007) and south in the deeper waters of the western Atlantic around the Grand Banks.

Labrador Sea Water and the deeper overflows combine to form NADW; approximately 12 Sv leaves the Subpolar Gyre and flows south in the Western Atlantic Basin as part of the global thermohaline circulation (Schott *et al.*, 2004). A part of the deep limb of the MOC flows south in the Eastern Atlantic Basin, as shown in Figure 2.2. Upon reaching the Southern Ocean, the NADW upwells in the Antarctic Divergence. Some of this upwelled water may return directly to the Atlantic, but much of it is transported eastwards by the Antarctic Circumpolar Current, spreading northwards into the deeper basins of the Indian and Pacific oceans. Eventually, vertical mixing and upwelling lift it back to the surface, where it flows west in the warm Agulhas Current around the Cape of Good Hope, with 14 Sv drifting northwards in the Benguela Current (Schmitz, 1995). Finally, it joins the Gulf Stream system and is transported northwards into the Nordic and Labrador seas to start the cycle again.

The deep North Atlantic Ocean is bordered by extensive shallow shelf seas. By and large, the dynamics of these shallow regions differ considerably from those of the deep ocean, primarily because of the effects of tidal stirring and bottom friction on the water column (Simpson, 2005). Examples include the southern North Sea and Irish Sea, as well as numerous other locations close to shore; in these areas, the tides are sufficiently strong to maintain a mixed water column throughout the year. On the outer shelves, such as the European Atlantic margin and parts of the American seaboard, where depths exceed ~50 m, with tidal currents in the order of 10 cm s^{-1}, the upper layers become stratified in summer. The variable nature of windstress over shelf seas, and the steering that comes from varying depths and coastal boundaries, limits the ability of wind to drive sustained currents (Brink, 2005).

In the Barents Sea, a northern shelf sea, additional processes act on the water column: cooling through heat loss to the atmosphere; ice melt and freezing; and freshwater gain from the coastal current and rivers, which contributes to water-mass modification. One result is the formation of the cold, dense bottom water that enters the Arctic Ocean, where it may sink to ca. 1000 m depth (Rudels *et al.*, 1994).

Most of the long-term circulation on shelves is in the form of density-driven currents, which are driven by a balance between the offshore pressure gradient and the Coriolis force, and which emanate from the major river systems (Hill, 2005). Examples of these currents include the Scottish Coastal and the Irish Coastal currents, which transport water around Britain and Ireland and towards the southern North Sea, and the outflow from the Rhine and other rivers along the north coast of Europe that combine with the outflow from the Baltic to form the Norwegian Coastal Current, which flows north towards the Arctic.

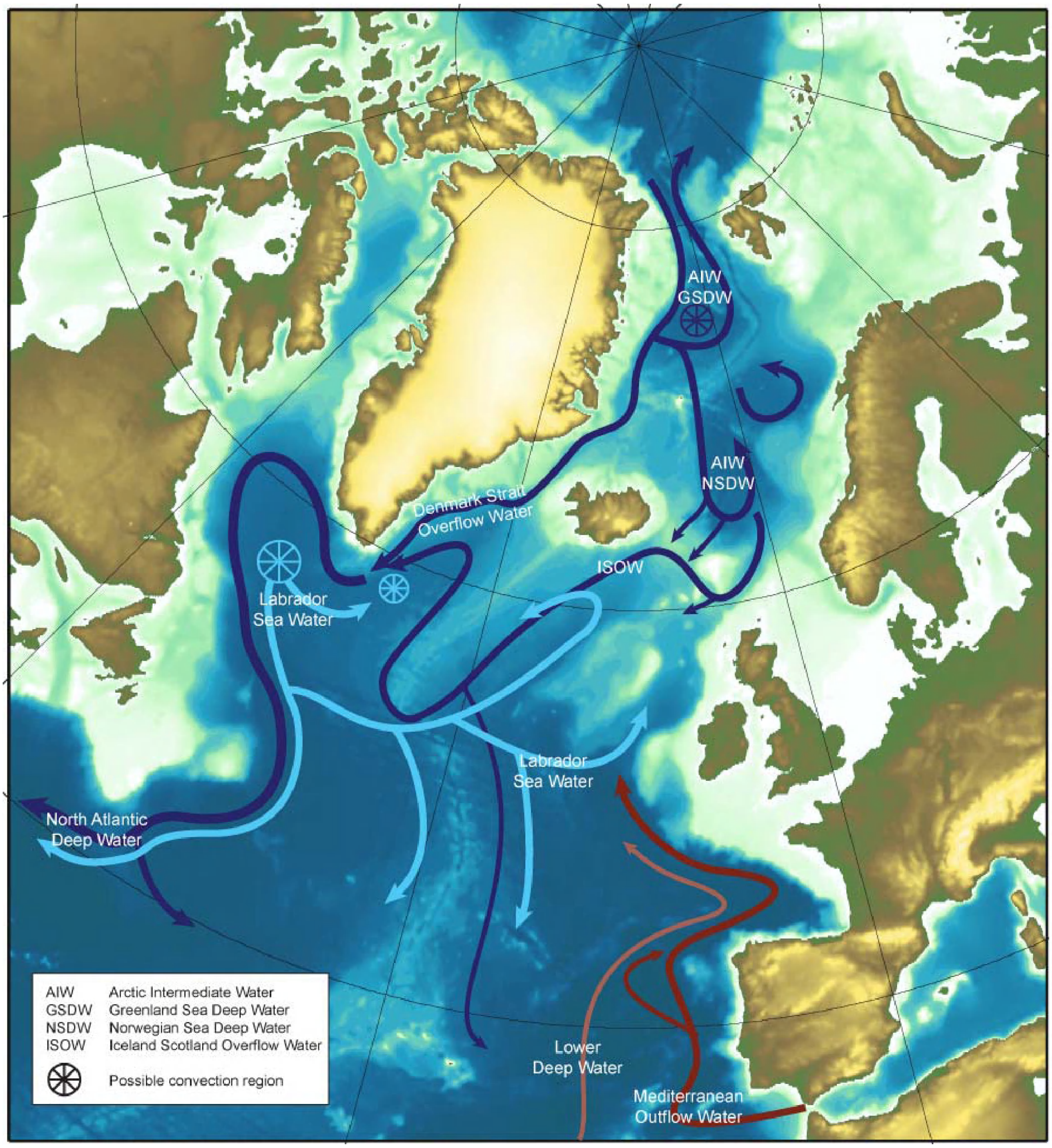

Figure 2.2. Schematic of the major pathways of the intermediate and deep waters of the North Atlantic superimposed on a map of bathymetry.

2.2 Exchanges between the ocean and atmosphere

The atmosphere is the source of most of the ocean's momentum and energy, with surface winds being the main driver of upper-ocean circulation through windstress. In the mid- to high-latitude North Atlantic, the mean pattern is of eastward stress from the westerly winds (Figure 2.3). This pattern varies on annual and shorter time-scales; some dominant seasonal to annual patterns, including the NAO, are discussed below. Shorter time-scale features, such as the mid-latitude storms, or "extra-tropical cyclones" (ETCs), are also described here.

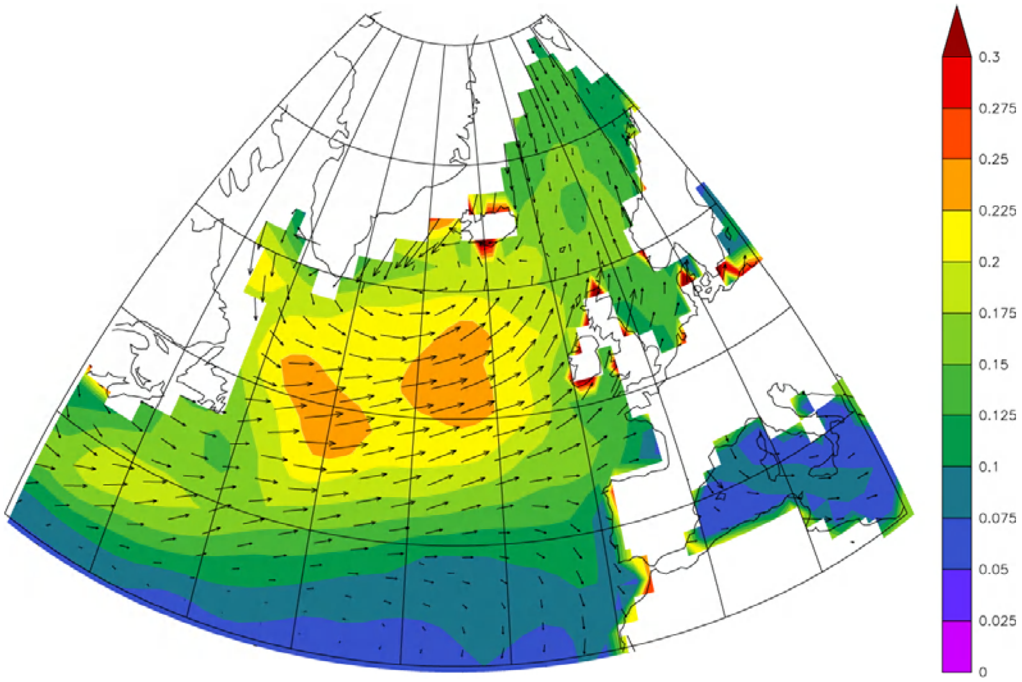

Figure 2.3. Annual mean of daily windstress (N m^{-2}) for 2009 over the North Atlantic Ocean. Arrows give windstress direction, and colour shading and length of arrows indicate the windstress value (N = Newton, the unit of the drag force). (Source: National Center for Environmental Prediction: NCEP1.)

The net heat flux at the ocean surface is a balance between a loss of heat through evaporation, long-wave radiation, and turbulent sensible heat flux, and a gain of heat through short- and long-wave radiation. Each of these components depends on a variety of ocean and atmospheric processes; measuring and describing them and their variations spatially and temporally over the ocean is a research activity that is vital to the improvement of climate simulations. The subpolar North Atlantic is a region with an average negative heat flux, i.e. the ocean gives off heat to the atmosphere (Figure 2.4).

Water is exchanged between the ocean and atmosphere by evaporation and precipitation. Evaporation is controlled by the temperature difference between the atmosphere and ocean, and by turbulence in the surface layer, which brings dry air into contact with the sea surface. Precipitation can be direct (rain or snow) or indirect (i.e. river run-off, ice-melt discharge from land, sea-ice melt). The high-latitude North Atlantic has a net gain of freshwater, whereas the subtropical North Atlantic is mainly evaporative (Figure 2.5). The surface salinity does not affect evaporation or precipitation, but changes in surface salinity can be indicative of changes in the hydrological cycle.

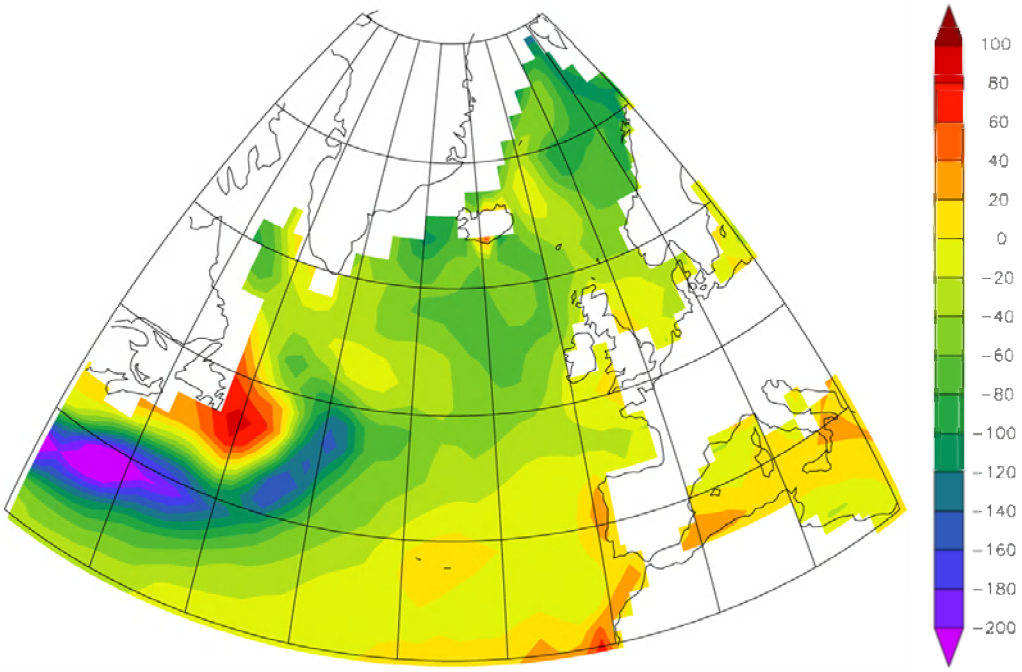

Figure 2.4. Annual mean of daily net heat flux (W m^{-2}) for 2009 over the North Atlantic Ocean (W = Watt). (Source: National Center for Environmental Prediction: NCEP1.)

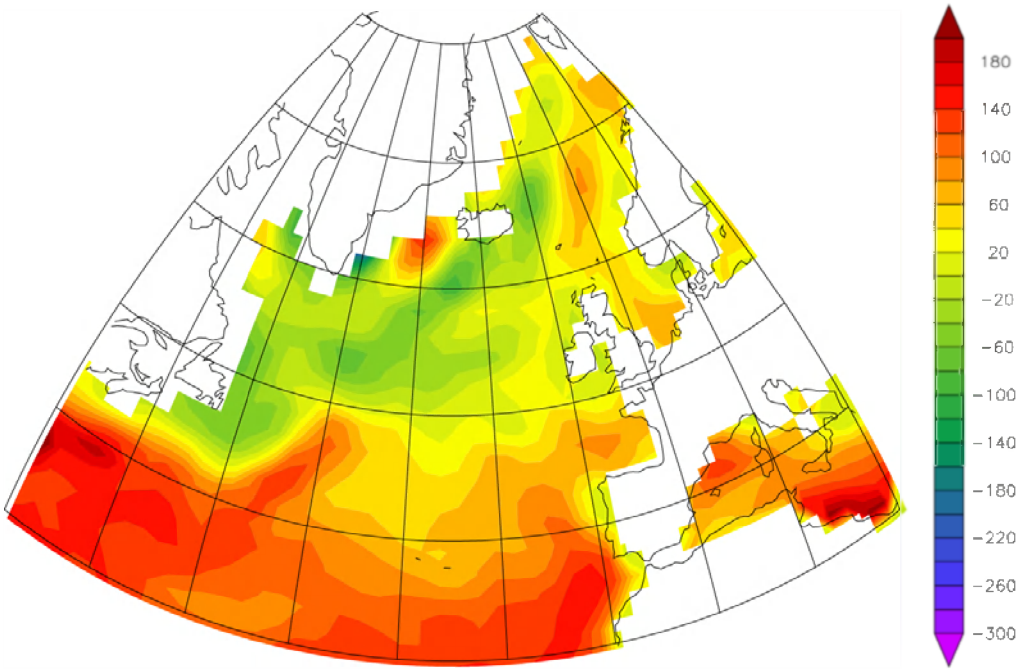

Figure 2.5. Annual mean of daily evaporation minus precipitation (E – P, cm year^{-1}) for 2009 over the North Atlantic Ocean (Source: National Center for Environmental Prediction: NCEP1.)

The ocean is also a major reservoir of CO_2, and because it is able to absorb more CO_2 from the atmosphere at lower temperatures, the northern North Atlantic is a net sink region. It is also a region where the surface acidity of the ocean has been most affected by anthropogenic CO_2 emissions (see Section 5).

2.2.1 Extra-tropical cyclones and storm tracks

Extra-tropical cyclones (ETCs) are the most prominent atmospheric feature over the mid-latitude North Atlantic. They strongly affect ship and air carrier routing over the region and lead to the predominantly westerly flow of the western European weather and climate. Thus, the question arises whether or not the frequency, intensity, and pathways (tracks) of ETCs may change. Here we review knowledge of past, present, and possible future changes in ETC occurrence and track locations for the mid-latitude North Atlantic. For a more detailed assessment, the reader is referred to overviews by Weisse and van Storch (2009) and Ulbrich *et al.* (2009).

Historical studies of 20th century ETCs relied on subjective detection from weather charts. More recently, numerical detection algorithms are used to search for these features in modern reanalysis products, such as NCEP or ERA-40 (Uppala *et al.*, 2005), and in the output of coupled general circulation models (GCMs) for predictions. The algorithms track mean sea level pressure (SLP) or vorticity (Greeves *et al.* 2007), and the success of cyclone detection depends on the method and the resolution of the underlying dataset (Raible *et al.*, 2008; Ulbrich *et al.*, 2009). The typical structure and life cycle of ETCs in terms of characteristics, such as depth, axis tilt, vorticity, windspeed, and precipitation, is of particular value for predictive analysis.

The present-day cyclone situation over the North Atlantic, as demonstrated by the track density and genesis density of ETCs, is given in Figure 2.6. A broad band of high track-densities spans almost the entire mid-latitude ocean south of Greenland from east to west, with decreasing values starting west of the UK and Ireland. The storms are extracted from the high-resolution, ERA-Interim reanalysis product applying the method of Hoskins and Hodges (2002). ERA-Interim is an "interim" reanalysis, by the European Centre for Medium-Range Weather Forecasting (ECMWF), for the period 1989–2009 in preparation for the next-generation extended reanalysis to replace ERA-40 (http://www.ecmwf.int/research/era/do/get/era-interim). This reanalysis has, among other features, a higher spatial horizontal resolution (T255, ca. 50 km) and improved physics. The extended resolution provides a better detection of cyclones and their genesis locations.

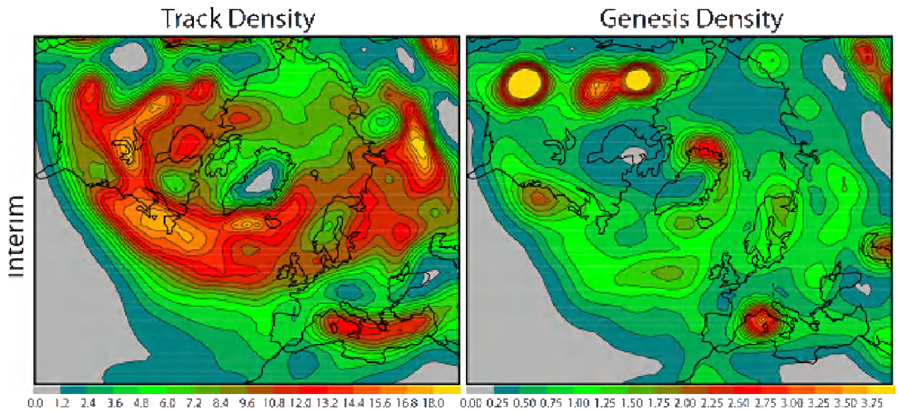

Figure 2.6. Left: track density, and (right) genesis density of extra-tropical cyclones (ETCs) over the North Atlantic region from ERA-Interim for the period 1989–2009. The densities are presented in units of number density per month per unit area, where the unit area is equivalent to a 5-degree spherical cap (~106 km^2). (Figure from Kevin Hodges, University of Reading, pers. comm.)

There is still uncertainty whether or not the intensity or frequency of North Atlantic ETCs has undergone a specific long-term trend in the recent past. Unfortunately, trend analyses for the past decades based on high-resolution reanalysis data are not yet available. There is some evidence from observational data that activity has increased since the 1960s, possibly associated with natural multidecadal variability (Leckebusch *et al.*, 2008). Negative trends have been found in 1958–1999 cyclone numbers over the North Atlantic, but no trend has been observed for northern Europe, and a positive trend has been found over higher latitudes (Ulbrich *et al.*, 2009). Some studies found an increase in the frequency and intensity of extreme cyclones during the second half of the twentieth century (Ulbrich *et al.*, 2009). However, Raible *et al.* (2008) did not find significant trends in mean cyclone intensities over the North Atlantic. The difference in these studies appears to be the result of contrasts in methodology and between the individual datasets (NCEP, ERA-15, ERA-40, JRA25), which raises doubts over the robustness of their findings.

Teleconnection studies relating North Atlantic cyclone features to the NAO (see below), the Pacific Decadal Oscillation (PDO), and the *El Niño* Southern Oscillation (ENSO) are reviewed by Ulbrich *et al.* (2009). Again, there is currently no clear result, but the NAO alone may not be sufficient to explain the variability of cyclone counts in the North Atlantic region. A number of recent studies report a noticeable poleward shift in storm tracks over the entire northern hemisphere (McCabe *et al.* 2001) and especially over the North Atlantic (Geng and Sugi, 2001; Weisse and van Storch, 2009).

With this uncertainty in mind, extracting an anthropogenic signal from changes in the cyclone data is not straightforward. Some studies demonstrate a consistency between observations and expected patterns of anthropogenic changes. For example, Wang *et al.* (2009) analysed trends in windspeed indices and SLPs for the second half of the 20th century, and claim a detectable response from anthropogenic and natural forcing combined.

Studies concerning future changes in ETCs over the North Atlantic rely on the use of coupled general circulation models driven by emission scenarios alone. Detection and tracking of the cyclones in low-resolution datasets are not simple; therefore, several methods have been employed. The existence of the different approaches to the study of storm tracks can be justified, because "mid-latitude storms are complicated features and as such require a variety of analytical methods to assess their representation in models" (Greeves *et al.*, 2007; Ulbrich *et al.*, 2008, 2009). In addition, different and partly competing processes acting on the genesis and evolution of cyclones may be represented in a different manner in models. Unsurprisingly, therefore, experiments with numerical models have led to a large range of results regarding the future variability of ETCs. Overall, the quality of detections is related to the resolution of the model in use; Bengtsson *et al.* (2009), in their analysis of intensive storms with a high-resolution climate model (T213, ca. 63 km), concluded that the results are in acceptable agreement with observations. Most of the published studies to date rely on models run with a coarser horizontal resolution.

Nevertheless, some consistent conclusions are emerging from recent studies. The first is that ETCs will shift towards the poles. In the northern hemisphere, there are indications of a poleward shift in the storm tracks (Meehl *et al.*, 2007) and a strengthening of the storm track north of the UK. In general, the shift in the extra-tropical storm tracks is associated with changes in the zonal sea surface gradient (Yin, 2005; Bengtsson *et al.*, 2006; Meehl *et al.*, 2007). Ulbrich *et al.* (2008) evaluated 23 runs from 16 coupled global climate models that were forced with a medium-emission scenario (A1B) with a focus on winter storm-track changes. Ensemble-mean changes include an increase in baroclinic wave activity over the eastern North Atlantic, amounting to 5–8% by the end of the twenty-first century.

A second conclusion is that there may be fewer or a stable number of ETCs. Several studies consistently note the possibility that fewer ETCs are likely to form in response to projected global warming over the twenty-first century. However, other studies show little change in cyclone number for similar scenarios (Weisse and van Storch, 2009).

Finally, several studies report an increasing number of more intensive mid-latitude cyclones in a warmer climate (Fischer-Bruns *et al.*, 2005; Bengtsson *et al.*, 2006; Pinto *et al.*, 2009). On the basis of the analysis of runs under an A1B scenario with nine coupled GCMs from the model pool of the Intergovernmental Panel on Climate Change (IPCC), Donat *et al.* (2010) found an increase in the mean intensity of cyclones associated with storm days of ca. 10% (±10%) in the ensemble mean over the eastern Atlantic, near the UK and Ireland, and in the North Sea.

In summary, a mixed picture is arising from studies of trends in ETCs and their properties over the North Atlantic. The large regional changes that have been observed are not inconsistent with natural variability. So, the question whether or not an anthropogenic signal can already be detected in observed ETC activity still remains open.

Regional details of storm-track changes are not well projected. A poleward shift in the ETC tracks and more frequent strong ETCs over the North Atlantic and Western Europe are results that are consistent with model-based studies of climate change in the twenty-first century.

2.2.2 North Atlantic Oscillation and other indices

The global climate exhibits a number of recognized oscillatory modes of variability on yearly–decadal time-scales. These alternate modes are referred to as atmospheric teleconnection patterns, and are linkages between centres of action over great distances. Atmospheric teleconnection patterns are typically expressed as an oscillation between high and low SLP centres and drive much of the interannual scale variability of both global and regional climatic conditions. Here we describe the dominant patterns of atmospheric variability significant to the North Atlantic; the NAO, the Arctic Oscillation (AO), and the East Atlantic Pattern (EAP).

Recent studies of the sea level pressure field over the North Atlantic (Cassou, 2008; Hurrell and Deser, 2010) suggest four typical winter atmospheric states (Figure 2.7). Two relate to the NAO positive and negative phases, one describes a "blocking" condition where high pressure dominates the European continent, with a trough in the Northeast Atlantic, and one describes an Atlantic Ridge state with a high pressure system in the Northeast Atlantic and a trough extending from Morocco to Scandinavia. The Atlantic Ridge state resembles the EAP described in Section 2.4.4 (Barnston and Livezey, 1987).

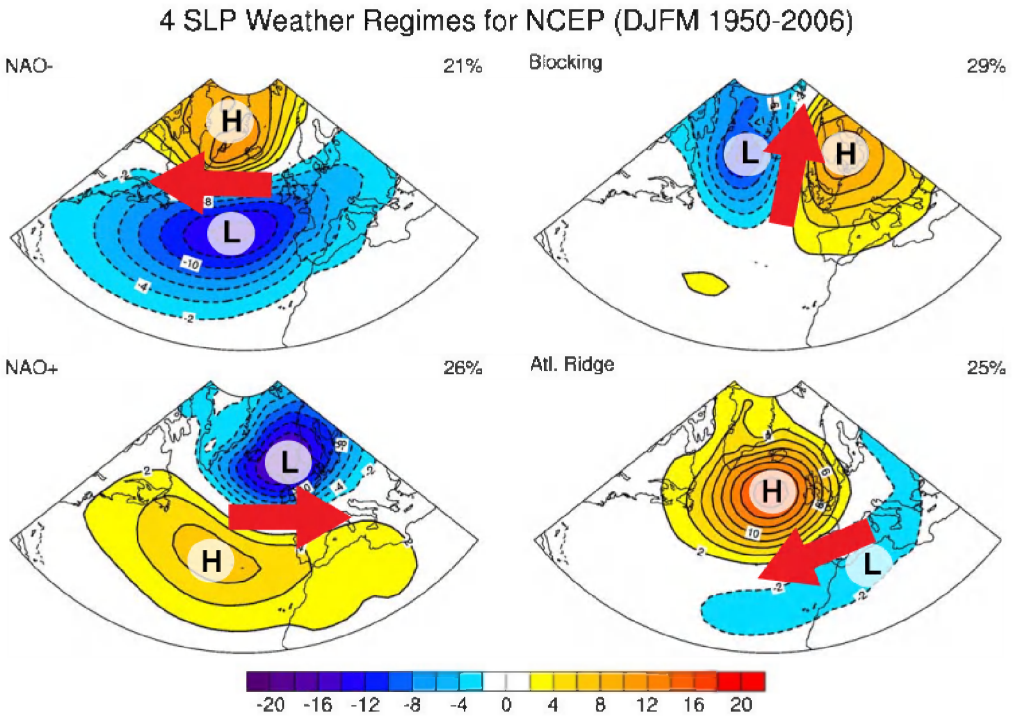

Figure 2.7. North Atlantic winter (December–March) climate regimes in sea level pressure (SLP; in hPa) using daily data from 1950 to 2006. The percentage at the top of each panel expresses the frequency of occurrence of a cluster out of all winter days since 1950. Contour interval is 2 hPa. Centres of high and low pressure and indicative wind direction (red arrows) are shown. (Adapted from Hurrell and Deser, 2010, Figure 9.)

The NAO is a pattern of atmospheric variability that has a significant impact on oceanic conditions. It affects windspeed, precipitation, evaporation, and the exchange of heat between ocean and atmosphere, and its effects are most strongly felt in winter. The NAO index is a simple device used to describe the state of the NAO. It is a measure of the strength of the sea-level air pressure gradient between Iceland and the Azores. When the NAO index is positive, there is a strengthening of the Icelandic low-pressure system and the Azores high-pressure system. This produces stronger mid-latitude westerly winds, with colder and drier conditions over the western North Atlantic and warmer and wetter conditions in the eastern North Atlantic. When the NAO index is negative, there is a reduced pressure gradient, and the effects tend to be reversed.

There are several slightly different versions of the NAO index, as calculated by climate scientists, but the Hurrell winter (December–March) NAO index is most commonly used. The Hurrell index is computed using the SLP difference between two stations. Other indices have been computed from gridded pressure fields, which allow the centres of the low- and high-pressure systems to move over time. Following a long period of increase, from an extreme and persistent negative phase in the 1960s to an extreme and persistent positive phase during the late 1980s and early 1990s, the Hurrell NAO index underwent a large and rapid decrease during winter 1995/1996 (Figure 2.8). Since then, the Hurrell NAO index has fluctuated around zero and has become a less useful descriptor of atmospheric conditions.

The ocean can respond quickly to the state of the NAO, particularly in winter, when atmospheric conditions affect the ocean so intensively that the effects are felt throughout the following year. Some regions, such as the Northwest Atlantic and the North Sea, are more responsive to the NAO than other regions, such as the Rockall

Trough. However, the NAO is not the only, or even the main, control on ocean variability. Over the Atlantic as a whole, the NAO still only accounts for one-third of the total variance in winter SLP. The chaotic nature of atmospheric circulation means that, even during periods of strongly positive or negative NAO winters, the atmospheric circulation typically exhibits significant local departures from the idealized NAO pattern.

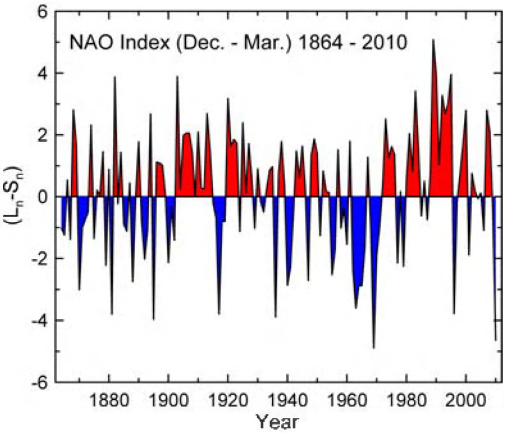

Figure 2.8. The Hurrell winter (December–March) North Atlantic Oscillation (NAO) index for the years 1864–2010. The index is based on the difference in normalized sea level pressure (SLP) between Lisbon, Portugal (Ln) and Stykkisholmur/Reykjavik, Iceland (Sn). (Data source: http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html (May 2011).)

It is essential to understand the mechanisms that control and affect the NAO and its temporal evolution. The evaluation of climate model ensemble experiments using a coupled ocean–atmosphere dynamics general circulation model reveals a small but consistent trend towards more positive values of NAO indices for a spread of greenhouse gas scenarios (Ulbrich *et al.*, 2008; Osborn, 2004). In chapter 10 of the Working Group I contribution to the IPCC's Fourth Assessment Report, Meehl *et al.* (2007) state a positive trend in the NAO indices in greenhouse gas scenario experiments.

Trends in the NAO over the past 30–50 years may already incorporate an influence from anthropogenic activities (Ulbrich *et al.*, 2008; Paeth *et al.*, 2008). An enhanced interannual NAO variability has been observed over the last half of the 20th century (Feldstein, 2002). However, not all models used for projections of future climate reveal a clear NAO pattern. In addition, only a subset of the models produces a realistic spectrum of the NAO variability (Stephenson *et al.*, 2006). In general, spatial shifts in the relevant pressure centres vary between the different models, so details of patterns and variability are extremely dependent on the model used (Ulbrich *et al.*, 2008). The absence of a proven skilful predictive model leaves significant uncertainty about NAO variability in future (Visbeck *et al.*, 2001). It has been demonstrated that there is potential for medium-range predictions of the NAO (2–4 weeks; Cassou, 2008), because NAO phases are affected by the main climate intra-seasonal oscillation in the tropics, the Madden–Julian Oscillation. For this to be realized, better observations and simulations of tropical coupled ocean–atmosphere dynamics are required.

2.2.3 Arctic Oscillation

The AO is another pattern of sea-level air pressure that explains ca. 25% of the pressure variability north of 20°N in the northern hemisphere (Ambaum *et al.*, 2001).

It has opposing centres of action over the Arctic and the mid-latitudes and, because it includes the entire northern hemisphere, it is sometimes referred to as the Northern Annular Mode. A negative AO index means weaker winds, lower winter pressures, and more sea ice (AMAP, 2009). From the mid-1980s to the mid-1990s, the AO, like the NAO, was strongly positive; since then, the AO has also fluctuated between weakly positive and negative values. By definition, the AO includes the NAO, and the two structures of variability are highly correlated (0.95 for monthly SLP anomalies; Deser, 2000). The AO may be dominated by the variability of the North Atlantic sector and may not be truly "annular" (Ambaum *et al.*, 2001; Deser, 2000).

2.2.4 East Atlantic Pattern

The EAP (Wallace and Gutzler, 1981; Barnston and Livezey, 1987) describes a significant pattern of variability of mean SLP over the North Atlantic. The EAP is important in all months except May–August, and is structurally similar to the NAO, consisting of a low-pressure centre in the Northeast Atlantic near 55°N, 20–35°W, and a high-pressure centre over North Africa or the Mediterranean Sea.

The EAP exhibits strong multidecadal variability and has demonstrated a tendency towards more positive values since 1970, with particularly strong and persistent positive values during 1997–2007 (Figure 2.9). The positive phase of the EAP is associated with above-average surface air temperatures in Europe throughout the year and below-average surface air temperatures over the southern USA during January–May and in the north-central USA during July–October. It is also associated with above-average rainfall over northern Europe and Scandinavia, and with below-average rainfall across southern Europe.

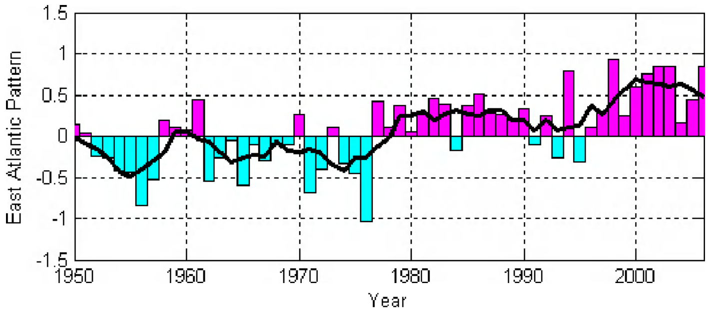

Figure 2.9. Time-series of the annual mean East Atlantic Pattern (EAP), from 1950 to 2006 (bars), overlain by a 5-year running mean (black line). (Data from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center, http://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml.)

3 Long-term physical variability in the North Atlantic Ocean

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3.1 Introduction

The North Atlantic Ocean is an ever-changing environment. From the surface ocean to the seabed, changes in temperature, salinity, currents, and chemical and biological properties occur on time-scales from as little as hours to as long as millennia. There are spatial changes too, not only from one side of an ocean basin to another, but also within patches as small as a few centimetres across. Making sense of all this variability is a major challenge; to understand regional change on climatic time-scales requires knowledge of the processes that take place over much shorter periods of time and space. New aspects of variability are being recognized as more data are collected and existing data are reanalysed, and knowledge of the physical mechanisms within the ocean and atmosphere that affect the environment is growing rapidly.

This section presents a contemporary overview of physical variability in the North Atlantic Ocean and adjacent seas (Figure 3.1). It describes the observed changes at seasonal, interannual, decadal, and longer time-scales, and discusses the mechanisms that influence them. It is important to recognize that physical variability includes the effects of natural variability as well as anthropogenic climate change. At present, it is rarely possible to successfully separate the effects of climate change from natural variability in North Atlantic observations, although ongoing research is addressing this issue.

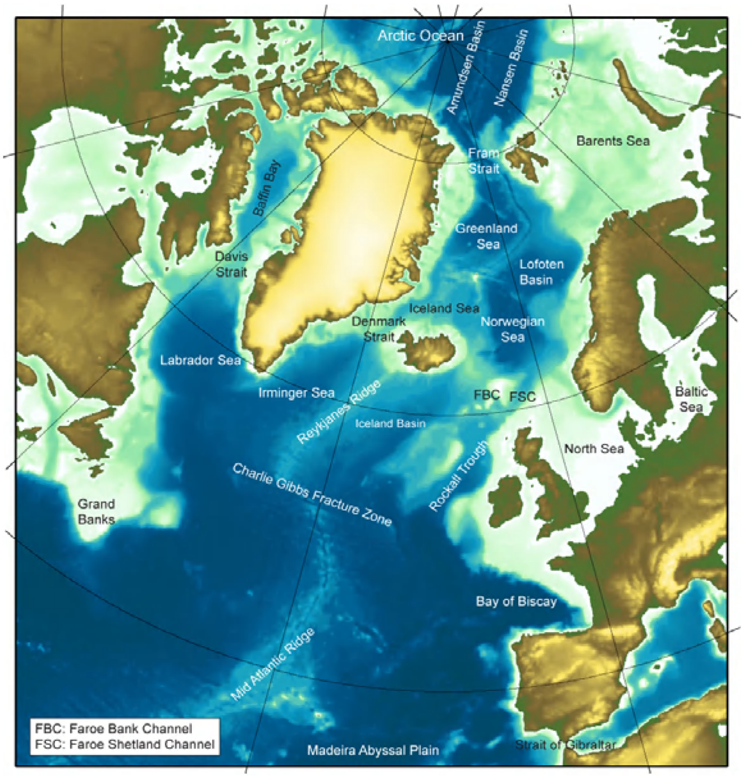


Figure 3.1. The main bathymetric features of the North Atlantic.

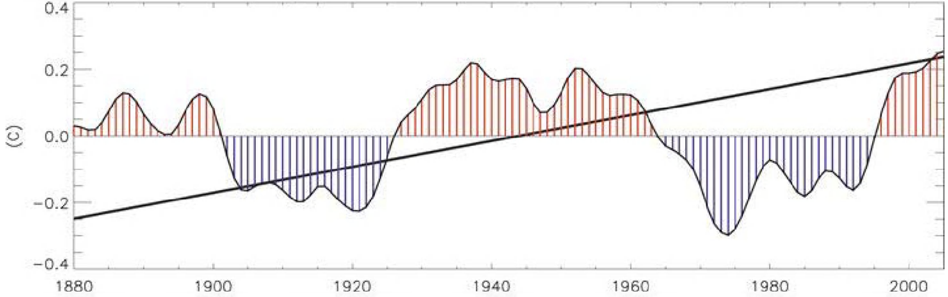
3.2 Large-scale temperature and salinity variability

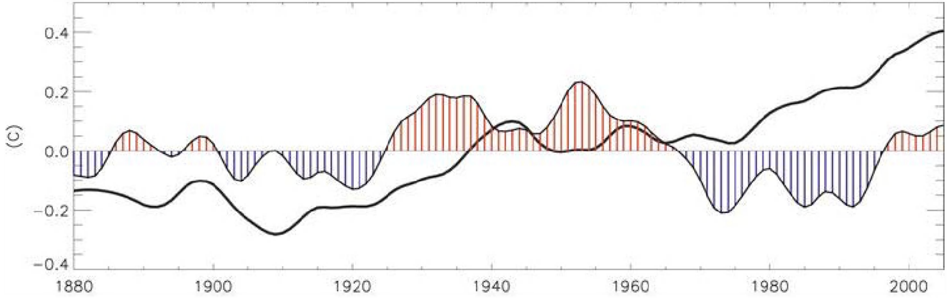
3.2.1 The sea surface and upper ocean

Variability in the sea surface temperature (SST) of the North Atlantic over the past 100 years is probably the most well-defined parameter because substantial effort has gone into the collation of high-quality datasets. Those datasets reveal that, in addition to the response to anthropogenic climate change and year-to-year changes, there is a decadal variability that affects the whole North Atlantic. This pattern has become known as the Atlantic Multidecadal Oscillation (AMO; after Kerr, 2000). A growing number of studies suggest that the AMO has an important impact on physical and biological processes. Examples include North American and European climate and precipitation (Enfield *et al.*, 2001; Sutton and Hodson, 2005), salmon recruitment (Friedland *et al.*, 2009), cod populations (Drinkwater, 2009), SST around Ireland (Cannaby and Hüsrevoğlu, 2009), temperature conditions in the Barents Sea (Skagseth *et al.*, 2008), and coastal phytoplankton distribution (Dixon *et al.*, 2009).

The AMO index is typically derived by averaging the SST of the North Atlantic and removing the fitted linear trend (upward), which is thought to represent the global warming response to an increasing concentration of CO_2 in the atmosphere (e.g. Enfield *et al.*, 2001; Knight *et al.*, 2006). The AMO is thus intended to represent variability resulting from mechanisms other than anthropogenic climate change. The index reveals periods of relative cold in 1900–1925 and 1970–1990, and relative warmth in 1930–1960 and in the present period since 1990 (Figure 3.2a). The multidecadal variability in SST is likely to be strongly related to large-scale oceanic circulation in the North Atlantic, such as the Meridional Overturning Circulation (MOC; see Section 3.4.2) as well as global atmospheric teleconnection processes (Hagen and Feistel, 2008; Sidorenkov and Orlov, 2008). The oscillatory nature of the AMO pattern has given rise to predictions that the coming decades may experience a cooling of the surface of the North Atlantic as the AMO index moves into a downward trend from the current high (Knight *et al.*, 2006).

However, alternative methods have been used to derive an AMO index, and these produce a slightly different pattern (Figure 3.2b, c). The methods differ in the way they calculate the signal of anthropogenic climate change; the method used by Kerr (2000) assumed the signal to be a linear trend. Two alternative methods use either the non-linear regressions of the global mean SST, or the global mean surface temperature (land and ocean), as a proxy for anthropogenic climate change (Mann and Emanuel, 2006; Trenberth and Shea, 2006; Ting *et al.*, 2009). These alternative AMO indices lead to a slightly different conclusion and prediction, namely that the AMO may still be in an upward trend and future decades may experience more warming (Ting *et al.*, 2009).


(a) Linear Trend and Detrended NASSTI(shading)


(b) NASSTI regressed onto SSTg index (shading: regression residual)

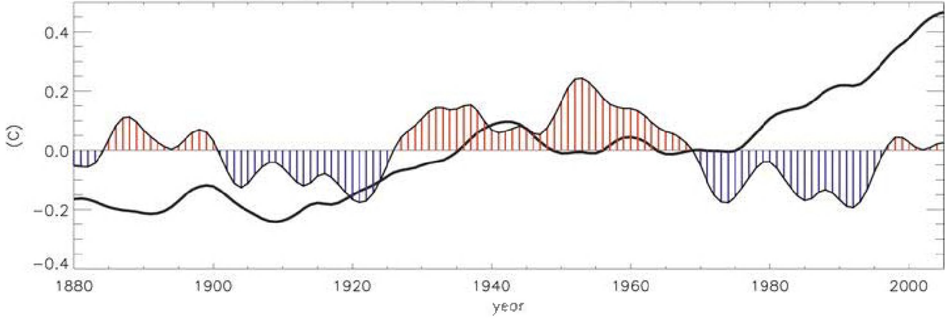

(c) NASSTI regressed onto Tg index (shading: regression residual)

Figure 3.2. The Atlantic Multidecadal Oscillation (AMO) index constructed by different methods. Initially, calculated from averaged North Atlantic sea surface temperature (SST) with: (a) the upward linear trend (black line) removed to adjust for the response to increased atmospheric CO_2; (b) the global mean SST pattern (black line) removed; (c) the global mean surface temperature (land and ocean) pattern (black line) removed. (Source: Ting *et al.*, 2009, Figure 2.)

A similar view of multidecadal variability in observed and modelled temperature in the North Atlantic was presented by Polyakov *et al.* (2010). The long-term trend is expressed as the non-linear first mode of surface and subsurface variability. The second mode of variability is multidecadal, similar to the AMO described above, and is related to the enhancement (warm phase) or slow-down (cool phase) of the MOC. The long-term trend reveals warming of the North Atlantic as a whole, but relative cooling in the subpolar region from 1920 to 2000. This trend was masked in the 1990s by a positive phase of the multidecadal variability.

Long-term variability of the surface salinity of the North Atlantic also reveals interannual and decadal-scale fluctuations, although records are not as complete as for temperature. Reverdin *et al.* (1994) provided the first comprehensive review, which is in the process of being updated. The data show that surface temperature and salinity in the Subpolar Gyre are usually correlated (warm periods are also saline). A regression of sea-surface salinity anomalies on the low frequency component (5-year running average) of the winter North Atlantic Oscillation (NAO) index is generally positive at zero lag in most of the basin, with maximum values in the east, although negative values are found along the western boundary at around 40–50°N.

Since the 1960s, the Nordic seas have demonstrated large-scale changes in the distribution of water masses, mainly because of changes in the atmospheric circulation (as indicated by changes in the NAO). From the 1960s to the 1990s, a cooling and freshening of the upper layer was observed, attributable to an increased supply from the East Icelandic Current (Blindheim *et al.*, 2000). Variations in wind direction and strength over the area are important for the release of freshwater from the East Greenland Current into the Nordic seas (Jonsson, 1992). The westward extent of the Arctic Front in the Norwegian Sea is also found to be less during a high phase of the NAO compared with the low phase (Blindheim *et al.*, 2000), and the difference between its broadest (1968) and its narrowest (1993) recorded extents exceeded 300 km (Figure 3.3). When the NAO winter index is high, the windstress brings the Atlantic Water closer to the slope, and continental shelf and the eastward extent of Arctic Water is increased. Decadal changes of salinity and ice cover in the Baltic Sea are a sensitive indicator for anomalies in the air pressure and windfields over the North Atlantic (Hagen and Feistel, 2005, 2008).

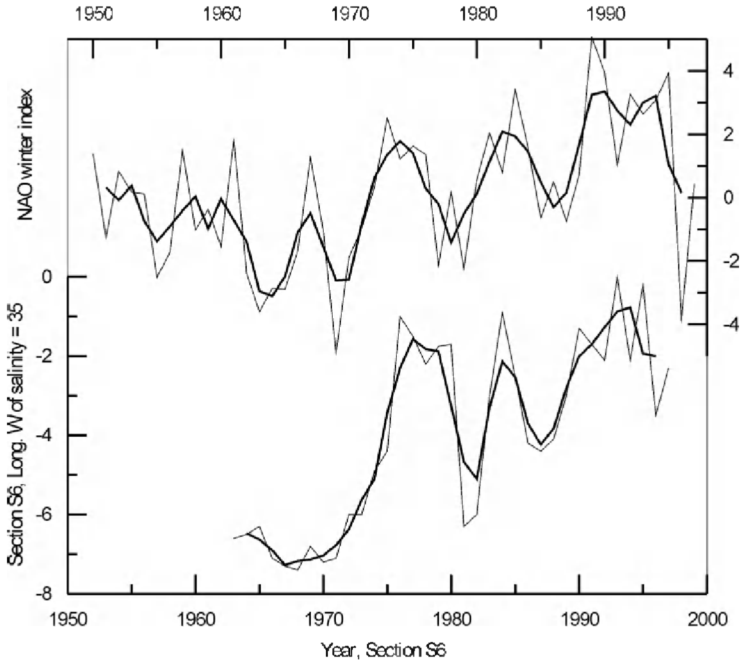


Figure 3.3. Three-year running means of the winter NAO index and the westward extent of Atlantic Water (in longitude) in the Norwegian Sea. (Source: Blindheim *et al.*, 2000, Figure 7.)

The freshening trend in the upper layer of the Nordic seas during the 1960s–1990s reversed in the 2000s, as the inflowing Atlantic Water increased in temperature and salinity (Holliday *et al.*, 2008). This has resulted in some record-high temperature and salinity values during 2003–2005. A similar trend has been observed since the mid-1990s in the upper layer of the Subpolar Gyre (in the Rockall Trough (Holliday *et al.*, 2008), along 20°W (Johnson and Gruber, 2007), above the Reykjanes Ridge (Thierry *et al.*, 2008), and even downstream near the Greenland coast). Because large-scale temperature and salinity anomalies are traceable along the current branches with a time-lag (Furevik, 2001; Holliday *et al.*, 2008; Eldevik *et al.*, 2009), there exists a potential for predictability.

The interannual–decadal variability of the upper ocean is summarized in one form in Figures 3.4 and 3.5, which show temperature and salinity time-series at specific locations. The upper ocean is defined as the part of the water column that lies above the permanent thermocline, typically 600–800 m in the deep ocean. In summary, at present, the Subpolar Gyre and Nordic seas (Holliday *et al.*, 2008) have elevated temperatures, the shelf seas of the Northwest North Atlantic have average temperature and low salinity, and the northwest European shelf seas have high temperature and average-to-high salinity (low surface salinity in the Baltic Sea).

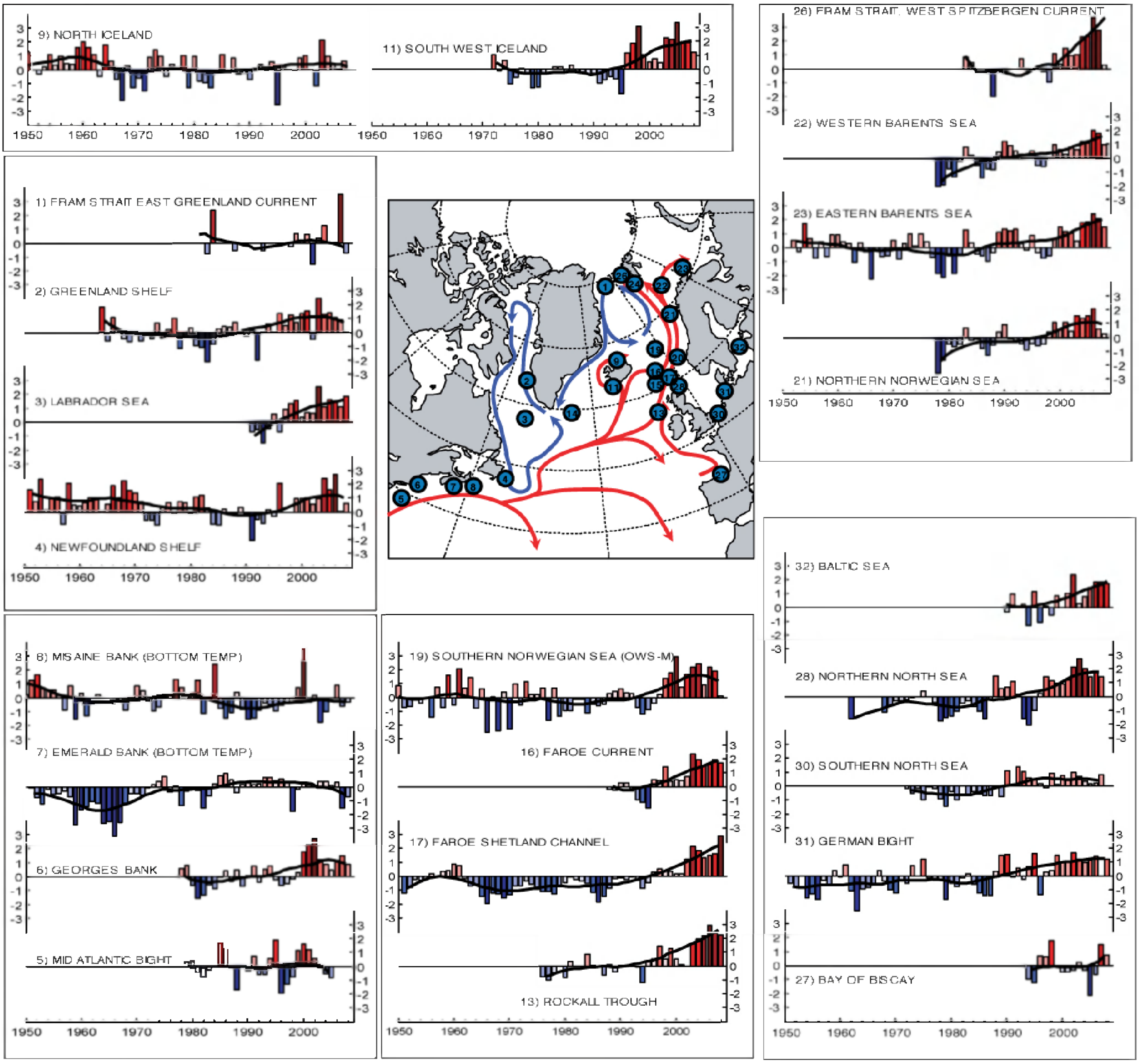


Figure 3.4. Upper ocean temperature anomalies at selected locations across the North Atlantic (including bottom temperatures over two shallow banks). The anomalies are normalized with respect to the standard deviation (e.g. a value of +2 indicates 2 standard deviations above normal). Colour intervals = 0.4; reds = positive/warm, blues = negative/cool. (Source: modified from Holliday *et al.*, 2009, Figure 1.)

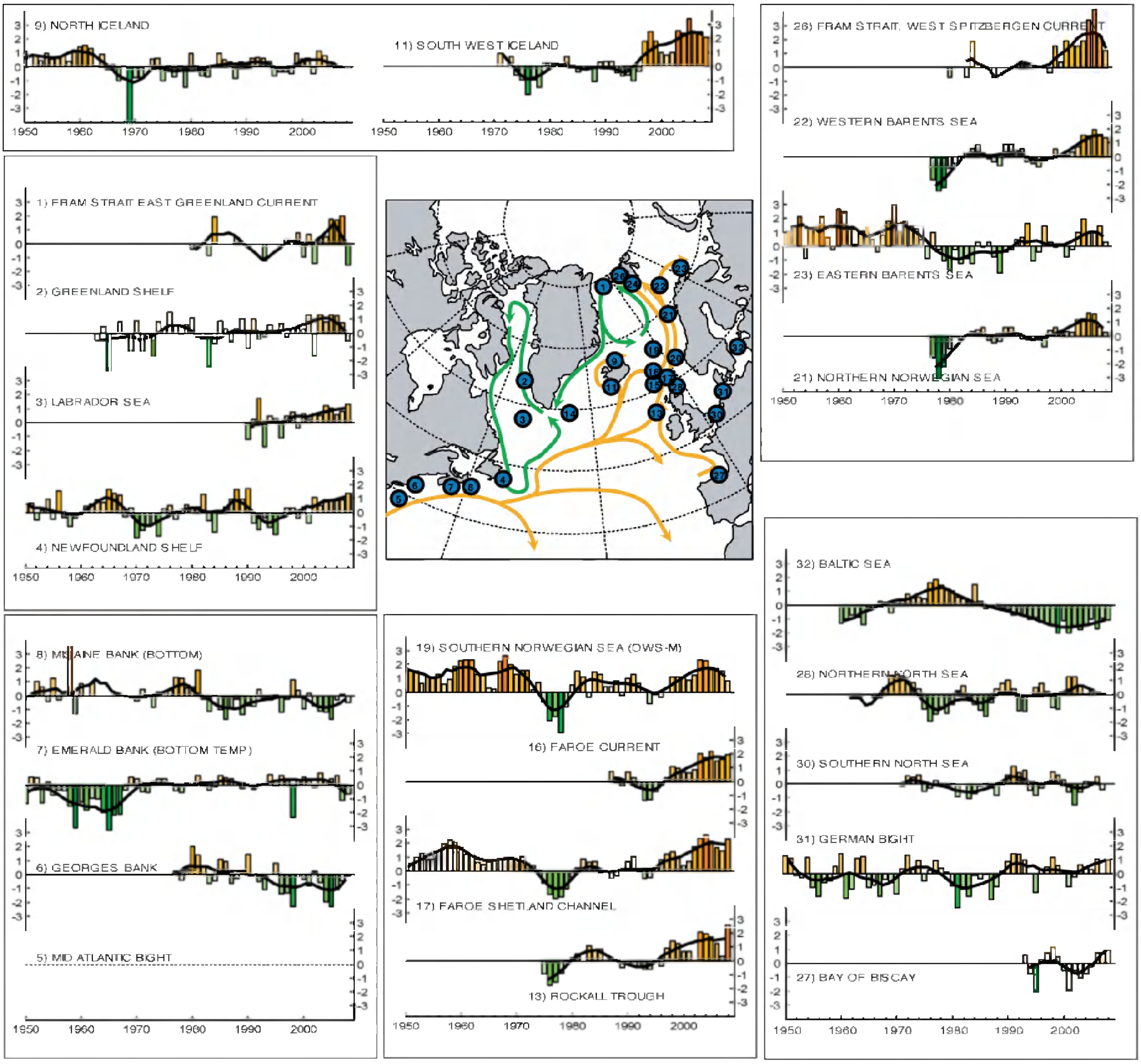


Figure 3.5. Upper ocean salinity anomalies at selected locations across the North Atlantic (including bottom salinities over two shallow banks). The anomalies are calculated relative to a long-term mean and normalized with respect to the standard deviation (e.g. a value of +2 indicates 2 standard deviations above normal). Colour intervals = 5; oranges = positive/saline, greens = negative/fresh. (Source: modified from Holliday *et al.*, 2009, Figure 2.)

An alternative way of considering temperature and salinity is to look at changes in heat content and freshwater content. This approach is typically used to represent average changes at a basin-wide scale and often uses measurements taken by instruments with lower precision than the station-based hydrographic data (e.g. expendable bathythermographs (XBTs) and profiling floats). An advantage of this approach is that more data with greater spatial coverage are available, but the analyses are prone to weaknesses, such as instrumentation and methodology bias (Levitus *et al.*, 2009; Palmer and Haines, 2009). Despite this, however, robust patterns are emerging from recent reanalyses. The North Atlantic has experienced an increase in upper ocean heat content since the 1960s, and the rate of increase has been greater there than anywhere else on the globe (Figure 3.6; Levitus *et al.*, 2009). During that period, there has been significant decadal-scale variability in the basin-scale mean and significant intrabasin spatial variability (Lozier and Stewart, 2008). This level of variability means that all reported trends need to be treated with caution; for example, Lozier and Stewart (2008) demonstrated a trend in cooling in the subpolar North Atlantic during the periods 1950–1970 and 1980–2000, a similar conclusion to that of Polyakov (2010). This appears to contradict their overall conclusion of a warming North Atlantic since the 1950s, but is actually compatible. The cooling trend is simply the result of the periods chosen for the comparison, and of the spatial variability.

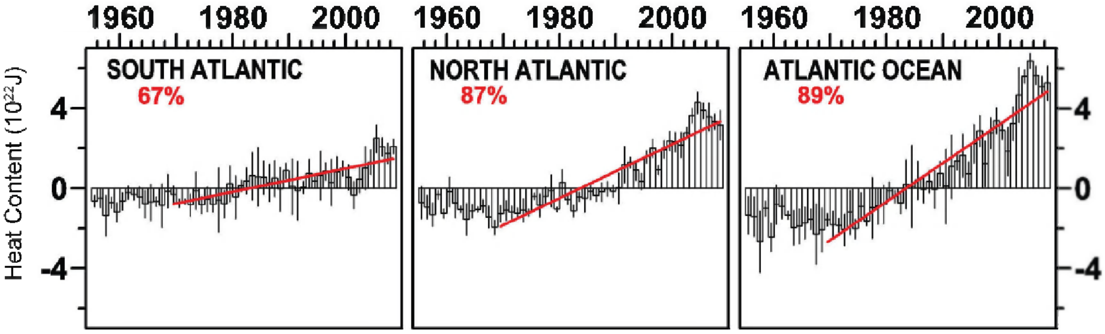


Figure 3.6 Time-series of yearly ocean heat content for the 0–700 m layer of the Atlantic Ocean (with percentage variance accounted for by the linear trend). (Source: Levitus *et al.*, 2009, Figure S11, upper panel.)

The freshwater content of the North Atlantic demonstrates similar variability on decadal scales. It was widely reported that the freshwater content increased from the 1960s to the 1990s, a change which was linked to the hydrological cycle in the subtropics (Curry *et al.*, 2003; Curry and Mauritzen, 2005) and the freshwater exchanges in the whole system, from the Arctic to the subtropical North Atlantic (Peterson *et al.*, 2006). As for the heat content, there is variability within these reported trends at temporal, horizontal, and vertical scales. From the mid-1990s to 2006, the freshwater content of the North Atlantic and Nordic seas was reduced (Boyer *et al.*, 2007). The change took place mainly in the upper ocean, whereas the water below 1300 m continued to demonstrate an increasing freshwater content to 2006 (Figure 3.7). It is currently being debated whether or not any global ocean warming trend is already exceeding the uncertainty of the scattered data (Lyman *et al.*, 2010; Trenberth, 2010). Between 1993 and 2008, a statistically significant increase in the heat content of 0.64 ± 0.29 W m^{-2} was observed for the upper 700 m of the global ocean water.

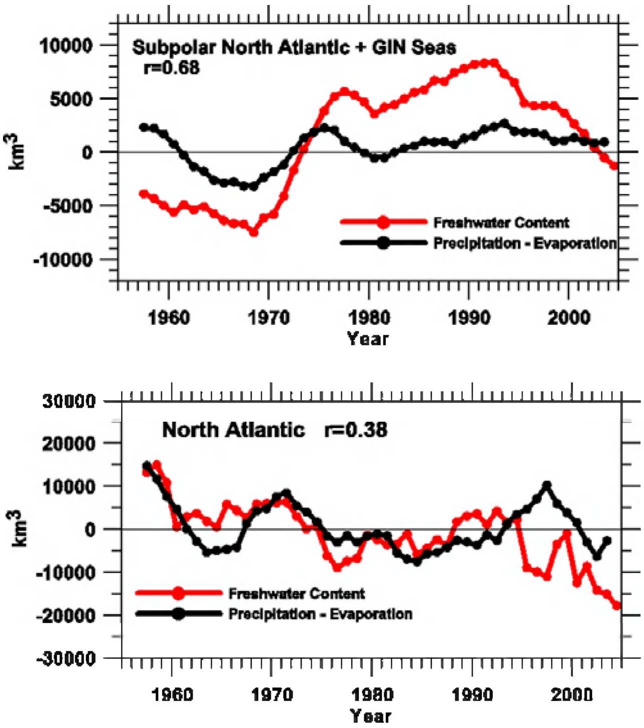


Figure 3.7. Equivalent freshwater content (0–2000 m, red) vs. precipitation minus evaporation from NCEP/NCAR reanalysis (black) for: (top) subpolar North Atlantic; and (bottom) North Atlantic (0–80°N). (Source: Boyer *et al.*, 2007, Figure 5.)

The broad correlation of temperature and salinity variability implies a dynamical origin to much of the decadal variability. For example, the decadal scale variations in the Northeast Atlantic are widely believed to be the result of changes in the circulation of the Subpolar Gyre (Hatun *et al.*, 2005; Hakkinnen and Rhines, 2009; Herbaut and Houssais, 2009). However, the spatial variability in temperature and salinity indicates that there is more than one mechanism at work. Changes in atmospheric patterns may account for changes in the broad heat content pattern (Lozier and Stewart, 2008), although the precipitation–evaporation balance can be invoked to explain changes in the freshwater content in some regions and during some periods (Josey and Marsh, 2005; Boyer *et al.*, 2007). Results from coupled climate models suggest that the recent increase in salinity in the subtropical North Atlantic may be a response to anthropogenic forcing (increased evaporation), but that subpolar changes in salinity are of similar magnitude to internal (non-anthropogenic) variability (Pardaens *et al.*, 2008; Stott *et al.*, 2008). More research is needed to untangle the complexity of the patterns of variability, their controlling mechanisms, and how they vary in space and time. In particular, it is not yet possible to say with confidence how much of the variability of the surface and upper ocean is the result of anthropogenic climate change, nor what future variability will resemble.

3.2.2 Intermediate water

The intermediate waters of the subpolar North Atlantic are dominated by the cold, fresh, and well-mixed Labrador Sea Water (LSW), which has long been known to demonstrate strong decadal variability of properties and of the depth of winter convection at its source (Lazier, 1980; Yashayaev, 2007). The LSW was warm and saline from the mid-1960s to the early 1970s, and fresh and cold between the late 1980s and mid-1990s, after which it has become warmer and more saline (Figure 3.8). The pattern of temperature variation is dominated by the flux of heat from the ocean to the atmosphere during very deep winter convection. Salinity is affected by precipitation, the inflow of freshwater at the surface, and by mixing with more saline water masses at depth. During prolonged periods of deep convection, such as in the early 1990s, large volumes of cold, fresh intermediate water are produced. As the LSW spreads through the Subpolar Gyre, it mixes with water of the same density as well as with water above and below; thus the properties of LSW at any location within the Subpolar Gyre depend on the original properties as well as the water with which it has mixed (Yashayaev *et al.*, 2007). Despite unexpected deep convection in winter 2007/2008 (Våge *et al.*, 2009; Yashayaev and Loder, 2009; see Section 4.3), the LSW is currently warm and saline.

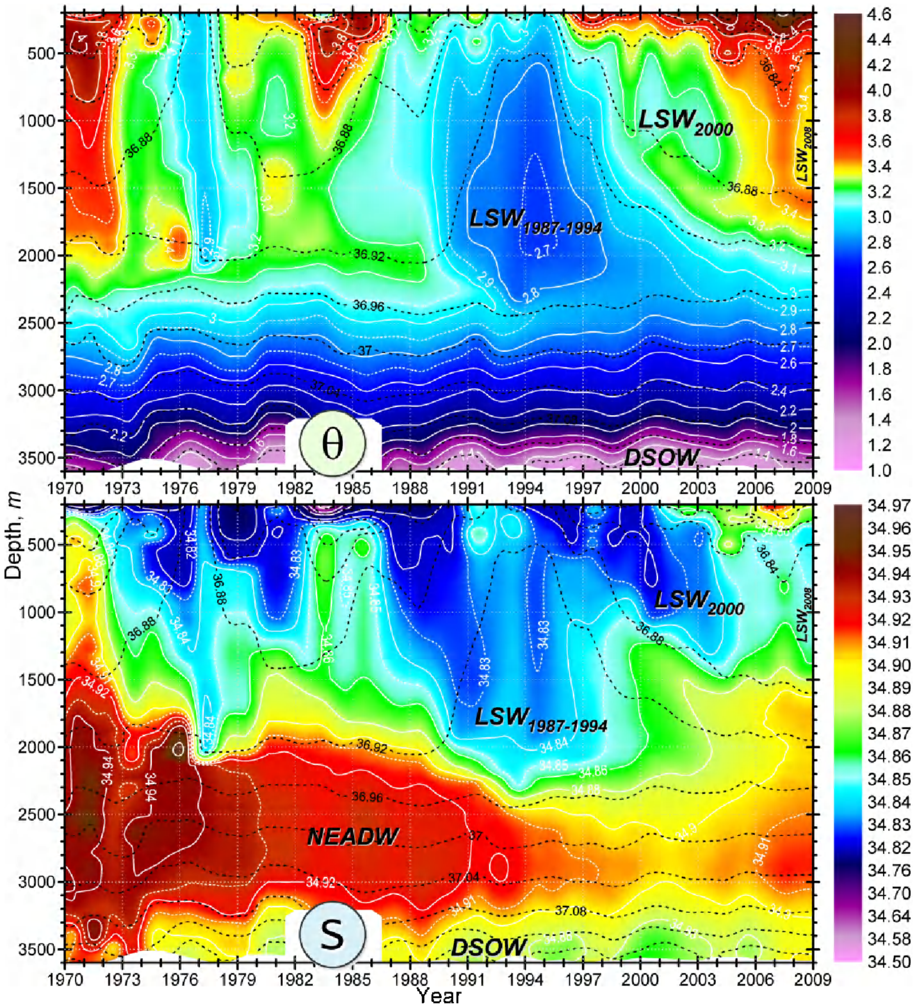


Figure 3.8. Time evolution of potential temperature (θ) and salinity (S) in the central Labrador Sea. Dashed lines indicate potential density anomaly (ref. 2000 db). LSW$_{2000}$ = Labrador Sea Water (LSW) produced in 2000; LSW$_{1987-1994}$ = LSW generated between 1987 and 1994; NEADW = North East Atlantic Deep Water (modified Iceland Scotland Overflow Water); DSOW = Denmark Strait Overflow Water. (Source: Yashayaev and Loder, 2009, Figure 2.)

Mediterranean Outflow Water (MOW) is another newly ventilated intermediate water mass that plays an important role in the climate system. This warm, saline water entrains surface Atlantic Water as it descends from the Strait of Gibraltar and carries heat, salt, and anthropogenic carbon into the high-latitude intermediate layers (Alvarez *et al.*, 2005). The properties of the MOW vary with time; from 1960 to 1994, the MOW near the Strait of Gibraltar became warmer and more saline, in sharp contrast to the rest of the Subpolar Gyre during that period (Potter and Lozier, 2004). The impact of the property changes of the MOW as it is distributed across the

Subpolar Gyre and mixes with other intermediate water is unclear. Recent analysis has demonstrated that the penetration of the MOW into the Subpolar Gyre varies with time in a way that may be related to the NAO (Lozier and Stewart, 2008). When the Subpolar Front moves east in response to a period of high NAO and stronger Subpolar Gyre circulation, the subpolar waters essentially block the northward penetration of the MOW into the gyre. The effect of this varying extent of MOW on the dynamics of the Subpolar Gyre is not yet understood.

In the Nordic seas, the most outstanding change in recent decades is the development of an intermediate layer of Arctic Water that is derived from the Greenland and Iceland Seas and has spread over the entire Norwegian Sea (Blindheim, 1990). The formation and pathways of the intermediate water are not fully understood, but with the absence of newly formed deep water in the Greenland Sea since the 1970s, production of intermediate water there will, at least partly, form and maintain the intermediate water in the Norwegian Sea. The lack of new formation of Greenland Sea Deep Water has led to greater influence by the warmer Arctic Ocean Deep Water, and therefore a considerable warming of the deep water in both the Greenland and Norwegian Seas (Peterson and Rooth, 1976; Østerhus and Gammelsrød, 1999).

3.2.3 North Atlantic Deep Water

The deepest layers of the subpolar North Atlantic are dominated by cold, dense overflow waters that exhibit a variability of their own that is not always in phase with the shallower layers. Overflow waters are the collective terms for cold, dense waters formed north of the Greenland–Scotland Ridge. After they flow over the Ridge, they sink below and mix with the lighter Subpolar Gyre surface waters, following pathways determined by bathymetry. There are two aspects to the pattern of variability of their end product, the North Atlantic Deep Water (NADW), which is exported from the Labrador Sea into the global ocean. First, temperature and salinity varies at the northern sills (Denmark Strait and Iceland–Scotland), but because they mix heavily with the surrounding water as they descend into the subpolar basins, they are greatly influenced by ambient properties. From the 1960s to the 1990s, the freshening of the overflows at the northern sills was maintained along its circulation path by mixing with intermediate water that was also freshening during that period (Dickson, B., *et al.*, 2002; Yashayaev and Dickson, 2008). Second, since the late 1990s, there has been an increase in the temperature and salinity of the overflow waters at the sills, a change resulting from the advection of anomalies brought into the Nordic seas in the Atlantic Inflow (Figure 3.9; Eldevik *et al.*, 2009). This is contrary to the earlier view that the overflow properties are largely determined by the depth of winter convection in the Greenland Sea. It is also contrary to the view that regional modification processes dominate the properties of the overflow source waters both in the Nordic seas and the Arctic Ocean (Mauritzen, 1996; Dickson B., *et al.*, 2008). In summary, the potential source processes, regions, and water masses that contribute to the overflow waters are still open to debate.

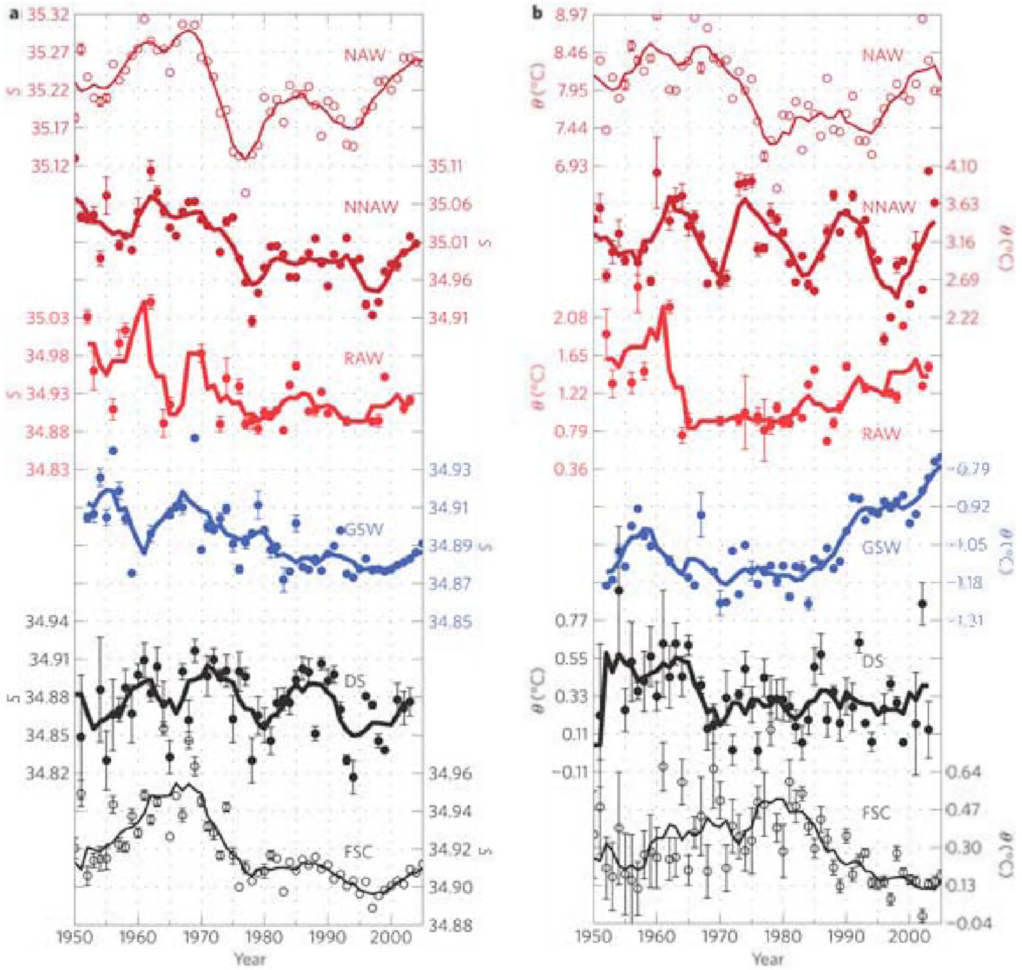


Figure 3.9. Time-series of the water masses in the Nordic seas and the properties of the dense overflows. NAW = North Atlantic Water flowing north through the Faroe Shetland Channel; NNAW = Norwegian North Atlantic Water in the western Norwegian Sea; RAW = Return Atlantic Water heading south in the Greenland Sea; GSW = central Greenland Sea Water; DS = Denmark Strait overflow water at the sill; FSC = overflow water within the Faroe–Shetland Channel. (Source: Eldevik *et al.*, 2009, Figure 2.)

As the overflow waters mix with upper and intermediate waters en route to the Labrador Sea, their properties are modified. Both the upper ocean of the Subpolar Gyre and the LSW have become warmer and more saline since the mid-1990s, as described above. So, although there is a time-lag of a few years as the waters circulate around the Subpolar Gyre, the result is that the NADW is also beginning to warm and become more saline (Yashayaev and Dickson, 2008). This is evident in the temperature and salinity of the deep Labrador Sea (>2500 dbar) from around 2003 onwards (Figure 3.8).

The NADW is exported from the Labrador Sea into the deep western boundary current and is considered to be the south-flowing limb of the MOC. The changes in temperature and salinity in the overflow waters and the NADW have associated changes in density and stratification (Yashayaev and Dickson, 2008), but it is not yet known what effect the changes might have on the MOC, now or in future.

3.2.4 The Baltic Sea

The brackish Baltic is a hydrodynamically and thermodynamically critical regime that is highly sensitive to climatic changes and fluctuations (Feistel and Feistel, 2006).

Permanent strong horizontal and vertical salinity gradients drive lateral transport and inhibit vertical transport. The Baltic response to climate signals and anthropogenic impacts is complex, non-linear, and not yet fully understood. The causal cascade includes physical, chemical, biological, and geological processes that reveal fluctuations and transitions with extreme amplitudes, such as in the nutrient and oxygen conditions, and in the abundance of certain algae or fish species. The conditions of the Baltic Sea were recently reviewed (e.g. BACC, 2008; Leppärenta and Myrberg, 2009), and observational data of monthly salinity, temperature, nutrients, and ice cover for at least four decades are digitally available from the Baltic Atlas of Long-term Inventory and Climatology (BALTIC; Feistel *et al.*, 2008).

The salt content of the Baltic Sea is a result of the balance between inflow and outflow through the Øresund and the Danish Belts. Sporadic inflow events steeply increase the deep-water salinity and the height and the strength of the halocline (Figure 3.10), although vertical transport and outflow gradually decrease it. Surface salinity follows that of the deep water, with a delay of a decade and a smoothed amplitude (Feistel *et al.*, 2006; Reissmann *et al.*, 2009). An alternative explanation for the surface salinity variability was given in terms of changing freshwater supply (BACC, 2008).

Before 1978, sporadic barotropic inflow events were observed approximately once a year, mostly in winter (Matthäus *et al.*, 2008). They were driven by sea-level differences of typically 1 m, lasting for 10 days or longer, between the Kattegat and the southern Baltic. Owing to changes in atmospheric circulation patterns, such events disappeared completely between 1978 and 1993. During this stagnation period, the deep-water salinity demonstrated a pronounced minimum (Figure 3.10). Since 1993, inflow events have occurred approximately once a decade. Other baroclinic inflow events (driven by lateral salinity gradients under lasting calm-weather conditions) have gained increasing importance after their first and unexpected observations in 2002 and 2003 (Feistel *et al.*, 2003, 2004; Borenäs and Piechura, 2007; Matthäus *et al.*, 2008) and eventually returned the deep-water salinity to values found in the 1970s (Figure 3.10). Reflecting this trend reversal, surface salinity has continued to increase to the end of 2010.

The average SST of the Baltic increased by +0.97 °C from 1990 to 2006 and is probably related to the global warming of the atmosphere (Siegel *et al.*, 2008). Air temperatures at Warnemünde revealed a trend of ca. +4°C over the last century in January–March and almost no trend in September–December (Hagen and Feistel, 2008). In the Baltic Deep Water, an extended warm period since 1997 was caused by the transition between the saline inflow regimes. The warm period started with the major inflow in September 1997. Despite the cold major inflow of 2003, baroclinic inflow events of 2002, 2003, and 2006 have maintained the unusually high deep-water temperatures (Figure 3.10; Feistel *et al.*, 2004, 2006). Owing to the high salinity gradients, temperature acts as a passive tracer in the Baltic.

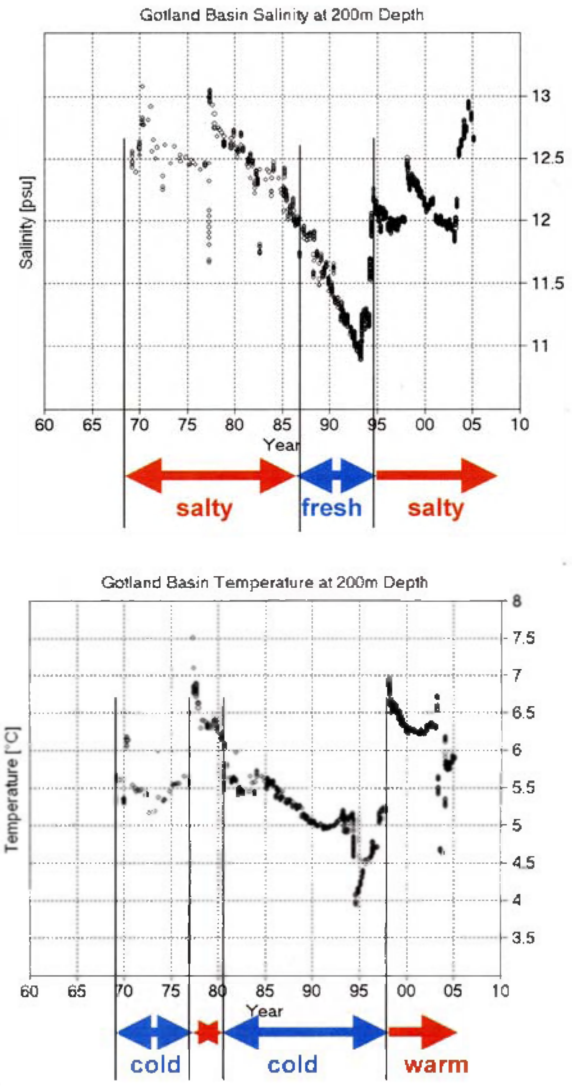


Figure 3.10. Deep-water salinity (upper) and temperature (lower) at the Gotland Deep station BY15; data from the BALTIC atlas (Feistel *et al.*, 2008). The long salinity stagnation phase of 1978–1993 without major inflow resulted in a pronounced salinity minimum. The trend was reversed with the barotropic inflow events of 1993, 1997, and 2003, and baroclinic inflows since 2002. Temperature transitions are controlled by the changing inflow regime from the North Sea.

Baltic Deep Water is ventilated by major North Sea inflow events in winter or late autumn, by vertical deep convection in late winter in regions where the salinity is low and the vertical stratification is weaker (gulfs of Finland and Bothnia, Karlsö Deep), and by baroclinic lateral transport in the Bornholm and Gdańsk deeps, and in the Słupsk Channel. With fewer major inflows, the other ventilation processes have gained increasing relevance and are affecting larger areas. In the regional or temporal transition phase between different mechanisms, anoxic conditions may occur, depending on the rate of oxygen depletion and eutrophication. For example, the anoxic region grew after the major inflow of 2003 (Savchuk, 2010). The inflow was just strong enough to ventilate the eastern Gotland Basin and pushed residual anoxic waters into the deeps west of Gotland, where the increased salinity prevented significant vertical convection. In subsequent years after the inflow, the eastern Gotland Basin returned to anoxic conditions, which still prevailed in 2010.

The ice cover of the Baltic Sea reveals large interannual variations, as shown in Figure 3.11. Generally higher values of maximum ice extent were observed in the 1960s and from the late 1970s to early 1980s. During the first half of the 1990s, winters were mild and the ice cover small. The linear trend since 1960 is negative, and the lowest value observed is for the ice season 2007/2008. The climatic variability of the ice cover is well reflected by the Baltic Winter Index (Hagen and Feistel, 2005, 2008). A detailed regional analysis of climatological ice conditions was given by Schmelzer *et al.* (2008).

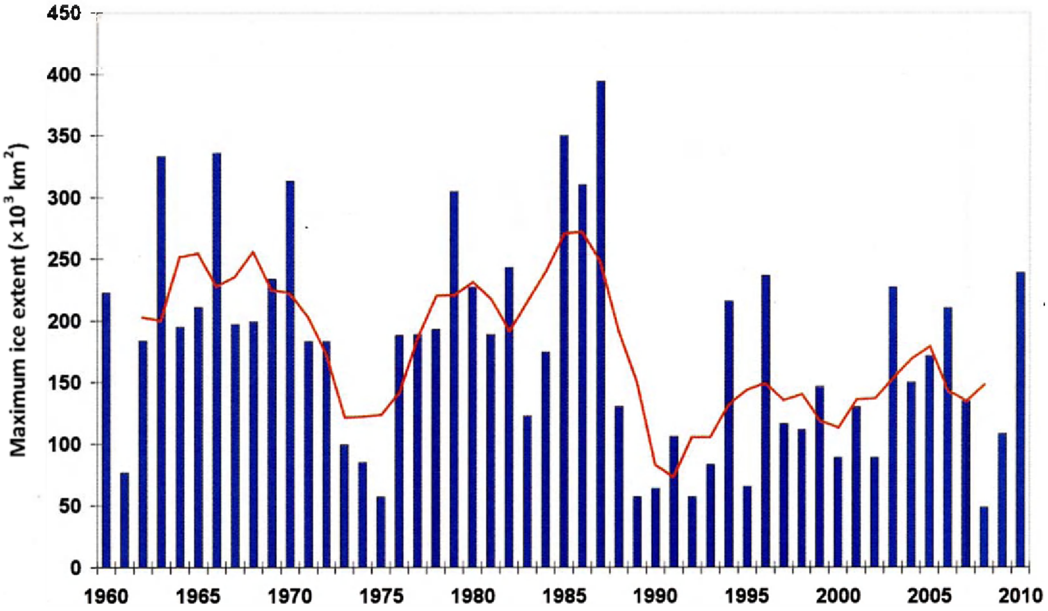


Figure 3.11. Maximum extent of sea ice in the Baltic Sea. Red curve = 5-year running mean. The long-term mean value of 214 000 km^2 from 1720 to 1987 has rarely been exceeded since. (Source: Sveriges Meteorologiska och Hydrologiska Institut (SMHI).)

3.3 The global water cycle

The oceans play a central role in the global water cycle because they are the major reservoir of freshwater and nearly 90% of global evaporation comes from the ocean. Variations in precipitation on land have been linked with large-scale changes in the ocean (especially SST), but the global water cycle and the exchange of freshwater between the atmosphere and ocean is poorly understood. Observations of the salinity of the North Atlantic have led some authors to suggest that the hydrological cycle may have changed (e.g. Curry *et al.*, 2003; Gordon and Giulivi, 2008; Durack and Wijffels, 2010; Helm *et al.*, 2010). It has been predicted that increasing global temperatures will lead to an enhanced global water cycle, and that a fresher North Atlantic may lead to a reduced overturning circulation. However, model predictions are currently unreliable because they can neither simulate the process of increased freshwater at the coastal boundaries, nor the effect of freshening on stratification and mixing in the ocean. The global water cycle is expected to become a major focus for climate research in coming years.

3.4 Ocean circulation

3.4.1 The Gulf Stream

The transport and location of the Gulf Stream provides a key link between processes in the subtropics (and tropics) and the Subpolar Gyre. Understanding the variability of the Gulf Stream, which mechanisms are important, and the impact of changes, is a key issue. The high level of variability in transport within the Gulf Stream was demonstrated by Rossby *et al.* (2005), who showed that, over an 11-year period, there was no overall trend in transport, but that the range was over 20% of the mean. The short time-scales of this variability suggest wind-driven forcing from the subtropics and tropics. In contrast, the north–south displacement of the Gulf Stream may be influenced by thermohaline forcing; in a period of cooler, fresher water and a slight increase in transport, the Gulf Stream was displaced to the south (Rossby *et al.*, 2005). In addition, it has previously been noted that the Gulf Stream may be displaced to the south during periods of low NAO index (Taylor and Stevens, 1998) or enhanced North Atlantic low pressure (Hameed and Piontkovski, 2004). The common thread between these results is that the position of the Gulf Stream is affected by the production of cold freshwater in the Labrador Sea and surrounding shelves. When conditions there generate more cold freshwater, it spreads south in intermediate levels and along the shelf break, where it meets the Gulf Stream and, being unable to cross it, must turn east. It has also been suggested that increased amounts of cold freshwater are present on the shelf south of the Grand Banks during periods of a low winter NAO index because of increased transport in the Labrador Current and local cooling (Marsh *et al.*, 1999; Petrie, 2007).

3.4.2 The meridional overturning circulation

The Atlantic MOC is thought to be vulnerable to changes in global climate, with coupled climate models predicting a long-term (multidecadal) slowing of the MOC as carbon dioxide concentrations rise (although with a high level of uncertainty; Bindoff *et al.*, 2007). However, measuring the MOC in the past has been problematic, leading to conflicting results. Analysis of the decadal variability of the MOC from a small number of hydrographic sections taken over 30 years suggested that the overturning circulation fluctuated, although the sampling bias was recognized as being unknown (Bryden *et al.*, 2005). Sustained measurements of overflow waters in the Faroe Bank Channel revealed unchanging transport in the lower limb of the MOC over 50 years (Olsen *et al.*, 2008), in contrast to an earlier study that had implied a slowing of overflow waters over the same period (Hansen, B., *et al.*, 2001). Measurements of the fluxes of heat and salt in the upper layers through the Faroe–Shetland Channel towards the Nordic seas demonstrate no obvious trend in the period 1997–2008 (S. L. Hughes, pers. comm., 2010).

The observations are now improving through concerted efforts to measure the MOC. High frequency variability has been observed by a dedicated MOC monitoring system at 26.5°N since 2004 (Kanzow *et al.*, 2007). The first results from the monitoring array in 2004/2005 revealed significant variability in the total overturning, with an annual mean of 18.7 Sv and a range of 4.0–34.9 Sv (Figure 3.12; Cunningham *et al.*, 2007). Estimates of the MOC that utilize subsurface drift velocities from ARGO (Array for Real-time Geostrophic Oceanography) profiling floats, as well as from hydrographic data, suggest that there has been no significant change since 1957 (Hernandez-Guerra *et al.*, 2010).

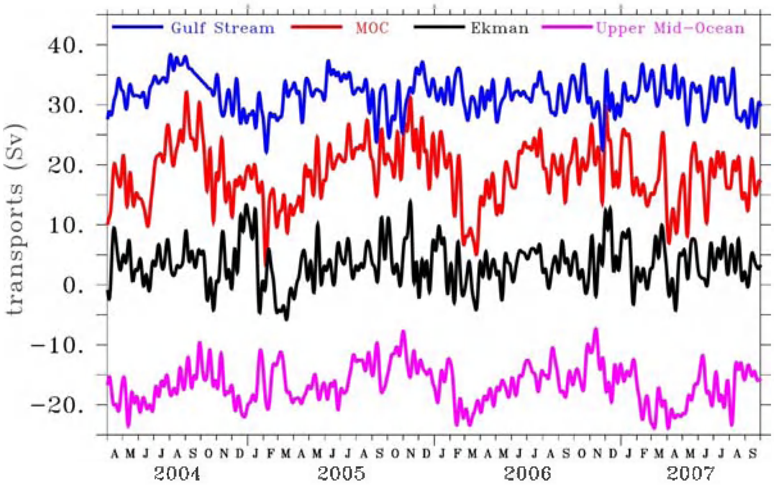


Figure 3.12. Daily time-series transports at 26.5°N from April 2004 to October 2007, with coloured lines representing different elements of the total transports across the section, including the western boundary current. Blue = Gulf Stream; red = Meridional Overturning Circulation (MOC); black = Ekman or wind-driven surface layer; pink = upper layer of the mid-ocean. (Source: RAPID-MOC website, http://www.noc.soton. ac.uk/rapidmoc/, October 2009.)

Although accurate measurements of the MOC are just beginning, predicting the future strength of the MOC is still problematical, at both decadal and centennial time-scales. At present, predictions on these time-scales differ considerably between models and between studies that essentially use the same model, demonstrating the need for further development. In order to predict future North Atlantic conditions, coupled climate models must be able to reproduce natural fluctuations in the MOC and other elements of the oceanic and atmospheric circulation.

3.4.3 Circulation of the Subpolar Gyre

During the 1990s, the repeated hydrographic sections of the World Ocean Circulation Experiment, combined with new data from satellite missions, demonstrated that the circulation of the Subpolar Gyre could change on interannual and decadal time-scales (Curry and McCartney, 2001; Bersch, 2002; Hakkinen and Rhines, 2004). One important mechanism for change is the baroclinic response to the dynamic height difference between the Labrador Sea and the centre of the Subtropical Gyre. The resultant sea surface slope induces geostrophic currents in the top 800 m that vary in strength as a delayed response to changes in windfields. Concurrently, the Subpolar Gyre may expand or contract, leading to changes in the location of key features such as the Subpolar Front. This front moved west in the mid-1990s, and the consequence for the Iceland Basin, the Northeast Atlantic, and the Atlantic inflow to the Nordic seas was an increase in temperature and salinity within the entire upper ocean (Figure 3.13; Holliday, 2003; Hatun *et al.*, 2005; Holliday *et al.*, 2008).

However, a delayed baroclinic response of the Subpolar Gyre to the Labrador Sea conditions may not be the only mechanism at work. An idealized study by Eden and Willebrand (2001) suggested that the response to a high NAO index could be a combination of a fast barotropic effect that acts to slow the currents near the Subpolar Front, and an opposing delayed baroclinic effect that acts to increase the circulation intensity of the Subpolar Gyre. Herbaut and Houssais (2009) reached a rather different conclusion than earlier studies: that changes in the eastern Subpolar Gyre are the result of a local response to windstress, which acts to increase the heat flux into the region, rather than the result of the enhancement of the entire gyre system.

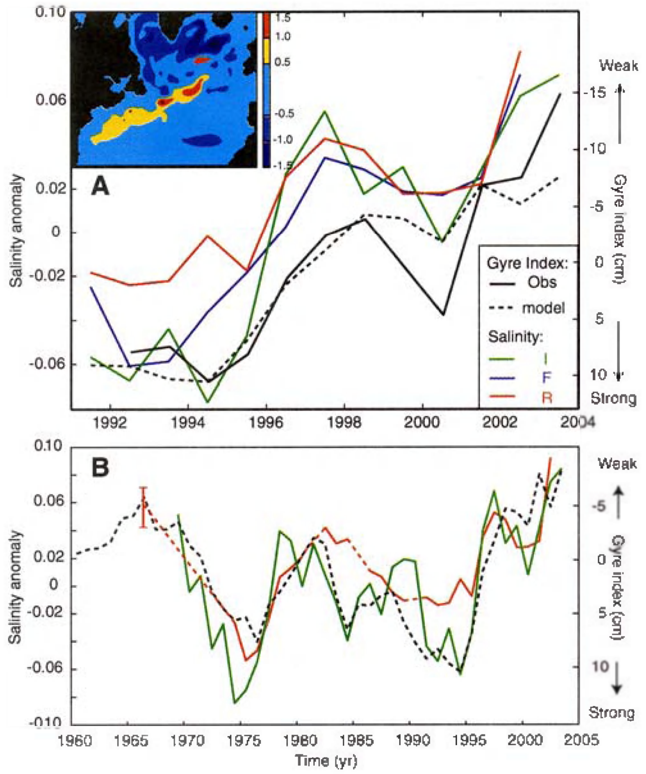


Figure 3.13. An index of Subpolar Gyre circulation intensity. Solid black line = the gyre index (inverted), associated with the leading North Atlantic sea-surface height mode, as obtained from altimetry observations; dashed line = the gyre index (inverted) obtained from the MICOM model; coloured lines = annual averages of the observed salinity anomalies in inflow areas Rockall Trough, Faroe Current, and Irminger Current. The Rockall and Faroe Current time-series are moved 1 year backwards, and the Irminger Current time-series is moved 2 years backwards to account for advective delays. (Source: Hatun *et al.*, 2005, Figure 2).

3.4.4 Circulation in the Nordic seas

The weak stratification and deep basins in the Nordic seas lead to a topographically controlled and wind-forced flowfield (e.g. Nøst and Isachsen, 2003), where mean advection is usually in narrow boundary currents (Søiland *et al.*, 2008). For the Greenland and Norwegian basins, windforcing and bottom friction were found to be important mechanisms for this variation, although other processes, such as baroclinic effects, may be more important for the Lofoten Basin. The strong seasonal variations within the Nordic seas are in contrast to the reduced seasonal signal in the water exchanges between the North Atlantic and the Nordic seas (Østerhus *et al.*, 2005), but the variability in the gyres of the basins seems to be local and not connected with the import and export to the North Atlantic (Jakobsen *et al.*, 2003; Isachsen *et al.*, 2003). Exchanges between boundary flows and gyres in the basins are instead dominated by eddy dynamics rather than advection (Isachsen *et al.*, 2003), but more studies are needed here. With stronger windforcing, an increase in the circulation within the Nordic seas is expected, but on longer time-scales, a reduction in local buoyancy effects may reduce the thermohaline circulation.

3.4.5 Open-ocean deep convection

In the North Atlantic, there are two globally important sites of deep open-ocean convection: the Labrador Sea and the Greenland Sea. They contribute intermediate and deep water, which are exported as NADW, and in this way, they dominate the northern lower limb of the MOC. Changes in convective activity can have a profound influence on the North Atlantic as a whole through the dynamic effects of changes in volume and properties. As described in Section 4.3, the dynamic height of the Labrador Sea affects the intensity of the Subpolar Gyre circulation (Curry and McCartney, 2001; Hakkinen and Rhines, 2004). The properties of the intermediate waters affect mid-depth circulation and mixing (Yashayaev *et al.*, 2007), whereas the properties of the deep water affect the strength of currents in the lower limb of the MOC (Boessenkool *et al.*, 2007). In recent decades of high-quality measurements, prolonged deep convection has occurred in the Labrador Sea during 1972–1976, 1987–1994, and 1999–2000. The depth of winter convection in the Greenland Sea reached a maximum of 3500 m in 1971 and has decreased steadily since. There was no convective renewal of waters below 1600 m during the 1980s (Dickson, R., *et al.*, 1996), and the time-series in Figure 3.14 shows convection has rarely reached even that depth since then. Deep convection has been observed in the Irminger Sea (Bacon *et al.*, 2003; Pickart *et al.*, 2003), although the basin-wide significance of this ventilated water may be small compared with that formed in the Labrador Sea.

The NAO is thought to be an important modulating mechanism for convection in the North Atlantic (Dickson, R., *et al.*, 1996), with changes in the windstress curl influencing the heat loss in the convective regions. However, there are other complicating factors. Preconditioning will play a role in regulating the depth of mixing (Yashayaev, 2007), and the properties are also influenced by variability in inflowing waters and the adjacent water masses with which they mix (Eldevik *et al.*, 2009). This complex mixture of regulatory factors makes it difficult to predict when and where deep convection may occur. In winter 2007/2008, an entirely unexpected deep convection was observed in the Labrador Sea (Våge *et al.*, 2009; Yashayaev and Loder, 2009). Cold winter winds, combined with a particular distribution of sea ice and storm tracks, led to deep winter convection taking place, despite unfavourable preconditioning and a neutral NAO index (Våge *et al.*, 2009). It is yet to be seen whether or not the most recent deep convection will lead to a substantial body of newly ventilated LSW.

In the Greenland Sea, where no widespread winter convection below 1600 m has occurred since the 1970s, small features of deep convection are sometimes observed (Wadhams *et al.*, 2002; Karstensen *et al.*, 2005). The convective chimneys are just a few kilometres wide, but can reach 2400 m depth and persist for several months. Details of their formation and the impact on active convection are still unclear.

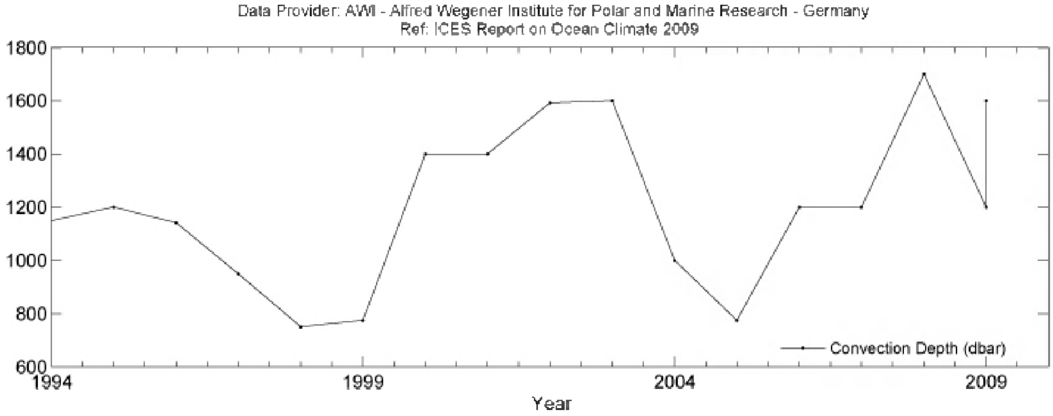


Figure 3.14. Time-series of the depth of winter convection in the Greenland Sea at 75°N. (Source: after Ronski and Budeus, 2005; updated in Holliday *et al.*, 2009).

3.5 Mixed layer depth

In the upper part of the ocean, there is a layer in which all tracers are almost homogeneous. This layer is known as the upper ocean mixed layer (ML), and its lower limit, referred to as the mixed layer depth (MLD), is one of the most intuitive and useful features used in upper ocean studies. The mixed layer owes its homogeneity to mixing processes caused by the exchange of turbulent energy and heat with the atmosphere. Changes within this layer affect the ocean-atmosphere as a coupled system through heat storage and its influence on surface currents (McCreary *et al.*, 2001; Seager *et al.*, 2002; Montegut *et al.*, 2004). In addition to physical and chemical properties, variability within this layer controls the biological productivity of the ocean. Therefore, understanding the processes that govern changes in the MLD may be a key factor to understanding physical controls on ecosystem processes.

Although the importance of the mixed layer is recognized for climate-change studies, there is no standard criterion to define its limits. The vague conceptual definition of the mixed layer as "the region in the upper ocean where there is little variation in temperature or density with depth" (Kara *et al.*, 2000) makes the search difficult for a precise mathematical definition of the MLD. Reviews of the performance of some methods used to determine MLD can be found in Thomson and Fine (2003), Montegut *et al.* (2004), and González-Pola *et al.* (2007).

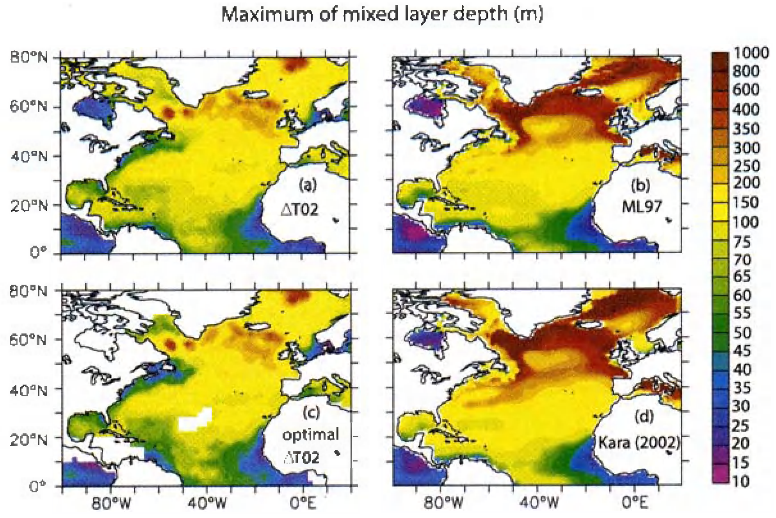


Figure 3.15. Maximum mixed layer depth (MLD) reached at the end of winter in the North Atlantic for different temperature threshold (DT) values: (a) the Montegut *et al.* (2004) climatology (DT = 0.2°C); (b) the Monterey and Levitus (1997) climatology (DT = 0.5°C); (c) the Montegut *et al.* (2004) MLD climatology corrected in barrier layer regions (DT = 0.2°C); and (d) the Kara *et al.* (2003) climatology (DT = 0.8°C). (Source: Montegut *et al.*, 2004.)

The use of a variety of methods means that the results from different analyses cannot be easily compared (Figure 3.15), and it is difficult to establish a MLD reference value for any region. However, different studies have reached similar conclusions about the main forces affecting MLD variability.

The convection processes governed by surface buoyancy fluxes are responsible for ML development during winter, although during summer, surface windstress is mostly responsible (Alexander *et al.*, 2000; Kantha and Clayson, 2000). At high latitudes, strong winds and heat loss from the ocean to the atmosphere are responsible for cooling and mixing. In these areas, ML during winter can reach more than 1000 m depth (see Section 4.3). In the mid-latitude open ocean, variability in energy exchange between the atmosphere and the ocean at seasonal time-scales is responsible for the typical cycle of a deep winter MLD and shallow summer thermocline. It oscillates between 150 and 300 m during winter and 20 and 40 m in summer, depending on the mid-latitude position considered. In subtropical latitudes, the amplitude of this seasonal cycle reduces in the upper waters.

As time-scales are increased from seasonal to multidecadal, MLD variability becomes less evident. Thus, MLD variability studies have focused traditionally on short-term time-scales, i.e. diurnal, intraseasonal, and seasonal. Even so, recent studies have reported long-term trends, suggesting in some cases that the MLD undergoes low frequency changes in the North Pacific and Atlantic oceans (Polovina *et al.*, 1995; Michaels and Knap, 1996; Freeland *et al.*, 1997; Timlin *et al.*, 2002; Deser *et al.*, 2003; Carton *et al.*, 2008; Henson *et al.*, 2009; Yeh *et al.*, 2009). Low frequency patterns of atmospheric variability appear to be linked to different MLD trends in subtropical and subpolar areas as follows. An important increase during the 1970s and 1980s, and a progressive reduction in MLDs in the Subpolar Gyre since the mid-1990s, has been described (Carton *et al.*, 2008; Henson *et al.*, 2009). These changes have been related to periods of strengthening or weakening of the NAO index. Opposing trends have been found farther south in the North Atlantic. Michaels and Knap (1996) studied ML variability at Hydrostation S in the Sargasso Sea (32°N 64°W) and found a shallowing of MLD from 1950–1960 to 1970 onwards, a feature also observed by Paiva and Chassignet (2002). This shallowing period ended during the 1990s, when a deepening of the ML took place (Carton *et al.*, 2008). In the Bay of Biscay, similar low-frequency variability of MLD has taken place in recent decades, also in opposition to that found in the Subpolar Gyre (Somavilla, *et al.*, 2011). In the Norwegian Sea, horizontal advection rather than surface forcing seems to determine MLD variability, although no temporal trend has been detected (Nilsen and Falck, 2006).

3.6 The seasonal cycle in the upper ocean

The seasonal cycle of the surface layer of the ocean results in changes in temperature, salinity, nutrients, and biological parameters that are far larger (in amplitude) than variability on interannual and longer time-scales. The World Ocean Atlases, regularly produced by the National Oceanographic Data Center (NODC), provide a basic description of the temperature and salinity cycle. For temperature, the seasonal cycle is the dominant feature of the variability in the upper layer and, in this cycle, the annual harmonic accounts for more than 95% of the variance in the latitude belt 20–60° of each hemisphere (Antonov *et al.*, 2004). The same authors demonstrated a similar distribution of the amplitude of this annual harmonic with latitude in the three oceans, with a maximum at latitude 40°, the northern maximum being stronger by nearly 50%. The space distribution of the first harmonic of the annual cycle of salinity is totally different, demonstrating maximum amplitude in the tropical band, at high latitudes (the Arctic Ocean and around Greenland), and along the western boundary currents (Boyer and Levitus, 2002).

The ARGO array of profiling floats has considerably improved the description of the variability of the upper 2000 m of the water column, and after just a few years, the annual cycle produced appears to be reliable (Roemmich and Gilson, 2009). The SST cycle in particular is consistent with Reynolds *et al.* (2002). A similar analysis performed by von Schuckmann *et al.* (2009) on a better sampled period (2003–2008) describes the depth of penetration of the seasonal cycle as a function of latitude: at 40°N, the seasonal cycle of temperature still represents 20% of the variance at 200 m depth, and at 60°N, more than half of the variance at 400 m is the result of the seasonal cycle.

This mean cycle itself is subject to interannual variations (von Schuckmann *et al.*, 2009). The seasonal cycles of temperature extracted from analysed ARGO fields at 12 selected locations (Figure 4.16) are plotted in Figures 3.17 and 3.18, overlying the climatological cycle (in black) from the World Ocean Atlas (2005). In the southern North Atlantic, locations 1–5 and 12 (Figure 3.17) have annual cycles that are above the long-term average for the whole period. Summers tended to be particularly warm, indicating a change in the amplitude, although spatial variability leads to individual locations with maximum temperatures in different years.

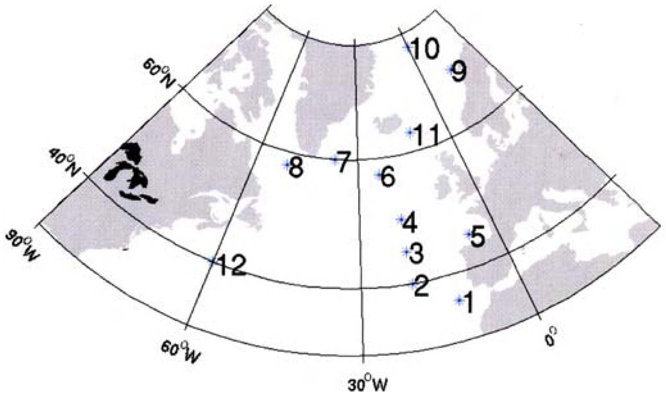


Figure 3.16. Location of the time-series sites from which the seasonal cycles shown in Figures 3.17 and 3.18 were derived.

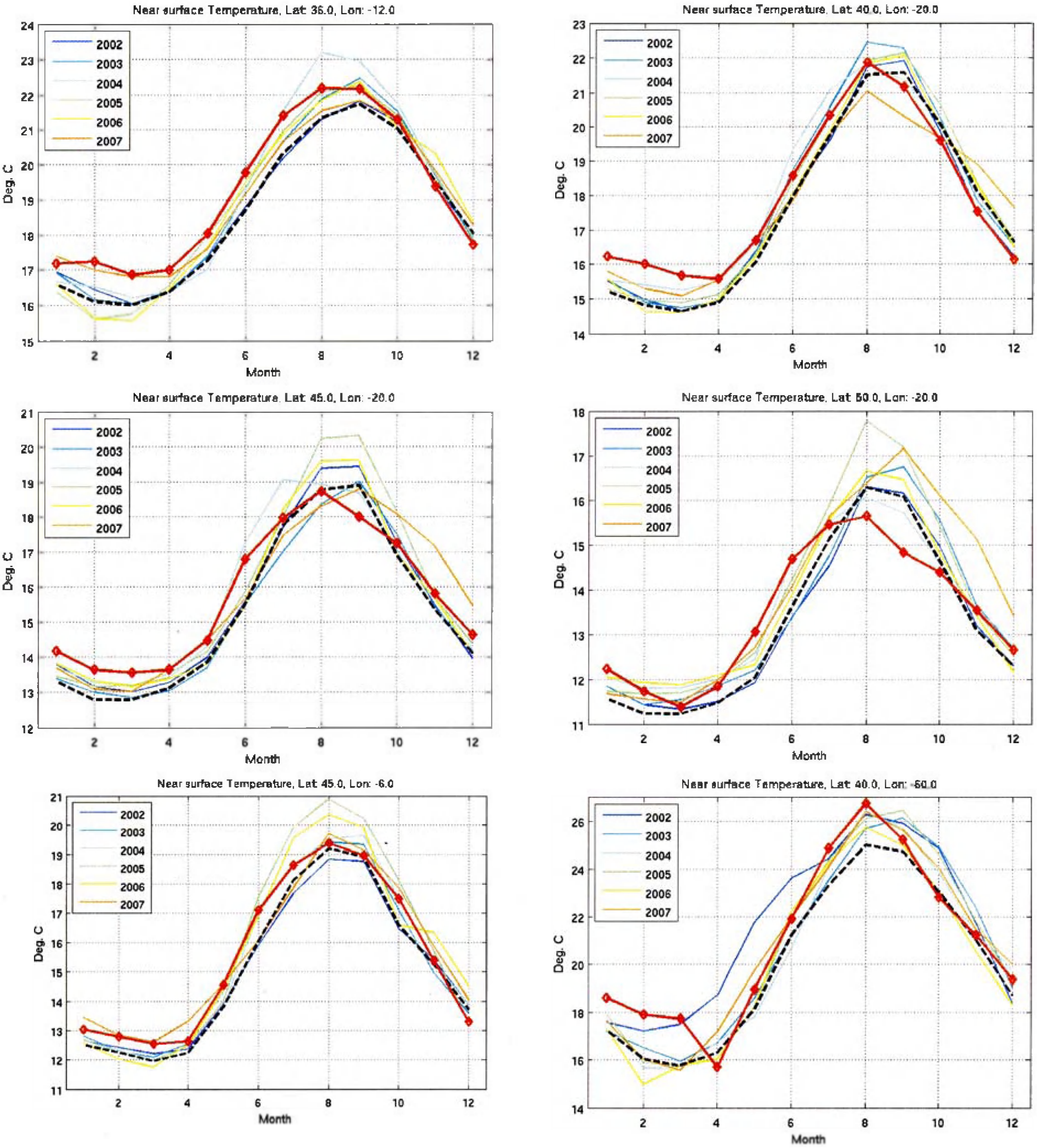


Figure 3.17. Seasonal cycles at locations 1–5 and 12 in the southern North Atlantic: from 2002 to 2007 (thin coloured lines), 2008 (thick red line), and the mean climatology from the World Ocean Atlas (Locarnini *et al.*, 2006;dashed black line). See Figure 3.16 for the locations.

In the northern North Atlantic, at locations 6–11 (Figure 3.18), all cycles are above the climatology by a nearly constant value, indicating a trend on which the change in seasonality is superimposed. In the Subpolar Gyre, all basins were warmer than average until 2008, when the cycle returned to the long-term average. In the Norwegian Sea, the warming was stronger in summer (up to 1 °C) than in winter (up to 0.5 °C), indicating a change in the amplitude of the seasonal cycle. In the Greenland Sea, the water was nearly 2 °C warmer than the climatology.

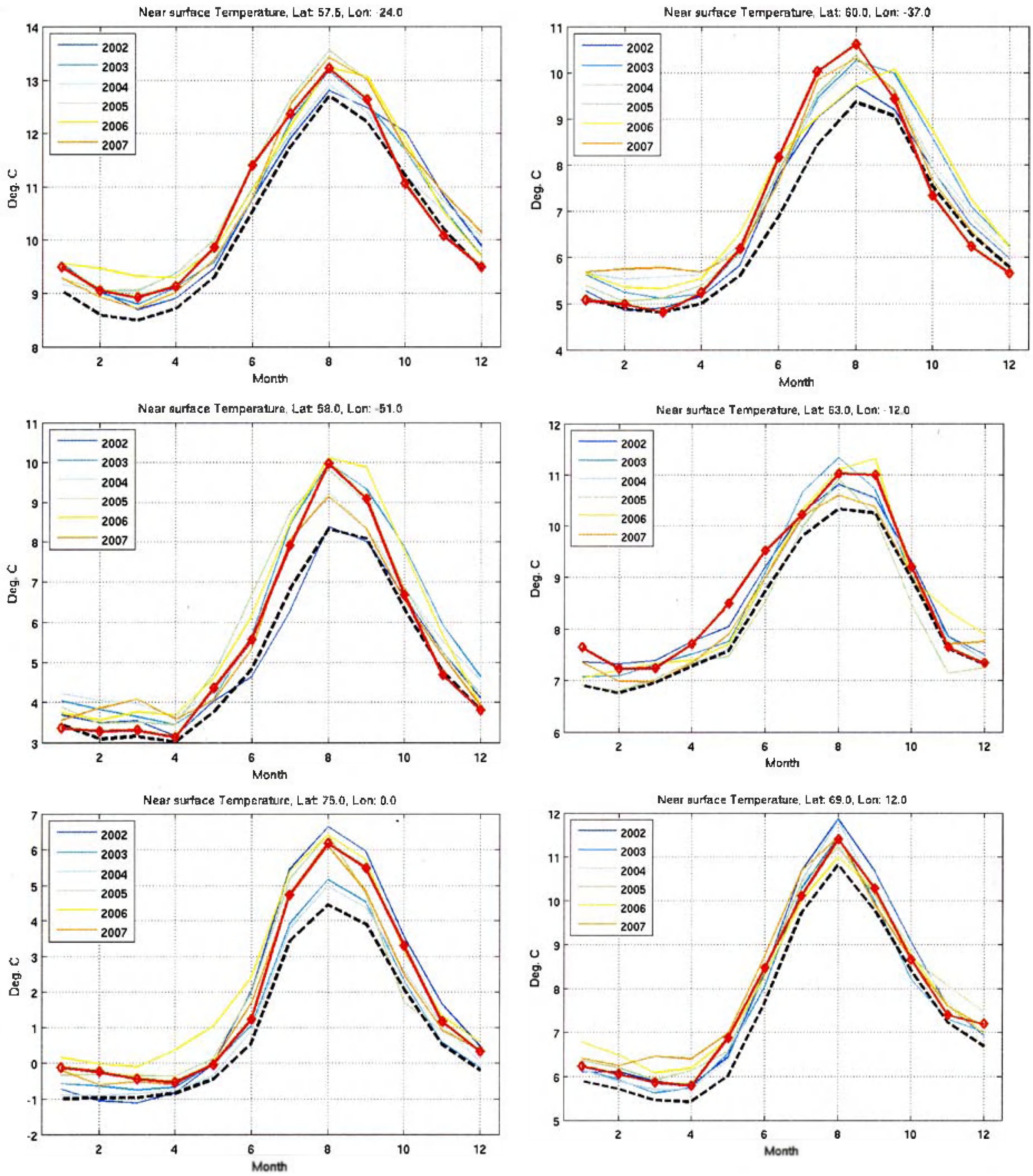


Figure 3.18. Seasonal cycles at locations 6–11 in the northern North Atlantic: from 2002 to 2007 (thin coloured lines), 2008 (thick red line), and the mean climatology from the World Ocean Atlas Locarnini *et al.*, 2006; dashed black line). See Figure 3.16 for the locations.

3.7 Conclusions

The physical properties and circulation of the North Atlantic undergo significant variability at all depths. In this section, we have described variability at seasonal–decadal time-scales and summarized the present-day understanding of the causes and mechanisms of variability. The patterns described include the effects of anthropogenic forcing as well as natural variations, although distinguishing the two in any one time-series is a matter for ongoing research. The main conclusions of the section are as follows.

- The Atlantic Multidecadal Oscillation (AMO) describes a pattern of decadal variability in the sea surface temperature of the North Atlantic, although different methods for deriving an AMO index give slightly different results. The AMO index is a statistical pattern that represents changing conditions, but as yet there is little understanding of the processes that might have contributed to the apparent oscillation.
- The temperature and salinity of the upper ocean in the northern North Atlantic have a broadly correlated pattern of decadal variability. Likely control mechanisms include changing atmospheric fields and changing ocean circulation, as well as anthropogenic forcing. More work is needed, however, to untangle the complexity in the patterns of temperature and salinity variability, the controlling mechanisms, and how they vary in space and time. On the time-scales for which observations exist (at most the past 50 years), it is not yet possible to say with confidence how much of the variability of the surface and upper ocean is the result of anthropogenic climate change, nor what future variability will look like.
- Changes in the temperature and salinity in the Nordic seas are primarily determined by variations in the large-scale atmospheric circulation, combined with the properties and volume of the inflowing Atlantic Water.
- The temperature and salinity of the dominant subpolar intermediate water mass, Labrador Sea Water (LSW), is strongly controlled by air–sea fluxes and mixing at its source. Saline Atlantic Water contributes to restratification after deep convection. Across the Subpolar Gyre, the LSW properties are modified by mixing with other water masses. The freshwater budget of the Labrador Sea requires further investigation in order to establish how the interaction between atmospheric fields and freshwater influx at the surface and at depth work to produce the observed temperature and salinity variability.
- From 1960 to 1994, the Mediterranean Outflow Water (MOW) close to the Strait of Gibraltar became warmer and more saline, in sharp contrast to the rest of the Subpolar Gyre during that period, but the impact of the property changes across the Subpolar Gyre is unclear. Penetration of the MOW into the Subpolar Gyre varies with the movement of the Subpolar Front, which may block the spread of warm, saline intermediate water. The effect of this varying extent of MOW on the dynamics of the Subpolar Gyre is not yet understood.
- The dense cold overflow waters that enter the North Atlantic from the Nordic seas demonstrate decadal-scale variability, which can be traced along its circulation pathway from inflow to outflow. The overflows have been warming and increasing in salinity since the late 1990s. However, the potential source processes, regions, and water masses for the overflow waters are still open to debate. In addition, the effect of changing properties, density, and stratification of the North Atlantic Deep Water on the strength of the Meridional Overturning Circulation (MOC) is not yet known.
- Accurate measurements of the MOC in the subtropical North Atlantic over the past five years have revealed significant variability on time-scales as short as days.
- The circulation intensity of the Subpolar Gyre responds to large-scale changes in the windfield, including the North Atlantic Oscillation (NAO).

However, the details of the mechanisms by which the Subpolar Gyre responds to changes in atmospheric fields may be only partially understood.

- Deep winter convection in key locations, such as the Labrador and Greenland seas, is heavily influenced by atmospheric circulation (including the NAO) because changes in the windfield determine the heat loss at the surface of the ocean. The depth of convection has a profound impact on the North Atlantic and the global circulation through the production of deep-water masses. However, the control mechanisms for deep winter convection are still poorly understood; consequently, the occurrence of deep convection and its subsequent impacts on ocean circulation are largely unpredictable.
- The mixed layer is the upper part of the ocean in which all tracers (especially density) are almost homogeneous. Its lower limit is referred to as the mixed layer depth (MLD). The MLD and seasonal stratification have a profound effect on primary production by affecting light levels and through the supply of nutrients. Understanding the variability of MLD is complicated by difficulties in establishing its true base because there is no single definition of the MLD that can be applied to all regions of the North Atlantic.
- In winter, mixing is dominated by surface buoyancy fluxes, although during summer, surface windstress dominates. It follows that temporal variations in the surface forcing (e.g. the NAO) will generate variability in the MLD on annual and longer time-scales. Decadal-scale patterns of variability have been detected in the Subpolar Gyre and the Subtropical Gyre, driven by changing atmospheric fields. Typically, the patterns are in anti-phase; MLDs have reduced in the Subpolar Gyre since the mid-1990s, although they have increased in the subtropics. Detailed studies of the annual-to-decadal variability of MLD and how it relates to surface forcing and biological productivity are scarce.
- There is a growing body of evidence that the general warming of the North Atlantic, which is more intensive in the northern region, is associated with changes in the amplitude (and, in some cases, the phase) of the seasonal cycle. However, these changes do not demonstrate an obvious coherent signal over the whole North Atlantic. A statistical analysis is necessary to separate the trend and the different spectral components of the seasonal cycle before the spatial coherence of the changes and their timing can be studied.
- The global water cycle and the exchange of freshwater between the atmosphere and ocean are poorly understood. Present-day model predictions are unreliable because they are able to simulate neither the process of increased freshwater at the coastal boundaries nor the effect of freshening on stratification and mixing in the ocean. The global water cycle is expected to become a major focus for climate research in the coming years.

3.7.1 Scales of variability

"Climate variability" is the variation of climate elements around the average state, which is usually defined as the mean over 30 years or more. Climate variations are much longer than those associated with weather events; they have time-scales of months, year-to-year (interannual), tens of years (decadal), several decades (multidecadal) to millennia. Natural elements of climate variability are those that are not directly attributable to the actions of humans and include changes in solar radiation, volcanic eruptions, or random changes in circulation. Climate variability is distinct from "climate change", which is any systematic change from one state to another in the long-term statistics of elements, and where the new state is sustained over several decades or longer. Climate change arises from both natural and human (anthropogenic) causes, such as those resulting from greenhouse gas emissions or land use.

Observed ocean variability includes the effects of climate change. Since 1750, the global mean temperature of the air and the sea surface has risen at a rate of ~0.074°C per decade. There is great complexity in the global and regional response to carbon emissions, and temperature rise is not the only oceanic consequence. Related effects include a decrease in the pH of seawater resulting from the uptake of carbon dioxide from the atmosphere; sea-level rise resulting from thermal expansion and ice-melt; changing precipitation–evaporation balance (including river run-off); changes in oxygen concentration; and changing wind-driven circulation.

The North Atlantic Ocean and Nordic seas are the most studied and densely sampled regions of the oceans. Multidecadal hydrographic records exist in many locations; indeed a few extend over 100 years, allowing description of the long-term variability of properties, circulation, and mixing processes. The most widespread data are sea surface temperature and salinity from ships of opportunity and drifters, and temperature and relative height from satellite missions. Subsurface measurements come from hydrographic stations, moored instruments, fisheries surveys, expendable instruments, and floats.

Using historical and recent data, it is generally possible to define variability on seasonal to decadal time-scales, and from a few kilometres to basin-scale for most areas of the North Atlantic. Decadal patterns tend to be driven by basin-scale changes in ocean circulation as a response to prolonged patterns of atmospheric forcing. Year-to-year patterns tend to be a response to shorter time-scale atmospheric forcing, such as winter windfields, net precipitation and evaporation, and sea-ice cover. Superimposed on these patterns are higher frequency variations caused by local processes, such as the changing positions of fronts, passing of eddies, river run-off, and the changing inflow of different water masses. Few datasets, however, describe variability at all desirable time- or space-scales, so there remain gaps in our understanding of variability and the processes that influence it. All datasets contain variability resulting from climate change, multidecadal patterns, decadal cycles, and interannual variations. It is rarely possible to distinguish the contribution of these elements in a single time-series, and this issue is an active area of research.

4 Sea level rise and changes in Arctic sea ice

N. Penny Holliday (corresponding author), Sarah L. Hughes, Markus Quante, and Bert Rudels

This section summarizes the present-day understanding of two key consequences of climate change: sea level rise and changes to sea ice in the Arctic. Research into these phenomena has not been a science priority for ICES, but sea level rise and the recent reduction in Arctic sea-ice extent and thickness can greatly affect processes in the ICES Area. The section provides an overview of recent research and outlines some of the key questions that remain to be addressed.

4.1 Sea level rise

There are a number of factors that contribute to variations in mean sea level (see box and Figure T4.1). On decadal–century time-scales, there are two main processes: (i) thermal expansion/contraction of ocean water in response to ocean warming/cooling, and (ii) exchange of water with land-based reservoirs such as glaciers, ice caps, ice sheets, etc. (Bindoff *et al.*, 2007). Melting of sea ice has no overall direct effect on sea level.

All of the above processes alter the volume of the oceans and thus global mean sea level on many temporal scales. On a regional or local scale, the picture may also differ as a result of variation in surface winds and ocean currents, location of atmospheric pressure systems, spatial variation in ocean heat uptake or salinity, and changes in the Earth's gravity field caused by changes in land ice masses (Katsman *et al.*, 2008; Vellinga *et al.*, 2009). A further factor that can affect local sea level change is adjustment in relative land height. The main causes of vertical movements are (i) rising of land caused by isostatic post-glacial rebound (observed in areas once covered by ice-sheets that have now melted), (ii) sinking of land caused by the additional weight of sedimentation (as in river deltas), and (iii) on longer time-scales, tectonic changes.

Isostatic adjustment affects some countries bordering the North Sea and the Baltic, as well as areas of Canada and the US that were glaciated. In Norway, Scotland, and the northern part of Ireland, landmasses are rising relative to mean sea level. Farther south, land masses are thought to be stable or sinking. This change in land level has resulted in an overall reduction in sea level relative to the coast, despite a rising global mean sea level (Figure 4.1). The effect is very pronounced in the Baltic, where the relative movements of land and sea level generate a rise of 9 mm year^{-1} in the north and 5 mm year^{-1} in the centre, and sinking in the southern Baltic, a region located in the transition zone between the Scandinavian Shield and the Central European Subsidence Zone, where isostatic uplift and neotectonic subsidence interact (Ekman, 1996; Rosentau *et al.*, 2007). Sinking of the land means that most of the US Atlantic coast has experienced higher rates of sea level rise over the past 100 years than the current global average, with the highest rates in the Mid-Atlantic between northern New Jersey and southern Virginia (Figure 4.2; CCSP, 2009).

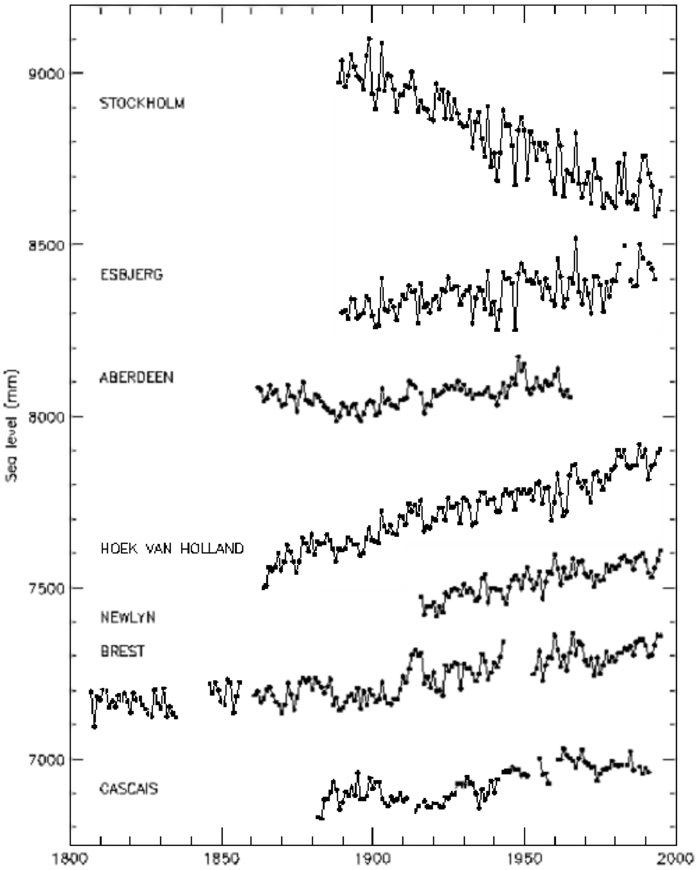


Figure 4.1. Relative sea levels (i.e. sea level relative to coastline and not adjusted for isostatic and sedimentation effects) from seven stations around Europe. (Source: www.pol.ac.uk/psmsl/images/euro.trends.gif, February 2010.)

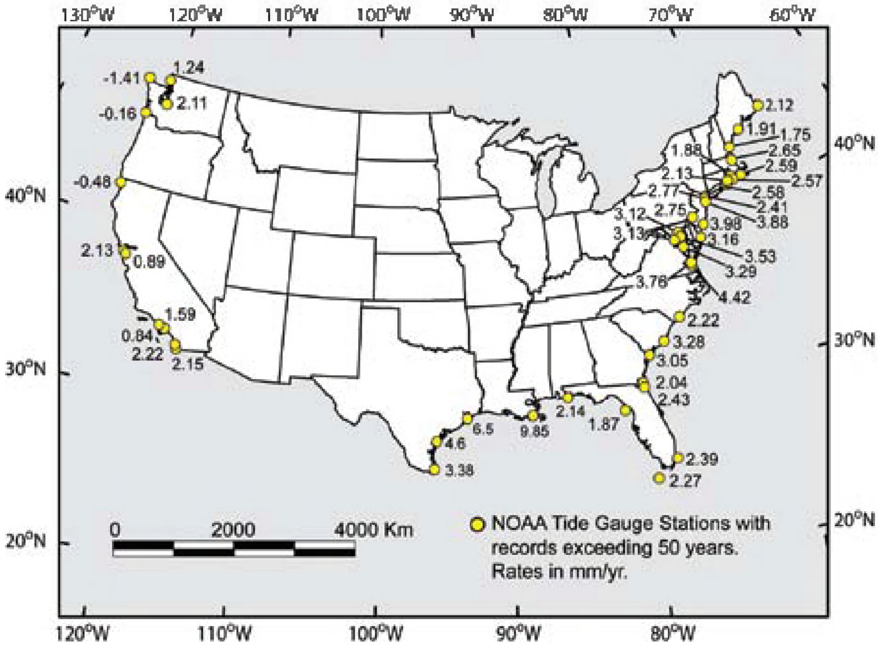


Figure 4.2. Map of annual relative sea level rise rates around the coast of the US in the 20th century. The higher rates for Louisiana (9.85 mm year^{-1}) and the Mid-Atlantic region (1.75–4.42 mm year^{-1}) are caused by land subsidence. Sea level is stable or dropping relative to the land in the Pacific Northwest, as indicated by the negative values, where the land is tectonically active or rebounding upwards in response to the melting of ice sheets since the last Ice Age. (Adapted from CCSP, 2009.)

The vulnerability of coastal areas to flooding varies; within Europe, the most susceptible regions are England, the Netherlands, Denmark, Germany, Italy, and Poland (Meehl *et al.*, 2007), because they have large areas of land already within 1 m of sea level, many of which are sinking. Areas with a lower tidal range, such as the Baltic and the Mediterranean, may also be more vulnerable to sea level rise than the Atlantic and North Sea coasts (Nicholls and Mimura, 1998). On the Atlantic coast of the US, shorelines south of 40°N have been shown to be the most vulnerable, owing to bluff and upland erosion, and to overwash and breaching of island barriers (CCSP, 2009).

4.1.1 Past and present (observations)

The total rise in global mean sea level over the 20th century was estimated to be ca. 0.17 m, with an average rate of 0.17 mm year^{-1} (Church and White, 2006; Bindoff *et al.* 2007). There is high confidence that the rate of observed sea level rise increased in recent decades (1.8 mm year^{-1} for 1961–2003 and 3.1 mm year^{-1} for 1993–2008; Merrifield *et al.*, 2009; Cazanave and Llovel, 2010). Whether the recent faster rate reflects decadal variability or an increase in the longer-term trend is unclear (Edwards, 2008; Jevrejeva *et al.*, 2008; Woodworth *et al.*, 2009). There are still some uncertainties in our understanding of how sea level has changed on decadal and longer time-scales, and of the contributions of the various processes involved (Church *et al.*, 2008).

Figure 4.3 shows the development of global mean sea level over the past 100 years as obtained from tide gauges and satellites. Where tide-gauge and satellite data overlap (1993–1999), the measured rate is similar, indicating that the acceleration observed since 1993 is not simply the result of the different method of observation (Church *et al.*, 2008).

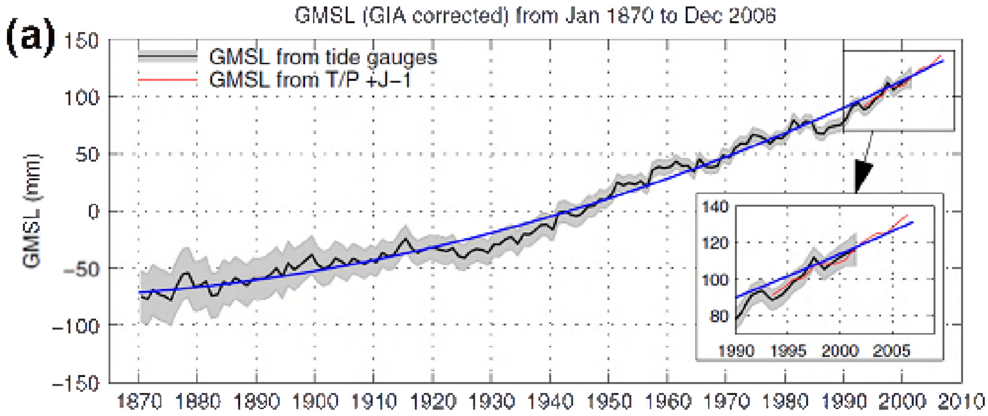


Figure 4.3. Global mean sea level (GMSL) from 1870 to 2006, with error estimates of one standard deviation. (Adapted from Church *et al.*, 2008.)

Melting land ice (including glaciers, ice caps, and the large ice sheets of Greenland and Antarctica) is thought to have provided 30% of the sea level rise during the 20th century compared with 55% from thermal expansion (Cazanave and Llovel, 2010). From 1993 to 2007, the largest contribution to sea level rise (39%) came from melting glaciers and ice caps, whereas 25% came from Greenland and Antarctic ice sheets, and 35% from thermal expansion. However, over the period 2003–2007, it is estimated that the combined contribution from melting land ice has increased from 64% to 80%, and that this is potentially the largest contributor in future (Church *et al.*, 2008; Cazanave and Llovel, 2010).

4.1.2 Future sea level rise (projections)

Projected warming caused by emissions of greenhouse gases during the 21st century will continue to contribute to sea level rise for many centuries because of thermal expansion and loss of land ice. These processes will continue for centuries or millennia even if radiative forcing were to be stabilized. In other words, future changes in sea level rise will be caused by past changes in temperature. There is high confidence in this projection (Meehl *et al.*, 2007). There remain uncertainties in the estimates of the future rate of rise, although the present scientific debate is about the upper range of estimates and not the lower range. As sea level rise was not geographically uniform in the past, it is highly likely that it will have similar variability in future.

Predictions of future sea level rise rely on accurate estimates of warming (thermal expansion) as well as of the mass balance in large ice sheets, such as the Greenland and Antarctic ice caps. Snow accumulation on an ice cap will have a negative effect on sea level rise, whereas melting of the ice cap will contribute to sea level rise. An ability to model the net effect of these processes is important to accurately predict the rates of change.

Estimates, from the Fourth Assessment Report (AR4) of the Intergovernmental Panel on Climate Change (IPCC, 2007a), of the likely range of sea level rise at the end of the present century, determined from a multimodel evaluation for different scenarios, are given in Table 4.1 (Meehl *et al.*, 2007). Overall, the range extends from 0.18 m to 0.59 m. In all scenarios, the average rate of rise during the 21st century very probably exceeds the 1961–2003 average rate (1.8 mm year^{-1}). In all scenarios, the largest contribution is obtained from thermal expansion (10–41 cm), whereas mountain glaciers and ice caps still provide the second largest contribution (7–17 cm) to projected global mean sea level rise.

Table 4.1. Projected global sea level rise at the end of the 21st century (in metres at 2090–2099 relative to 1980–1999). The model-based range excludes future rapid dynamic changes in ice flow. (Data from Meehl *et al.*, 2007.)

SCENARIO	LIKELY RANGE
B1	0.18–0.38
A1T	0.20–0.45
B2	0.20–0.43
A1B	0.21–0.48
A2	0.23–0.51
A1FI	0.26–0.59

Although an attempt to account for uncertainties related to land-ice response was made in the IPCC projections, there remain concerns in the scientific literature that the ice dynamic response to warming (the flow of ice directly into the ocean as opposed to melt and run-off) was significantly underestimated in IPCC AR4. This is partly caused by the observation that measured sea level changes from 1990 to the present have been larger than projected by the AR4 central value for the same period (Church *et al.*, 2008).

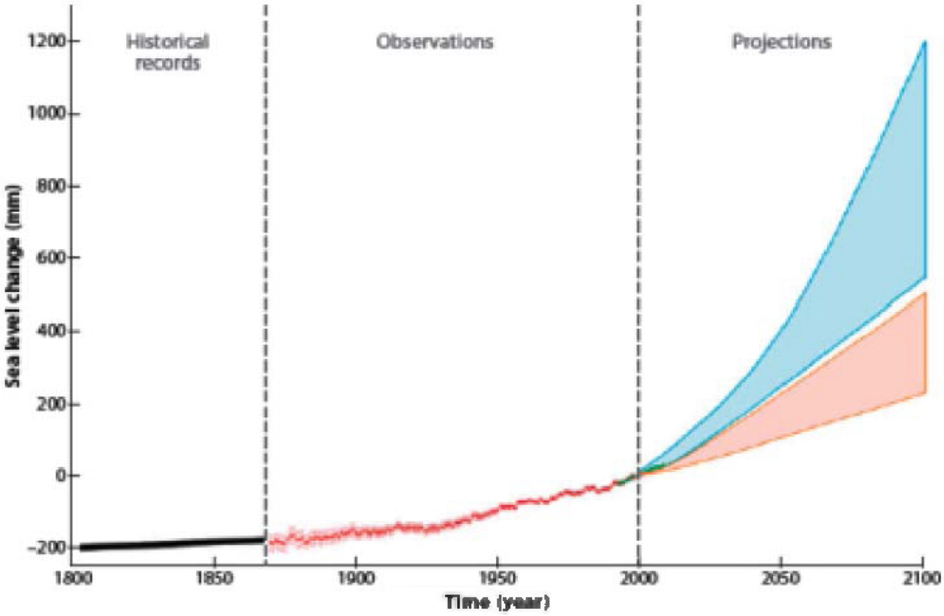


Figure 4.4. Evolution of the global mean sea level from observations (19th and 20th centuries) and model projections for the 21st century. The thick black line represents the long-term sea level based on various observations. The red line is based on tide-gauge data (Church *et al.*, 2004). The green line is from satellite altimetry since 1993. The pink-shaded region includes projections from coupled climate models (Meehl *et al.*, 2007). The light blue-shaded region includes projections from Rahmstorf (2007). (Figure from Cazenave and Llovel, 2010.)

A number of recent studies have presented projections of sea level rise without relying entirely on global climate models. Rahmstorf (2007) employed a semi-empirical model, based on a linear relationship between 20th century global mean sea level rise and temperature change, and applied this relationship to the 21st century using temperature projections based on IPCC scenarios. The reported sea level rise by 2100 ranged between 0.5 m and 1.2 m. These predictions have been contested (Holgate *et al.*, 2007, among others) and are still subject to scientific debate. Since then, more complex relationships or longer correlation datasets have been used to estimate future sea level rise driven by the IPCC temperature projections. For the A1B scenario, Grinsted *et al.* (2008) gave a range of 0.9–1.3 m for sea level rise up to the last decade of the current century. Vermeer and Rahmstorf (2009) applied an extended and improved version of the semi-empirical method developed by Rahmstorf (2007) in order to obtain a sea level projection up to 2100 of 0.75–1.9 m.

The possibility of extreme sea level rise of up to several metres has been brought into the discussion (Overpeck *et al.*, 2006; Hansen *et al.*, 2007). The studies refer to climate modelling and analogies in palaeoclimate records, which contain numerous examples of ice-sheet disintegration, yielding sea level rises of several metres per century. In a recent study, Pfeffer *et al.* (2008) report on kinematic constraints that limit land-ice contributions to sea level rise; they conclude that rises in excess of 2 m by 2100 are most unlikely if physically possible glaciological conditions are considered. Pfeffer *et al.* (2008) suggest that, even with large uncertainties in their assumptions, a range of 0.8–2 m is plausible for sea level rise during the 21st century.

The processes that determine regional changes in sea level are more complex and difficult to predict (see the box below). Projections based on ocean density changes indicate that the coastal regions of the ICES Area will be one of the most strongly affected by regional sea level changes, with the effect being greater at higher latitudes

(Cazenave and Llovel, 2010, Figure 12). At a regional level, understanding the relative sea level rise is the key issue, and this requires a multidisciplinary approach.

In summary, model projections of sea level rise during the 21st century (and beyond) still remain highly uncertain. The range provided in the IPCC AR4 appears to mark the lower bound of possible global sea level rise in response to future climate change. Aside from general model uncertainties, the dynamics of the land-based ice, especially the ice that flows into the ocean as icebergs, are poorly understood and limit the informative value of the projections. On a regional scale, the available model-based projections are even more uncertain, because they reflect only the regional variability caused by long-term climate signals. Decadal and multidecadal natural variability, which may differ from the global mean by a factor of 2–3, is poorly accounted for at present (Cazenave and Llovel, 2010). Further development of sea level projections that better represent the natural decadal and multidecadal variability is an important priority.

4.2 Arctic sea-ice cover

A feature associated with both climate change and global warming is the state of sea-ice cover in the northern hemisphere. With the advent of satellites and the development of sensors, the sea-ice extent has become one of the most easily observed and monitored environmental parameters. The shallow and deep outflowing water from the Arctic plays a major role in the North Atlantic and global circulation as part of the redistribution of heat and freshwater around the planet. Changes in sea-ice cover are closely related to the processes that form the polar outflow waters.

Arctic sea-ice extent has demonstrated a more or less steady reduction since the beginning of systematic satellite observations in the late 1970s (Figure 4.5). The mean sea-ice extent for the period 1979–2000 is commonly used as reference to evaluate anomalies of sea-ice cover. Large declines in sea-ice cover occurred in 2005, especially during the International Polar Year (IPY) 2007–2008. In 2007, the minimum ice extent, occurring in September, was 4.3×10^6 km^2, 15% below the previous minimum of 2005 and 30% below the long-term mean. Most climate models indicate that the Arctic Ocean could become ice-free in summer by the end of this century, but a summer extent as small as that observed in 2007 was not predicted until approximately 2040 (ACIA, 2005).

A combination of several forcing conditions appears to have contributed to the retreat of the summer ice in the Arctic Ocean in 2007. A high-pressure system with clear skies over the Beaufort Sea in June and July allowed for strong incoming solar radiation and large surface ice melt (Kay *et al.*, 2008). Advection of warm air from the Pacific sector, an unusual condition that prevailed in the early part of the 2000s, brought heat and moisture into the Arctic (Overland *et al.*, 2008). A pronounced high over the Beaufort Sea and Greenland, and a corresponding low over Siberia, led to strong winds from the Bering Sea/Chukchi Sea across the Arctic Ocean, driving the sea ice through Fram Strait into the Nordic seas (Nghiem *et al.*, 2007). The large ice-free area allowed surface water to be directly heated by incoming short-wave radiation, leading to exceptional basal melting (Perovich *et al.*, 2008). The inflow of Pacific water in 2007 was also found to be stronger and warmer than average (R. Woodgate, pers. comm., 2009). It is clear that no adequate and generally accepted understanding of the processes and interactions that determine the Arctic Ocean ice cover has yet been reached. The minimum ice extent in 2008 and 2009 was slightly greater than in 2007, but not by much.

Measuring long-term changes in sea level

There are two main data sources from which multiyear changes in mean sea level can be determined: tide gauges and satellite altimetry.

Tide gauges measure sea level relative to the seabed (relative sea level); these records are available for longer periods, but there are gaps in the spatial coverage, and the measurements can be affected by sudden changes, such as an earthquake, or gradual land movement, such as isostatic rebound.

Satellite altimetry measures sea level relative to the centre of mass of the Earth (absolute sea level). These data provide near-global coverage and are not affected by land movements. However, satellite measurements are available only from 1993 onwards, and the data need to be carefully analysed to ensure that errors are corrected (Cazenave and Llovel, 2010).

Recent developments in observation systems, such as the Argo programme (since 2000) and the GRACE (Gravity Recovery and Climate Experiment) satellite programme (since 2002), have provided additional data useful for understanding spatial and temporal variability in sea level rise. These data have already proven to be useful, and confidence in the new results will grow as the time-series get longer (Milne *et al.*, 2009).

All of the data sources have their limitations and sources of uncertainty, and much of the current research effort is focused on examining and understanding small differences in the various types of observations (Bindoff *et al.*, 2007; Milne *et al.*, 2009; Cazenave and Llovel, 2010). Despite these difficulties, the general conclusion of a climate-related rise in sea level since the early 1900s, with a recent acceleration in the last decade, remains solid.

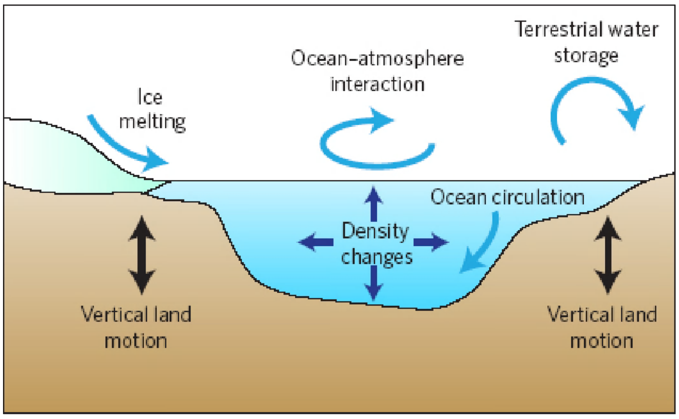


Figure T4.1. Processes that affect sea level rise. These processes can have significant regional and short-scale temporal variability. (Source: Milne *et al.*, 2009.)

One factor that might be decisive for the future fate of the ice cover is ice thickness. In the 1990s, ice-thickness observations from submarines were released with a sufficiently long time-series and enough spatial coverage to allow thickness trends to be determined. The observations demonstrated that not only was the ice extent reduced, but also that it was becoming thinner, by almost 40% over a 20-year period (Rothrock *et al.*, 1999). These analyses were initially contested because the ice is in motion, driven by the windfields, and the comparison between ice thicknesses at the same place 20 years apart does not necessarily reveal a time evolution but could indicate a redistribution of the thicker ice within the Arctic Ocean (Holloway and

Sou, 2002). More recent results from the past 5 years, however, have clearly confirmed that the sea ice is becoming thinner (Figure 4.6). The number and sizes of ridges have also decreased, and the ice cover has become more deformable. Ice is drifting more easily and quickly through the Arctic Ocean, as was strikingly demonstrated by the vessel "Tara", which in 2006–2008, as part of the DAMOCLES (Developing Arctic Modelling and Observing Capabilities for Long-term Environmental Studies) programme, repeated the drift of "Fram" in 1893–1896. The "Tara" drift lasted 18 months compared with 3 years for "Fram", and "Tara" reached a higher latitude than "Fram": almost to the North Pole, Nansen's original goal. The greater mobility of the ice has allowed ice export through Fram Strait, which accounts for >95% of the total ice export, to remain almost constant, despite the thinning of the ice (Kwok *et al.*, 2004; Dickson, R., *et al.*, 2007). As a result, the residence time for sea ice has decreased, perhaps by as much as 50%, and is now ca. 4–5 years.

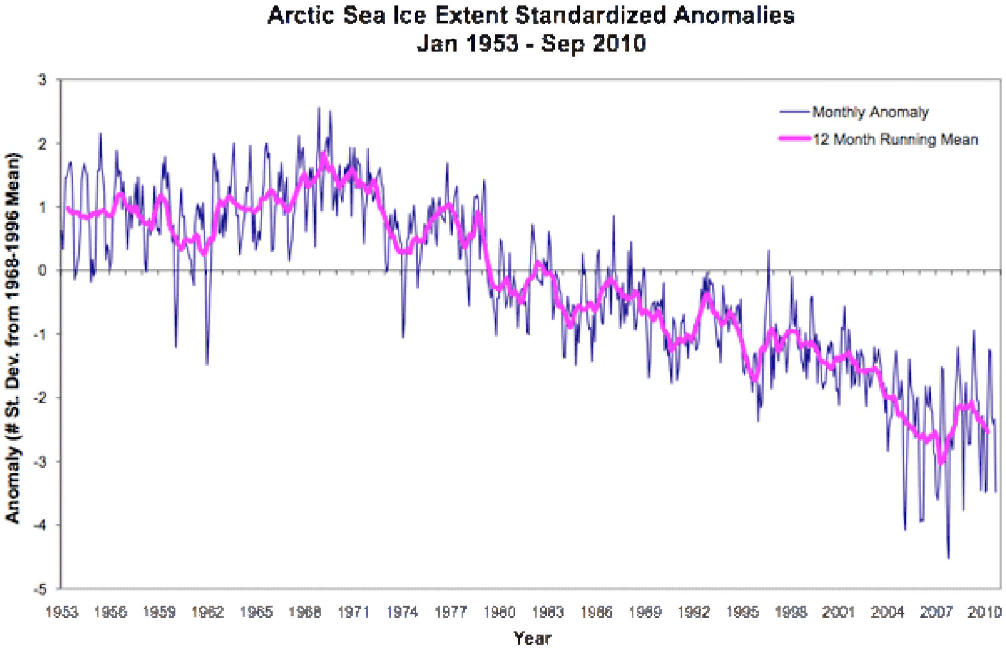


Figure 4.5. Mean sea-ice anomalies, 1953–2010: sea-ice extent departures from monthly means for the northern hemisphere. For January 1953–December 1979, data have been obtained from the UK Met Office Hadley Centre and are based on operational ice charts and other sources. For January 1979–September 2010, data are derived from passive microwave radiometry, (Scanning Multichannel Microwave Radiometer (SMMR) and Special Sensor Microwave/Imager (SMMR/I)). (Image by Walt Meier and Julienne Stroeve, National Snow and Ice Data Center, University of Colorado, Boulder. Image obtained from http://nsidc.org/sotc/sea_ice.html, March 2011.)

As the climate becomes warmer, the extent and thickness of sea-ice cover is expected to reduce further. A basic estimate of the thickness for landlocked ice achieved during winter can be derived from the number of freezing-degree-days, (θ; summing the days multiplied by their negative temperatures), which is a measure of the cooling during a winter season. The thickness is then related to θ as $\sim\sqrt{\theta}$. This expression can also be used as a rough indicator of ice growth in the Arctic Ocean (Gascard, pers. comm., 2009) and, obviously, a warmer winter leads to a thinner ice cover. Correspondingly, the ice thickness in autumn has been shown to be related to the length of the melting season. A longer melting season results in a thinner ice cover (Laxon *et al.*, 2003).

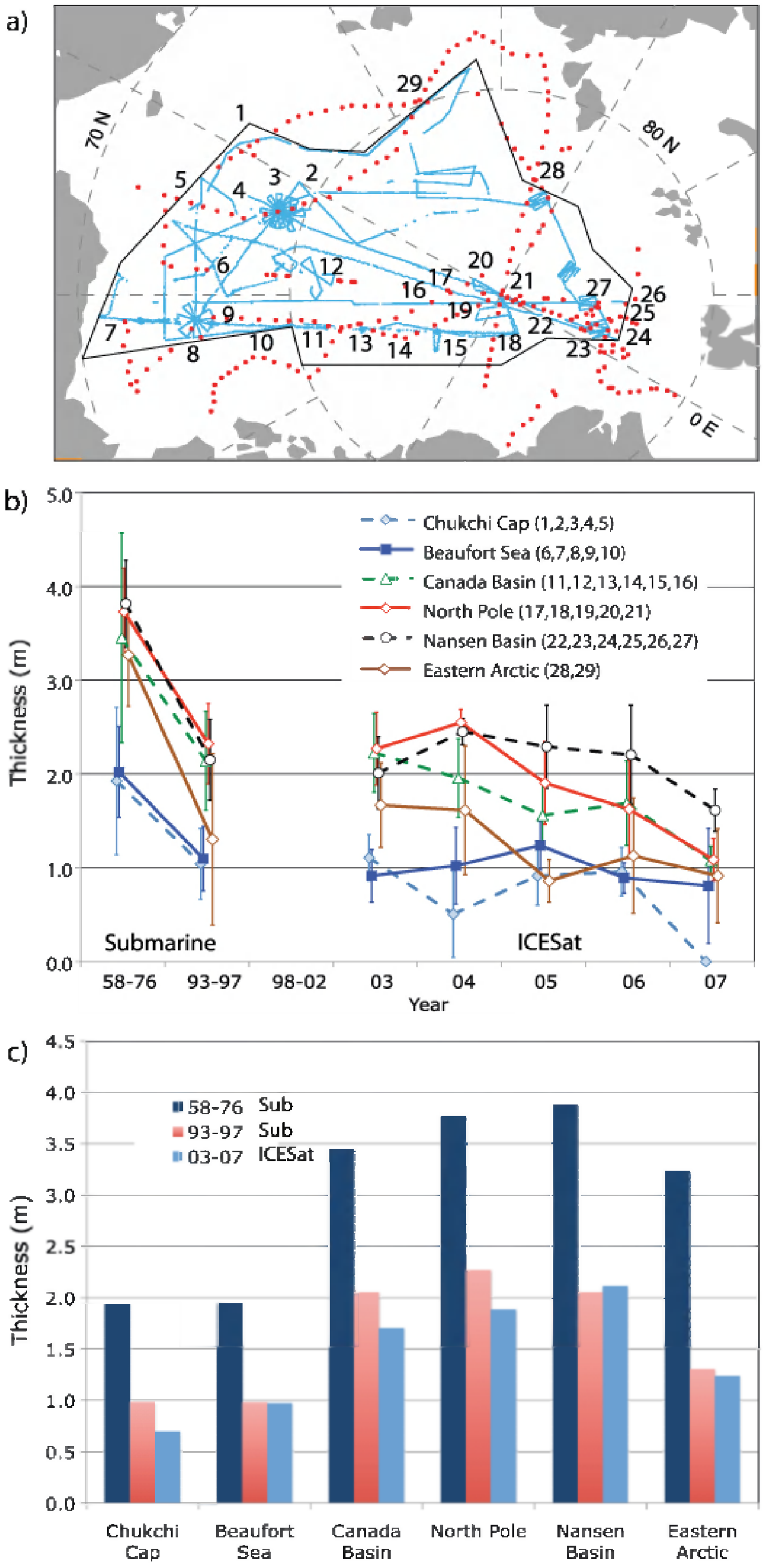


Figure 4.6. Analysis of sea-ice thickness. (a) Submarine cruise tracks and comparison locations. (b) Regional comparisons of the submarine data (1958–1976 and 1993–1997) and five years (2003–2007) of ICES thickness data. Vertical bars show the variability within each region. (c) Mean thicknesses of the six regions for the periods 1958–1976, 1993–1997, and 2003–2007. Thicknesses have been seasonally adjusted to September 15. (Source: Kwok and Rothrock, 2009, Figure 1.)

It should be kept in mind that the Arctic Ocean sea ice is not melting except in summer. Freshwater is supplied in liquid form, by river run-off and by net precipitation (Serreze *et al.*, 2006). The freshwater is then exported partly as liquid freshwater by the ocean currents and partly as sea ice. At present, approximately one-third of the freshwater input to the Arctic Ocean is exported as sea ice (e.g. Dickson, R., *et al.*, 2007).

The thinning and reduction of the ice cover, and its dynamical effect on the ice drift, has started a discussion about the tipping point or point of no return for the extent of Arctic sea ice (Lindsay and Zhang, 2005). A gradual thinning and a maintained ice export would eventually lead to such a small ice storage that a sudden large export of ice could reduce the ice cover so much that multiyear ice never recovers. Newly formed ice would not be kept sufficiently long in the Arctic Ocean to generate two-year and multiyear ice floes before it is exported, and the perennial ice would give way to a seasonal ice cover. Such a point of no return had been predicted to occur before the middle of the century (Holland *et al.*, 2006; Stroeve *et al.*, 2007), but following recent events, it has been suggested that such a state could be reached earlier, perhaps within a decade.

Oceanic heat transport, especially the inflow of warm Atlantic water through Fram Strait, has been suggested to have a critical impact on the sea-ice cover (e.g. Polyakov *et al.*, 2005). The inflow of exceptionally warm Atlantic water in the 1990s, and again in the early 2000s, could then have contributed to the reduction in ice thickness. However, the temperature of the Atlantic layer ($T > 0\,^{\circ}C$) in the Arctic Ocean has also increased during this period, indicating that most of the oceanic sensible heat transported by the Atlantic water into the Arctic Ocean does not reach the sea surface and the ice, but is stored in the interior of the water column, eventually to return to the Nordic seas through Fram Strait (Rudels *et al.*, 2008). In most parts of the Arctic Ocean, the heat of the Atlantic layer is isolated from the sea surface by a cold halocline and a low-salinity upper layer (Coachman and Aagaard, 1974). Only north of Svalbard, close to Fram Strait, does the Atlantic water interact directly with and melt sea ice. In the Nansen Basin, a direct communication between the Atlantic water and the ice cover exists in winter, but the heat exchange is probably small because the upper winter mixed layer is thick (>100 m), and the stirring is caused by brine rejection and haline convection (e.g. Rudels *et al.*, 2004). However, at the continental slope and at the shelf break, where the Atlantic water comes close to the sea surface and mechanical mixing processes, such as wind and internal tides, may entrain warmer water into the mixed layer, the Atlantic water could contribute to the heat balance at the sea surface and reduce the ice formation during winter.

The inflow of warm Pacific water through the Bering Strait in summer, namely the Bering Strait Summer Water (BSSW; Coachman and Barnes, 1961), may have an impact on the ice cover. In recent years, the BSSW has had a temperature maximum located between 50 and 100 m below the surface in the Canada Basin north of the Chukchi Sea. This is close enough to the surface to be brought into the mixed layer by interaction with the large-scale circulation (Shimada *et al.*, 2006), as well as by enhanced motions and upwelling generated at the ice edge and at the continental slope and shelf break (Carmack and Chapman, 2003). This heat input could contribute to ice melt, or at least reduce the ice formation. The largest retreat of the sea-ice cover has also been observed in the Canada Basin.

The low-salinity upper layer, and thus the freshwater input to the Arctic Ocean, is necessary for the formation and maintenance of the ice cover. It creates the strong stability that allows the surface water to be cooled to freezing temperature without attaining a density high enough for convection into the deep ocean. In global warming scenarios, the freshwater supply to the Arctic is expected to increase. If less freshwater is exported as ice, the stability of the upper layers will increase in future. The interactions with and the vertical heat flux from the underlying Atlantic water would then become even weaker than at present. An increased freshwater input thus favours stronger ice formation.

Another situation to unravel and model is the deformation of the ice cover and the ridge formation as the ice cover becomes thinner. More open water should then be generated, and the ice would move more rapidly. On the other hand, more open water would, in winter, lead to increased ice formation because the insulating effect of the ice cover is reduced. However, open water also leads to a higher evaporation rate and, hence, to a higher vapour content in the atmosphere that could reduce the outgoing long-wave radiation from the ice by radiating it back towards the surface. The cooling in winter would then be reduced. In summer, more open water implies a lower albedo and a larger input of heat from short-wave solar radiation to the upper layer of the ocean. The ice melt would increase, and the ice would melt not only as a result of solar radiation directly on the ice but also by the heating from below and from the sides by the surrounding water.

An intriguing point in this context is that the ice does not melt until the water temperature is above 0°C. At lower temperatures, but above the freezing point of the surface water, the ice is dissolved because ions penetrate and destroy the crystal structure (Notz *et al.*, 2003). Heating the surface water above 0°C could then result in a large increase in the basal ice-melt rate. As the temperature increases, the brine channels widen. This eventually leads to flushing and the replacement of high-salinity brine with low-salinity meltwater. The enlarged brine channels reduce the ice-to-ice contact and the ice strength. With sufficient seasonal heating, this could also happen with multiyear ice, causing it to fragment more easily. With present-day satellite observations, it is not easy to distinguish between strong, multiyear ice and weakened or "rotten" ice (Barber *et al.*, 2009).

The effects of the northward atmospheric transports of sensible heat and water vapour are difficult to assess. How much does the direct heating affect the ice thickness? What is the effect of the water vapour? The vapour transport contributes to the heat transport by condensation. It also affects the radiation balance in two ways: as water vapour, it reduces the long-wave back radiation, whereas, as water and clouds, it reduces the incoming solar radiation by increasing the albedo. As net precipitation falling as snow, it also increases the surface albedo of the ice and thus reduces the summer ice melt. However, the snow insulates the underlying water and reduces the heat loss and ice formation in winter.

More open water will lead to larger sensible and latent heat loss that not only increases, or at least preconditions, the ice formation, but could also affect, and perhaps change, the larger-scale atmospheric circulation and thus influence the overall atmospheric heat transport to the Arctic. The effects of such changes, should they occur, are unknown.

Most changes that could, and do, occur in the Arctic involve interactions and feedbacks that may be either positive (strengthening the change), or negative (reducing the change). Which effects will dominate are not obvious and might actually depend upon specific conditions prevailing as the changes occur. To parameterize these vaguely understood interaction processes is a difficult task, and its solution, should only one solution exist, may remain elusive far into the future.

The overall consequences of a less-extensive, less-compact ice cover and perhaps an ice-free Arctic Ocean in summer are hard to envisage, as are the analyses of the processes determining the fate of the ice cover. What changes will occur in the Arctic Ocean ecosystem and what surprises are in store for the local population? The changes in human activities, local living conditions, fisheries, and shipping, and the effects of future oil and mineral exploitation and tourism following a retreat of the ice cover, are likely to be huge and unforeseeable.

4.3 Conclusions

- Global mean sea level is known to have risen by ca. 0.17 m during the 20th century. An increase in the rate of rise, with an additional acceleration over past decades, has been observed. The recent acceleration is known to be mainly the result of climate-related effects, such as thermal expansion of seawater and melting of land-based glaciers, ice caps, and ice sheets.
- In some regions, such as the Mid-Atlantic coast of the US, sea level rise is greater than the observed global mean owing to sinking of the land surface. Satellite observations over the past 15 years reveal that sea level rise is highly variable at regional scales.
- Coupled climate modelling studies suggest that sea level will continue to rise throughout the 21st century (and beyond), with rates likely to exceed significantly those observed during the 20th century. The future impact of sea level rise is likely to be mainly socio-economic, owing to flooding of coastal areas. Direct environmental effects will be limited to intertidal, coastal, and wetland areas. Impacts will be greatest in countries with large populations living in low-lying coastal regions.
- Although global mean sea level has been estimated with some confidence, an accurate understanding of the temporal and spatial variability in sea level rise (past and future) requires a better understanding of the underlying oceanographic and climatic processes.

Arctic sea-ice extent has demonstrated a more or less steady decrease since the late 1970s, reaching a new record low in 2007. No adequate and generally accepted understanding of the processes and the interactions that determine Arctic Ocean ice cover has yet been reached. Observations reveal that the sea ice has become thinner by almost 40% over a 20-year period, leading to predictions that perennial ice may give way to seasonal ice cover within 10–50 years. The interaction between the warm oceanic inflows from the Atlantic and Pacific and the stratification and ice cover is not fully understood, so the impact of changes in the inflows is unclear. The feedback effects from more open water in summer and winter are complex and not well understood. More open water will lead to larger sensible and latent heat losses that may increase ice formation, but could also affect the larger-scale atmospheric circulation.

5 Acidification and its effect on the ecosystems of the ICES Area

Liam Fernand (corresponding author), Will LeQuesne, Joe Silke, Bill Li, Silke Kroeger, John Pinnegar, Jan Helge Fossä, and Xosé Anxelu G. Morán

5.1 Introduction

This section focuses on the impacts of ocean acidification (OA) on ecosystems and higher trophic levels in the ICES Area. One of ICES distinguishing features is its access to scientists across the entire marine field; this section is based on the Report of the Workshop on the Significance of Changes in Surface CO_2 and Ocean pH in ICES Shelf Sea Ecosystems (WKCpH; ICES, 2007c), updated to include recent research, using inputs from the chairs of ICES working groups.

A number of collections of papers have been published recently in peer-reviewed journals, notably "The ocean in a high-CO_2 world II" (Gattuso *et al.*, 2008; available online at: http://www.biogeosciences.net/special_issue44.html), and these are referred to in the text whenever relevant to impacts on ecosystems.

More general background on the chemical and physical effects of OA can be found in the freely available reports of scientific bodies or governmental institutions, such as the Intergovernmental Panel on Climate Change (IPCC, 2005), the National Oceanic and Atmospheric Administration/National Science Foundation/US Geological Survey (NOAA/NSF/USGS; Kleypas *et al.*, 2006), and the German Advisory Council on Climate Change (WBGU, 2006), as well as in recent journal articles about the historical context (e.g. Pelejero *et al.*, 2010), and in papers in the five 2011 special issues of the online journal *Biogeosciences* (available at: http://www.biogeosciences.net/volumes_and_issues.html.

Oceanic uptake of atmospheric CO_2 has led to a perturbation of the chemical environment, primarily in ocean surface waters, which is associated with an increase in dissolved inorganic carbon (DIC). The increase in atmospheric CO_2 from ca. 280 ppmv (parts per million by volume) 200 years ago to 390 ppmv today (2011) has most probably been caused by an average reduction across the surface of the oceans of ca. 0.08 pH units (Caldeira and Wickett, 2003) and a decrease in the carbonate ion (CO_3^{2-}) of ca. 20 μmol kg^{-1} (Keshgi, 1995; Figure 5.1). It has been estimated that the level could drop by a further 0.3–0.4 pH units by the year 2100 if CO_2 emissions are not regulated (Caldeira and Wickett, 2003; Raven *et al.*, 2005). A study of potential changes in most of the North Sea (Blackford and Gilbert, 2007) suggests that pH change this century may exceed its natural annual variability. Impacts of acidity-induced change are likely, but their exact nature remains largely unknown, and they may occur across the whole range of ecosystem processes. Most work has concentrated on open-ocean systems, and little research has been applied to the complex systems found in shelf-sea environments.

5.2 Evidence for pH change in the water column

A small number of long-term (>10 years) observatories have recorded atmospheric carbon dioxide (pCO_2) in both the atmosphere and the water column (Figure 5.2a). A strong seasonal cycle is observed in pCO_2, caused by variations in temperature and biological drawdown resulting from photosynthesis and respiration; therefore, a minimum record of 10 years is required to estimate a meaningful average and deduce any trend. These stations are relatively rare, with limited geographic coverage. The principal stations are the Hawaii Ocean Time-series (HOT, Figure 5.2 lower graph), the Bermuda Atlantic Time-series Study (BATS), and the European Station for Time Series in the Ocean (ESTOC), situated off the Canaries. All of these time-series demonstrate high natural variability, but all confirm that pH is decreasing. Owing to instrument limitation, many of the historical measurements of pH are of limited accuracy, and those prior to the 1970s are suspect and generally not reliable. Consequently, care must be taken when using pre-1970s datasets, because potential sampling bias and geographic variation can lead to erroneous interpretation of results. In the deep ocean, the natural pH range and likely future change is a function of depth, with the greatest variation at the surface. In contrast, in shelf seas, which are well mixed in winter, even benthic organisms are exposed to a full range of pH variation and will soon experience the effects of increased levels of atmospheric CO_2.

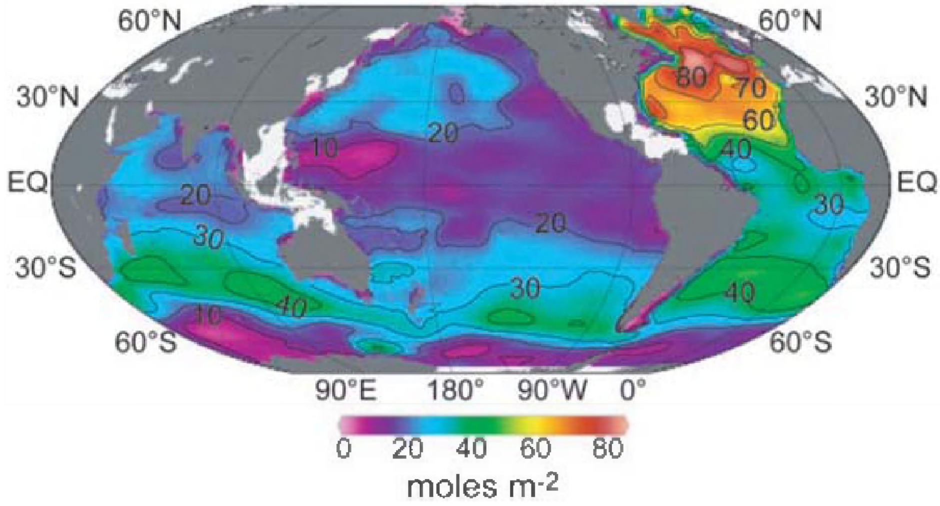


Figure 5.1. Worldwide distribution of Oceanic uptake of anthropogenic $C0_2$ (mol m^{-2}). This increase is greatest in the ICES region. (Source: Sabine *et al.*, 2004. Courtesy of *Science*.)

5.3 The historical context to changes in oceanic pH

Boron isotopes in fossil foraminifera from seabed sediment cores can be used to reconstruct past records of pH. The record (Figure 5.3) from the eastern equatorial Atlantic demonstrates the change in pH over the past 650 000 years, revealing a cyclical pattern that is associated with alternating glacial/interglacial periods. Present-day measurements of pH are comparable with the lowest values estimated in the past, with a transition from low to high pH states at intervals of ~50 000 years. From an historical perspective, the present levels of pCO_2 are already high, and anthropogenic emissions are further increasing the natural concentration. Natural cycles in seawater pH could enhance or mitigate the vulnerability of marine organisms to future OA. Catastrophic events in the past, associated with the Palaeocene–Eocene Thermal Maximum (PETM), suggest that the saturation state was important, and the record also suggests that, once established, high pCO_2 levels persist for thousands of years (Pelejero and Calvo, 2007).

5.4 Model predictions

The saturation depth (or horizon) is the depth at which a shell or bone made of calcite or aragonite would dissolve if there were no biological activity. Figure 5.4 shows a modelled estimate of the aragonite saturation horizon produced by Orr *et al.* (2005). The map shows that, in the Southern Ocean, aragonite in shells will dissolve at all depths. In the North Atlantic, bottom-dwelling organisms will be affected, and only those in relatively shallow areas will remain viable. The calcite/aragonite ratio is species-dependent; thus the difference between these two saturation conditions gives rise to species-dependent responses to future conditions. In waters below the saturation horizon, shell formation will be at a substantial metabolic cost.

In future, in upwelling areas, it is likely that intermediate waters from below the depth of the aragonite-saturation horizon, which are rich in CO_2, will be upwelled onto the shelf, as is now occurring off the Oregon coast (Chan *et al.*, 2008). In some cases, such as the Baltic, low saturation states are already occurring because the low-alkalinity waters in this brackish sea afford little buffering (Figure 5.5).

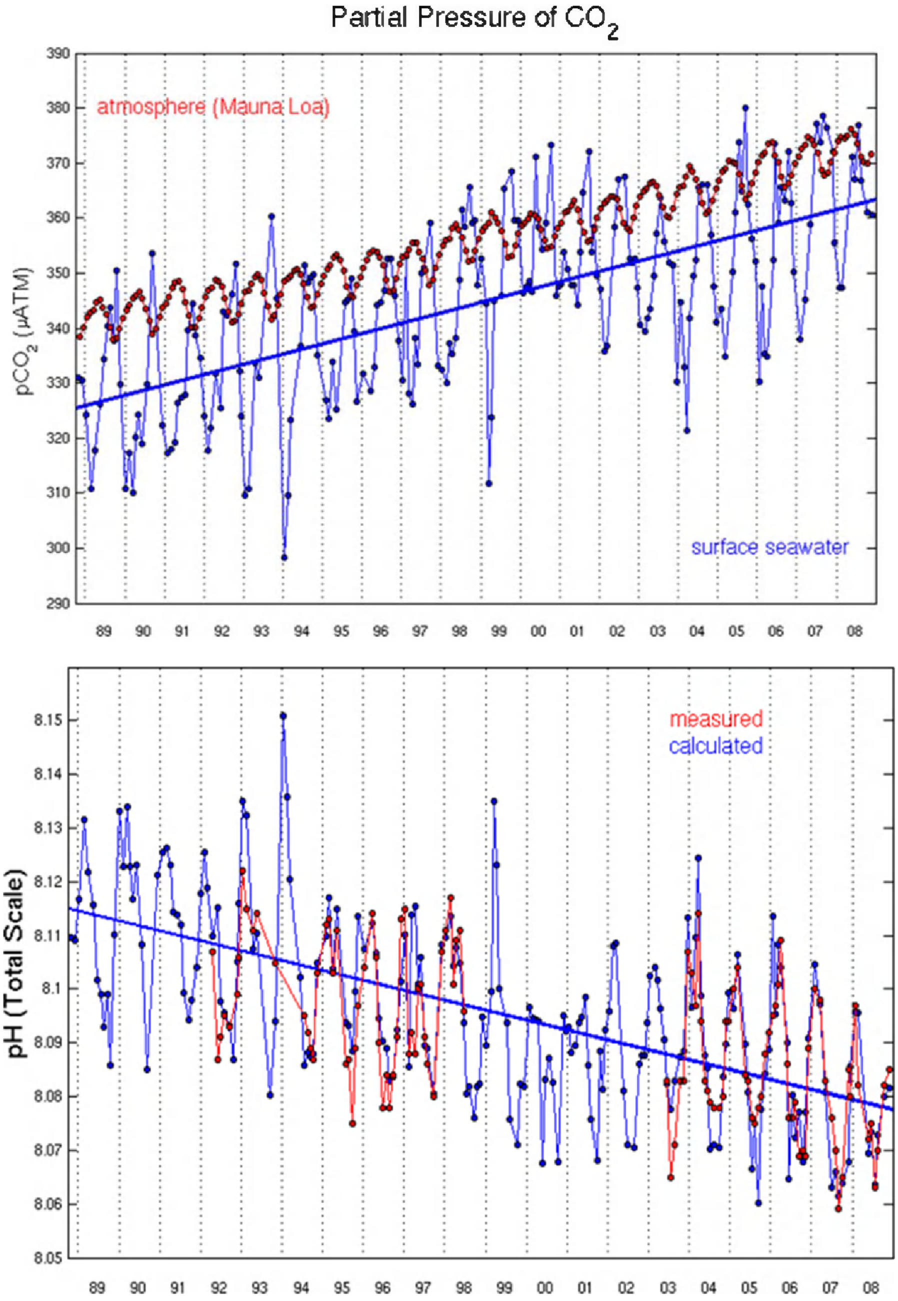


Figure 5.2. (upper graph) Time-series (1989–2008) of the change in pCO_2 (atmosphere and seawater). (lower graph) The pH change in seawater as recorded at the Hawaii Ocean Time-series (HOT) site, showing a decline in pH over 20 years of 0.03 units, which is approximately half the annual variability. (Figures supplied by HOT.)

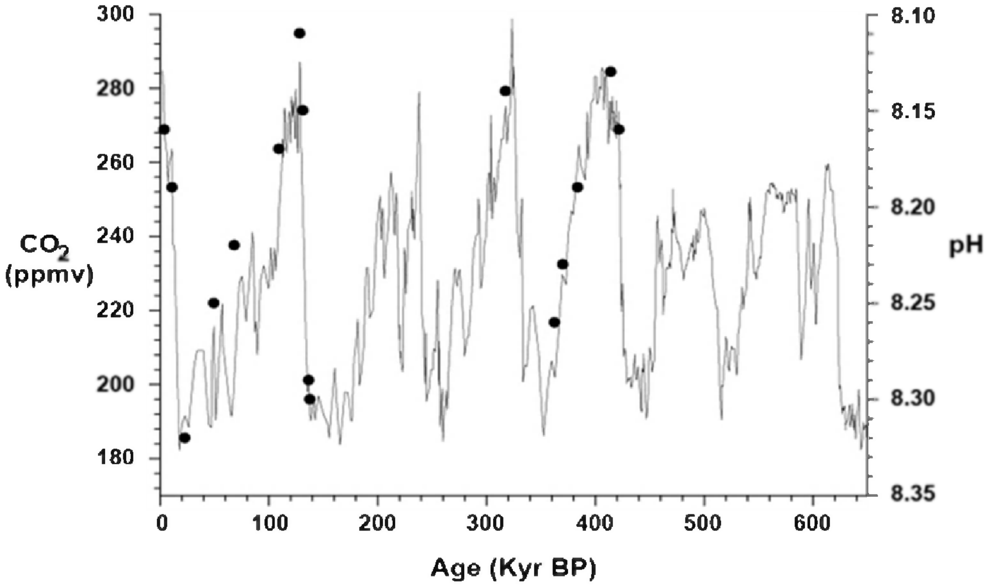


Figure 5.3. Estimated sea surface pH (solid circles) reconstructed using boron isotopes in planktonic foraminifera from a sediment core (ODP668B) retrieved in the eastern equatorial Atlantic (Hönisch and Hemming, 2005), superimposed on the record of atmospheric CO_2 (Petit *et al.*, 1999; Siegenthaler *et al.*, 2005). Redrawn from Pelejero and Calvo (2007).

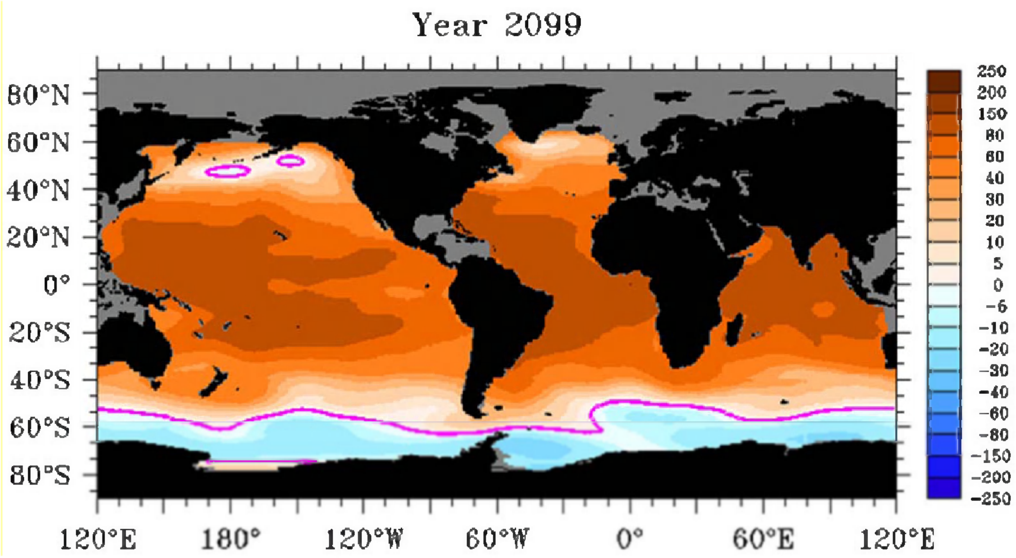


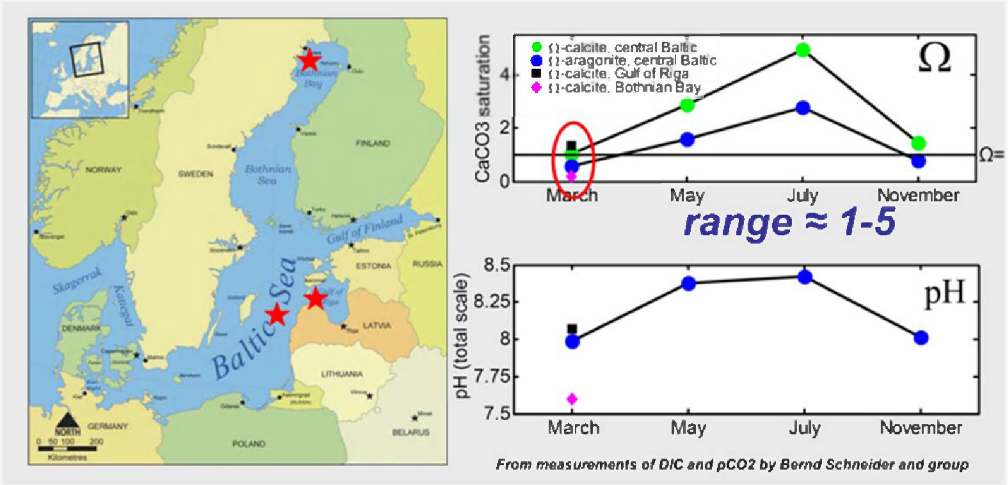
Figure 5.4. Global model predictions for 2099 of the depth (m) of aragonite saturation, i.e. the depth at which dissolution of aragonite occurs. (Source: Orr *et al.*, 2005; courtesy of *Nature*.)

5.5 Effect of pH (and temperature) changes on metals and contaminants

In addition to the chemical changes within the carbonate system of the oceans, other potential impacts on chemical speciation (e.g. metal and contaminant availability) must also be considered. Many metals and organic contaminants in the marine environment are bound, either by adsorption onto particles (of inorganic sediment, or of suspended or dissolved organic matter) or by complexing agents, such as metal-binding ligands. They may even be adsorbed onto plastic particles, which are commonly found in sediments and the water column. Their availability to biota or other chemical reactions depends on their binding coefficients (i.e. their adsorption–desorption behaviour). Temperature and pH are the key parameters in the regulation of binding processes. The predicted decrease in pH and increase in temperature may not be significant in regulating the availability of many organic contaminants in the short-to-medium term, but in some circumstances, such as metal complexation, the changes could lead to increased bioavailability of previously bound metals. In certain circumstances, some metals that are essential trace nutrients (e.g. iron) may be limiting to phytoplankton growth or toxic (e.g. free copper or organotins).

Organic metal complexes are known to play a significant role in the geochemical cycle of reactive trace metals (Hirose, 2002), and changes in the equilibrium between bound and free-metal ions result from an increase in hydrogen ion concentration. Importantly, marine microalgae process and excrete metal-binding ligands that allow them to obtain competitive advantages over other species in sequestering metals (Vasconcelos *et al.*, 2002); consequently, they can have an important influence on heavy-metal concentrations in seawater (González-Dávila, 1995). It is, therefore, likely that future changes in pH will influence metal complexation, which in turn may have a substantial impact on biota, either toxicologically or via ecosystem processes, such as microalgal bloom dynamics.

The potential for increased concentrations of CO_2 to alter the fate and transport of trace metals in sediment and seawater has recently been investigated in controlled experiments by Ardelan *et al.* (2009). Toxicological effects of changes in contaminant availability and fate caused by climate change have been described by Noyes *et al.* (2009), and the specific case of a climate impact on contaminants in the Arctic was the subject of a paper by Donald *et al.* (2005). It can be concluded that there are still many uncertainties regarding the exact influence of acidification on ocean chemistry with respect to metals and contaminants, but that the topic is worthy of consideration when trying to evaluate potential impacts of climate change and acidification on marine ecosystems.



From measurements of DIC and pCO2 by Bernd Schneider and group

Figure 5.5. Low saturation state (Ω) in the Baltic. Note: aragonite saturation is below 1, although pH is not very low, because of low total alkalinity. (Source: Tyrell *et al.*, 2008.)

5.6 Impacts on calcifying organisms in the water column

Research into water-column processes has focused primarily on those organisms that calcify. This group includes the coccolithophores, pteropods, and foraminifera, of which the first two are important in the carbon cycle but do not constitute a major food source.

5.6.1 Coccolithophores

Emiliania huxleyi is numerically the most abundant coccolithophore in the ocean and became prominent during glacial periods of enhanced ocean productivity. The species, which is ubiquitous in the ICES Area (De Bodt *et al.*, 2010), forms a major sink of carbon and is responsible for one-third of the production of marine calcium carbonate (Iglesias-Rodríguez *et al.*, 2008). Coccolithophores are important because they both fix carbon and photosynthesize (Figure 5.6).

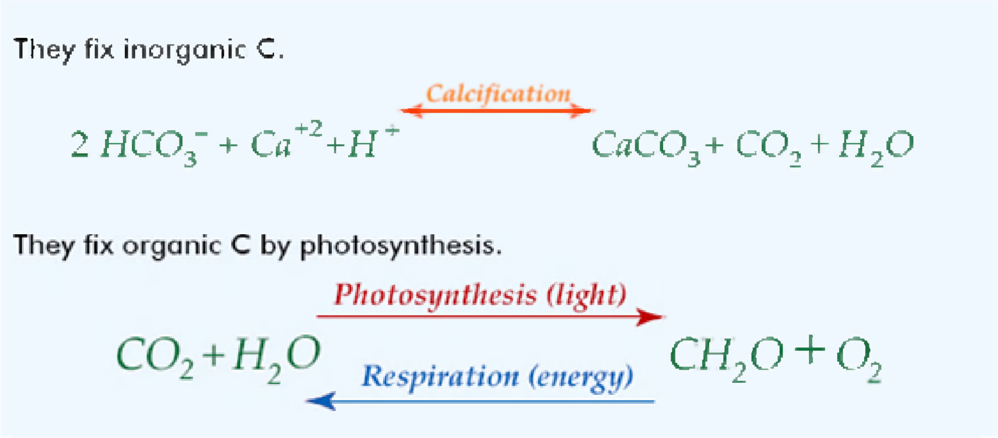


Figure 5.6. The function of coccolithophores in the fixing of carbon from the oceans and the drawdown of CO_2.

The majority of experiments (Riebesell *et al.*, 2000; Suggett *et al.*, 2007; also Figure 5.7) demonstrate the dissolution of liths when exposed to increased concentrations of CO_2. Others demonstrate reduced calcification rates (De Bodt *et al.*, 2010) corresponding to a reduction in the availability of carbonate ions. Other recent work, looking at changes over a longer term, indicates that, despite a decreasing pH, the net primary production is increasing, with a 40% increase in coccolithophore mass over the past 220 years (Iglesias-Rodríguez *et al.*, 2008). This apparently contradictory message may be the result of differences in methodology or in the time-scale associated with the experiments. The sudden changes in pH experienced by organisms in experiments may not be representative of possible adaptation over a longer natural time-scale. However, it should be noted that predicted changes in pH over the next 80 years, as simulated by many experiments, are much greater than those experienced over the past 220 years.

An additional consideration is that the increase in aqueous CO_2 will favour an increase in photosynthesis and thus increase the energy available to a cell. Depending on the species involved, this increase may offset the additional metabolic cost of making liths because of the reduced availability of carbonate ions. Different strains of *E. huxleyi* have responded in different ways (Suggett *et al.*, 2007), so although one strain may suffer from acidification, the species is likely to survive and, more broadly, may be replaced by another with a similar function.

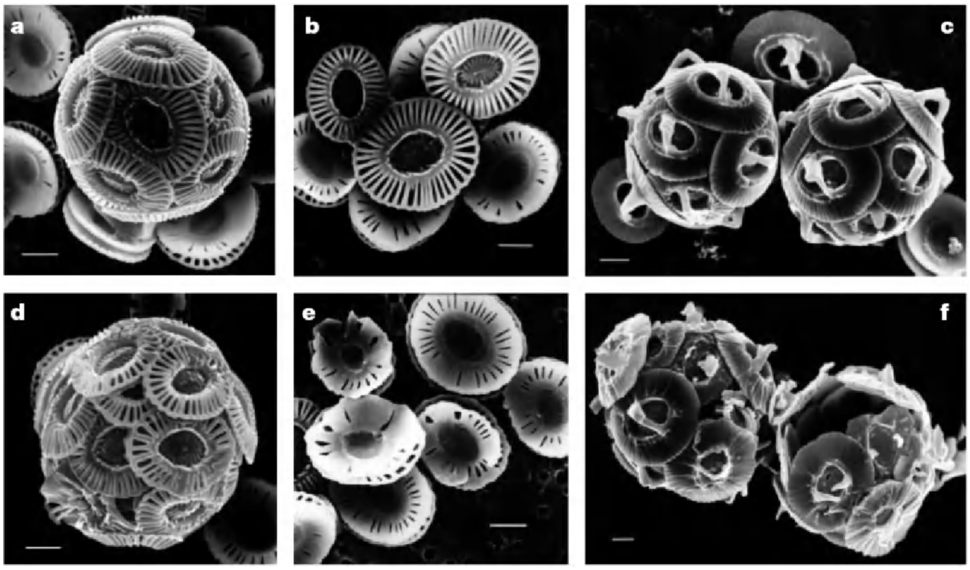


Figure 5.7. Scanning electron microscopy (SEM) photographs of coccolithophorids under different CO_2 concentrations: *Emiliania huxleyi* (a, b, d, and e) and *Gephyrocapsa oceanica* (c and f) collected from cultures incubated at levels corresponding to pCO_2 levels of about 300 ppmv (a, b and c) and 780–850 ppmv (d, e, and f). Scale bars represent 1mm. Note the difference in the coccolith structure (including distinct malformations) and in the degree of calcification of cells grown at normal and elevated CO_2 levels. (Source: Riebesell *et al.*, 2000; courtesy of *Nature*).

5.6.2 Pteropods

In the Barents Sea, pteropods (sea butterflies), which have calcareous shells, are a significant food source for herring (*Clupea harengus*), cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*), whereas, in the Southern Ocean, they are consumed by zooplankton and whales. Herring are an important part of the ecosystem because the adults are commercially valuable and the juveniles are an important food source for fish such as cod, and for marine mammals and seabirds. As the saturation of aragonite, the mineral that constitutes most of the shell, falls below 1, the shell should begin to dissolve (Figure 5.8). Thus, by 2040, there could be notable effects on pteropods in northern waters. When saturation is <1, these organisms are likely to experience an enhanced metabolic (sublethal) cost to maintaining their skeleton. A recent paper (Comeau *et al.*, 2009) has quantified this effect and suggests a 28% reduction in calcification at the pH values predicted to occur by 2100.

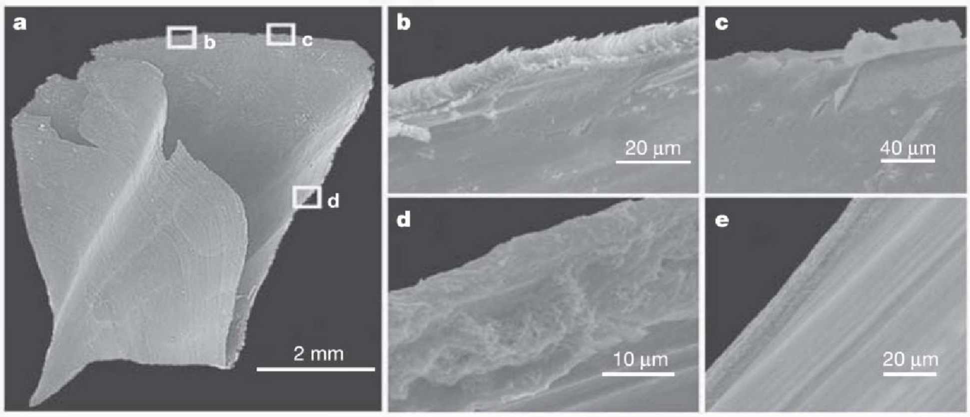


Figure 5.8. The effects of higher pH on the shell formation of pteropods. (Source: Orr *et al.*, 2005; courtesy of *Nature*.)

Ocean acidification can have multiple impacts on marine phytoplankton, either directly (by affecting their metabolism) or indirectly (by changing the ecosystem around them to make them more or less competitive). Direct effects include the speciation of nutrients that are strongly pH-dependent (e.g. nitrogen, phosphorus, and silicon). As successful growth depends on nutrient affinity, particular groups of phytoplankton can be positively or negatively selected (Turley *et al.*, 2009). The process of photosynthesis is favoured by an increase in CO_2 and may enhance plant growth. Thus, there will be winners and losers (Figure 5.9), depending on which species or groups are affected, in what manner these changes can alter productivity, and on feedback from biogeochemical cycles. Phytoplankton also play an important role in the stabilization of climate by influencing the partitioning (exchange) of climate-relevant gases (e.g. CO_2) between the ocean and atmosphere (Rost *et al.*, 2008). The potential direction (positive or negative) of this exchange is at present unknown.

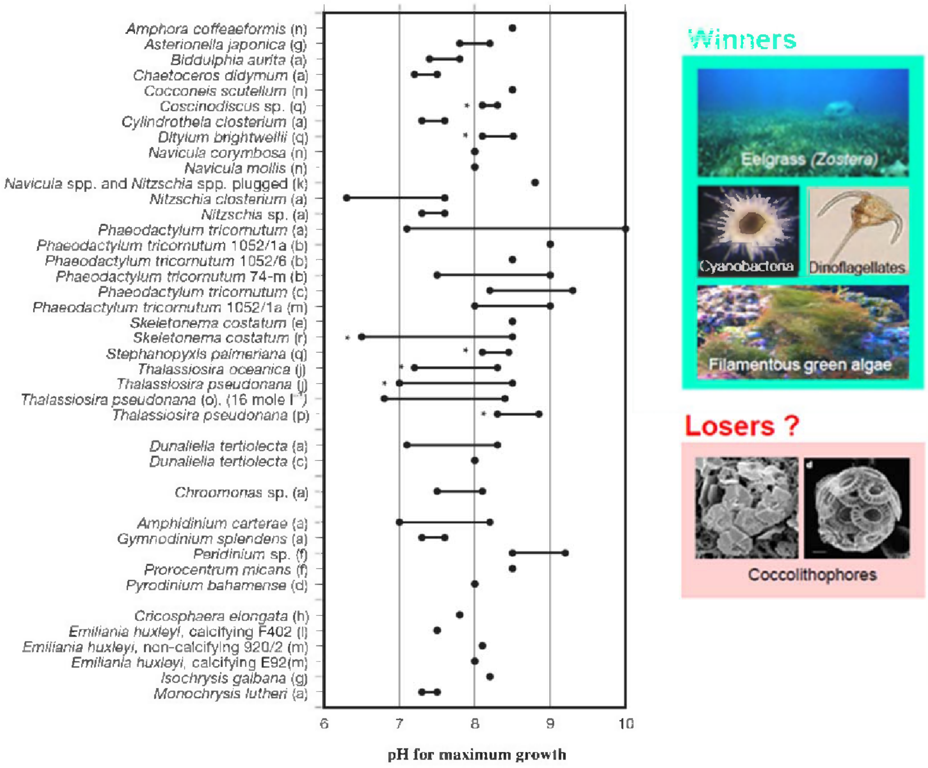


Figure 5.9. There will be winners and losers in a response to future change. Preferred pH range for a number of phytoplankton species/taxa. (Source: Hinga, 2002.)

5.6.3 Diatoms

Experimental studies of diatoms have demonstrated a resilience to changes in CO_2 concentration with respect to the process of silicification (Rost *et al.*, 2008), although shifts in their composition and dominance in phytoplankton communities in the equatorial Pacific and the Southern Ocean have been observed at different levels of CO_2 (Tortell *et al.*, 2002; Tortell and Long, 2009). These studies have demonstrated that elevated CO_2 concentrations lead to an increase in primary production and favour the growth of larger chain-forming diatoms.

5.6.4 Dinoflagellates

Although this group is ecologically and economically important, knowledge of the uptake of inorganic carbon by dinoflagellates is relatively limited (Hansen, P.J., *et al.*, 2007). Dinoflagellates are known to be able to accumulate inorganic carbon by involving the active uptake of either CO_2 or bicarbonate (HCO_3), or both, at up to 70-fold the ambient concentration (Berman-Frank *et al.*, 1998). In communities where other phytoplankton populations decrease in response to low pH, dinoflagellates, with greater resilience to acidification, may prosper. One subgroup of dinoflagellates form calcareous resting cysts (e.g. *Calciodinellum levantium*; Meier *et al.*, 2008). Calcification rates for these dinoflagellates may be affected in future by an expected change in the saturation state of the ocean.

5.6.5 Cyanobacteria

Nitrogen-fixing cyanobacteria provide a biological source of new nitrogen for large parts of the ocean (Barcelos e Ramos *et al.*, 2007) and are involved in photosynthesis, being responsible for up to 60% of primary production in low-productivity areas (Iturriaga and Mitchell, 1986). This group is one of the potential winners under projected climate conditions of high pCO_2. Experiments (Barcelos e Ramos *et al.*, 2007; Hutchins *et al.*, 2007; Levitan *et al.*, 2007) have demonstrated enhanced cell-division rates, increased CO_2 fixation (up to 128%), and increased N_2 fixation (100%) under future scenarios of CO_2 concentration compared with present conditions. Such changes could enhance the productivity of nitrogen-limited oligotrophic oceans and increase biological carbon sequestration.

5.6.6 Bacteria, Archaea, and viruses

The increase in CO_2 in the surface ocean and the concomitant reduction in pH may have many direct and indirect effects on microbes and the ecosystem processes in which they are involved (Hutchins *et al.*, 2009). At the organism level, physiological transformations, such as inorganic carbon fixation (photosynthesis by cyanobacteria, chemosynthesis by nitrifying proteobacteria and Archaea, and dinitrogen fixation by diazotrophs, such as *Trichodesmium* and *Crocosphaera*), depend on the availability of dissolved CO_2. However, physiological enhancement is taxon-specific and may not be evident if the present-day pCO_2 is already saturated by virtue of carbon-concentrating mechanisms. Whether or not these mechanisms might be relaxed to compensate for higher pCO_2 is another, as yet unresolved matter.

At the community level, the effect of raised pCO_2 in perturbation experiments suggests little impact on heterotrophic bacterial diversity (Woolven-Allen, 2008). However, experimental simulation of OA indicates the potential for a weakened biological carbon pump because of increased microbial respiration associated with enhanced degradation of polysaccharides (Piontek *et al.*, 2009). More importantly, it is known that the acid–base balance in seawater affects the availability of nutrients to all microbes, not just those that fix CO_2. In a scenario of future losers and winners, ocean nitrification may become inhibited at lower pH because of a reduction in the availability of ammonia to chemoautotrophs; however, more ammonia may be diverted to other microbes, such as photoautotrophic picocyanobacteria, that are well adapted to assimilate this form of reduced nitrogen. However, most marine microbes are not obligate autotrophs but are heterotrophic or parasitic (viruses); thus, the effect of acidification is via propagation through the microbial loop and the viral shunt. In other words, because they do not get energy from photosynthesis but feed on other organisms, they rely on their hosts.

It appears, therefore, that the impact of OA on microbes cannot be predicted solely from the outcome of isolated cause-and-effect relationships. Exogenous disturbance of microbial foodwebs can lead to counterintuitive changes because of complexity in system constraints, such as elemental stoichiometry (Thingstad *et al.*, 2008). Plausible scenarios may be developed based on knowledge of structure and function in present-day microbial foodwebs, but biological adaptation and evolution may limit the time-domain to which these scenarios apply.

Some definitions

Phototrophs get their energy from sunlight, *lithotroph*s from inorganic compounds, and *organotrophs* from organic compounds. The *viral shunt* is the process that moves material from heterotrophs and photoautotrophs into particulate organic matter (POM) and dissolved organic matter (DOM). The *microbial loop* describes the process by which bacteria consume DOM and thus balance the viral shunt. These systems are important for the control of macronutrients to pico-, nano-, and phytoplankton.

In terms of the secondary effects of microbial processes, ecological interaction becomes an important consideration in assessing the pathway and strength of the acidification signal through the system. It may be presumed that the net outcome of these potentially opposing effects will predict the fate of a virus specific to a given host. However, a contradictory association of lower viral production with higher host abundance has been found under conditions of elevated CO_2, apparently because of altered host–virus interaction (Larsen *et al.*, 2008).

5.7 Impacts of high CO_2 on the physiology of invertebrates and fish

A range of direct physiological impacts of OA have been suggested (Fabry *et al.*, 2008; Figure 5.10); some may be common across many higher taxa, whereas others are specific to individual species or limited groups of species. Although notable work on physiological impacts has been conducted, knowledge is still limited to a few species and often to only short-term experiments. Some studies have reported apparently contradictory results. It is not yet clear whether these contrasts represent methodological differences or reflect true physiological features.

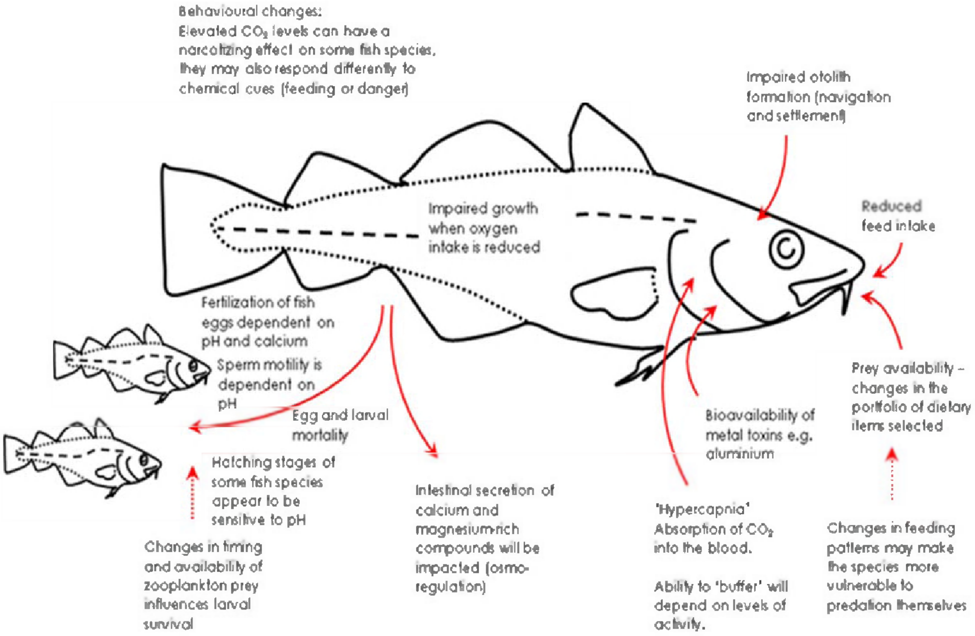


Figure 5.10. The potential mechanisms by which ocean acidification (OA) may affect fish throughout their life cycle. (Courtesy of John Pinneager.)

The physiological impacts of acidification, as reviewed by Fabry *et al.* (2008), are grouped into three categories: (i) impacts on reproduction and early development, (ii) calcification (see Section 5.9), and (iii) broad impacts on physiology caused by changes in the balance of the internal acid–base balance.

5.7.1 Reproduction and early development

Reproduction and early life stages (fish eggs and larvae) are expected to be particularly sensitive to the direct impacts of OA (Ishimastu *et al.*, 2004; Fabry *et al.*, 2008; Melzner *et al.*, 2009b). As the sperm and eggs of broadcast-spawners are directly exposed to changes in seawater chemistry, the more specialized buffering mechanisms found in more fully developed organisms are not found in the early life stages, which are known to be most susceptible to environmental toxicants (McKim, 1977).

Experimental results for reproduction and early development stages so far exhibit a range of sensitivities to OA. Among invertebrates, there is almost a complete spectrum of sensitivities, ranging from brittlestars that die with only minor changes in pH (Dupont *et al.*, 2008), to sea urchins that demonstrate abnormal development under moderate levels of CO_2 enrichment (Kurihara and Shirayama, 2004), and to tunicates that exhibit improved development under CO_2-enriched conditions (Dupont and Thorndyke, 2009). To date, no theories have been put forward to explain the relative sensitivity of different taxa. The onset of OA will proceed alongside global temperature change. A study of fertilization and development of the rock oyster (*Saccostrea glomerata*) under co-varying pH and temperature found that fertilization and development were reduced under elevated CO_2 conditions, and that fertilization and development were more sensitive to CO_2 at temperatures above and below the optimal temperature for fertilization (Parker *et al.*, 2009).

Comparatively little work has been conducted on the effects of environmentally realistic levels of OA on fish reproduction and development. Studies conducted at high levels of CO_2 enrichment, in relation to potential effects of oceanic carbon sequestration, have demonstrated that fish larvae are sensitive to high levels of CO_2 enrichment and that, under extreme conditions, death can occur (Hayashi *et al.*, 2004; Ishimatsu *et al.*, 2004). However, experiments under highly elevated CO_2 conditions have only limited applicability to realistic scenarios of OA. A study of two species of reef cardinal fish (*Ostorhinchus doderleini* and *O. cyanosoma*) found that there was no impact on egg hatch rate, size at hatching, or developmental time at levels up to 1030 ppmv CO_2 (Munday *et al.*, 2009b). In additional, unpublished preliminary work on cod, it was demonstrated that developing eggs and larvae did not die as a direct response to elevated CO_2 concentrations up to 4000 ppmv (A. Frommel, IFM-GEOMAR, pers. comm.; W. Le Quesne, Cefas, pers. comm.). This suggests that many marine fish larvae may be unlikely to die as a direct result of OA. Sublethal effects require more detailed investigation; a study on white sea bass (*Atractoscion nobilis*) found enhanced otolith growth under elevated CO_2 conditions (Checkley, D. M., *et al.*, 2009).

5.7.2 Internal acid–base balance

An emerging theory of the general sensitivity of species to changes in acid–base balance predicts that active organisms, and species with large amounts of extracellular fluid, such as blood, will be less sensitive to OA (Melzner *et al.*, 2009b). Active animals (e.g. fish, squid, and some crabs) may be pre-adapted to cope with OA because (i) CO_2 builds up in the body during exercise, and (ii) they possess specialized structures to control and maintain internal CO_2 levels. The metabolic costs of regulating acid–base balance have yet to be investigated; if regulation of acid–base balance comes at a notable metabolic cost, this could have implications for individual performance and energy flow through foodwebs.

The onset of OA will occur over a period of decades and will proceed alongside changes in global temperature; therefore, acidification impacts need to be considered in light of a parallel development in climate change. Increasing water temperatures have led to an observed shift in the geographic range of a number of species, including commercially targeted fish (Perry *et al.*, 2005). The upper thermal limit of the spider crab (*Hyas araneus*) decreases by at least 1.5°C under the CO_2 conditions expected by 2100 (Walther, K., *et al.*, 2009). This indicates that OA may reduce the thermal tolerance window within which species can survive (Pörtner and Farrell, 2008) and could exacerbate changes in biogeographic range as a response to warming.

5.8 Impacts on deep-water corals

Within the ICES Area, there are extensive reefs of cold-water corals, especially in Norwegian and Canadian waters, and the full extent of their distribution was only begun to be realized in the past decade (see Section 8.3.3). In the North Atlantic, *Lophelia* (Figure 5.11) is the dominant deep-water colonial coral. It is a true hard coral, formed by a colony of individual coral polyps that produce a calcium carbonate skeleton. It feeds by catching food from the surrounding water. Unlike its tropical relatives, *Lophelia* does not need algae and light for survival, and it is found mainly at depths between 200 and 1000 m. The record for the deepest reef is 3000 m, and the shallowest living *Lophelia* reef is found at 40 m in Trondheim Fjord, Norway.

Figure 5.11. ***Lophelia*, a typical cold-water coral that feeds by extracting food particles from the surrounding water. (Courtesy of Jan Fossa.)**

Lophelia reefs provide habitat for a large number of invertebrate species (e.g. crustaceans, molluscs, starfish, brittlestars, and sea urchins), and a wide variety of animals (e.g. sponges, bryozoans, hydroids, and other coral species) grow on the coral itself (Mortensen and Fosså, 2006; Roberts *et al.*, 2009a). Fish (e.g. redfish (*Sebastes marinus*), saithe (*Pollachius virens*), cod, ling (*Molva molva*), and tusk (*Brosme brosme*)) are also found in the coral habitat (Husebø *et al.*, 2002; Costello *et al.*, 2005). Although experimental fishing with longlines has demonstrated that catches of redfish are greater in coral habitats than in surrounding areas (Husebø *et al.*, 2002), it is still uncertain whether or not this habitat is important for fish or fish stocks (Auster, 2005). Up to the present, the largest threat to *Lophelia* reefs has been bottom-trawling (Fosså *et al.*, 2002; Hall-Spencer *et al.*, 2002; Grehan *et al.*, 2005), but in future, OA may become a serious problem if anthropogenic CO_2 emissions are not markedly reduced or halted in order to stabilize pH in the oceans (Orr *et al.*, 2005; Guinotte *et al.*, 2006).

The largest reef system in Norway, the Røst Reef, grows along the continental break off the Lofoten Islands at ca. 300–350 m depth. Model scenarios (Orr *et al.*, 2005) reveal that undersaturated conditions may be reached at the end of the century. Under these conditions, *Lophelia* will most probably have serious difficulties in producing a skeleton. Severe stress levels may occur even before the seawater becomes undersaturated. Preliminary results indicate that *Lophelia* may reduce its calcification rate with even a small change in pH (Maier *et al.*, 2008). Lowering the pH by 0.15 and 0.3 units reduced coral calcification by 30 and 56%, respectively. Also, the effect of changes in pH (0.3 units lower than in ambient water) on calcification rate was stronger for fast-growing young polyps (59% reduction) than for older polyps (40% reduction). This implies that the young and fast-calcifying corallites exhibit the most negative response to OA (Maier *et al.*, 2008). It has also been demonstrated that the metabolic rate in *Lophelia* increases threefold for a temperature increase of only 3 °C (Dodds *et al.*, 2007). *Lophelia* therefore seems to be sensitive to changes in both pH and temperature. Given these concerns, there is an urgent need for further studies on the potential direct physiological effects on *Lophelia*, particularly growth and calcification under altered pCO_2 and pH in interaction with anticipated changes in temperature (Roberts *et al.*, 2009a). In addition, the potential indirect ecological effects of OA (e.g. changes in primary production, food supply, and benthic–pelagic coupling) may play a role in a future changing environment.

5.9 Impacts on shellfish: calcification

Many marine invertebrates, including commercially important wild-harvest and aquaculture species, form shells hardened by calcium carbonate. The process of calcification is particularly sensitive to OA, because the concentration of available carbonate in seawater decreases as pH decreases, so that the formation of calcium carbonate structures becomes increasingly expensive in terms of energy. Calcium carbonate can be laid down in a number of ways and in varying chemical forms; therefore, different calcifying species may have different sensitivities to lower pH conditions. Ries *et al.* (2009), in a study of 18 calcifying species using 60-day exposures, found a range of responses, including both increases and decreases in the rate of calcification under elevated CO_2 levels. They also found that calcification by mussels (*Mytilus edulis*) was insensitive to CO_2 enrichment over the range tested; this contrasts with the linear decline in calcification by *M. edulis* with increasing CO_2 reported by Gazeau *et al.*, (2007), which was based on a short-term exposure. However, both sets of authors report linear declines in calcification by the oyster (*Crassostrea virginica*) in response to elevated CO_2. In experiments using slightly different techniques, Findlay *et al.* (2009) came to an alternative conclusion. These experiments, which were performed on a number of species, as well as *M. edulis*, displayed no significant change in the ability of mussels to calcify at high levels of CO_2; although the rate of dissolution increased, the net result was a greater shell weight. Other work on mussels (Beesley *et al.*, 2008) has demonstrated that, although growth is not reduced, it does come at an energetic cost, with an associated reduction in health. Mussels are easily able to survive short periods of low pH, but may suffer energetically from long periods of exposure. These results suggest that animals can rapidly adapt by changing their internal biology. In the long term, adaptation may come at the cost of overall growth; however, this will be a function of other factors, such as food availability and other stresses.

Arnold *et al.* (2009) studied the survival of the four larval stages of the European lobster (*Homarus gammarus*) at high CO_2 levels (1200 ppm) and pH 8.1. No effect was observed on carapace length or the duration of the larval stages, although the pH was not especially high.

5.10 Impacts on shellfish aquaculture

The global aquaculture industry continues to expand rapidly, producing more than US$35 billion (€27 billion) of marine aquaculture products in 2008, when molluscs and crustaceans (Figure 5.12) accounted for more than 40% of marine aquaculture production by value.

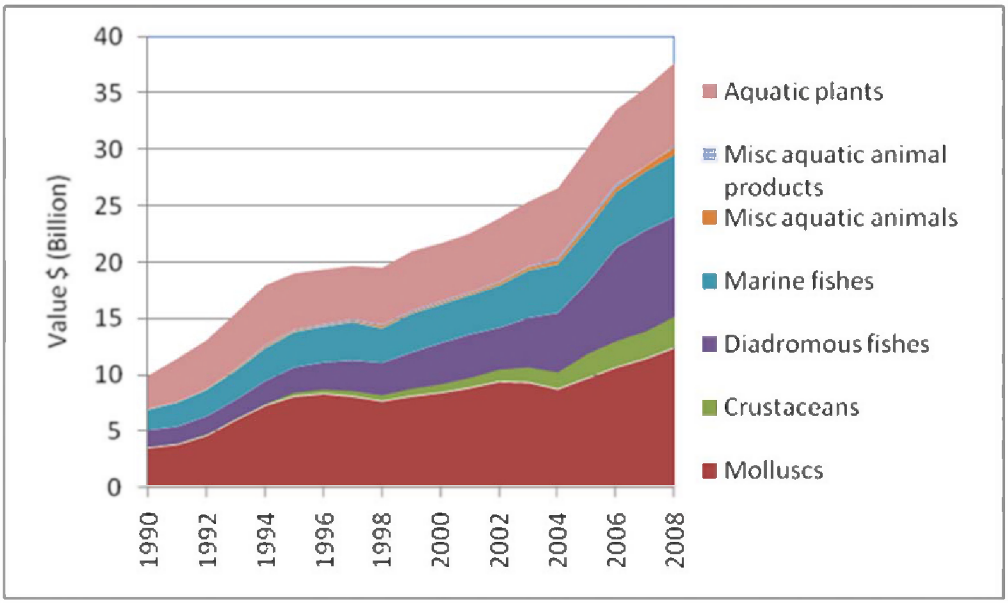


Figure 5.12. Global value of marine aquaculture products; note the increasing proportion of shellfish (molluscs and crustaceans). (Source: FAO.)

As noted above, calcifying organisms may be especially susceptible to the effects of OA. A reduction in growth rate in a farmed species would therefore affect the operations of the industry, although a more detailed, linked bioeconomic assessment would be required to gauge the implications in terms of production and profitability. Assessments of the impacts of acidification on calcifying species consistently find variations in sensitivity and response (Miller *et al.*, 2009). It may be possible, therefore, to replace sensitive aquaculture species that are negatively affected by acidification with alternative, more resilient species. However, there are likely to be transition costs associated with changing to production of a different species.

Commercial oyster hatcheries on the Pacific coast of the US are finding it difficult to keep the larvae of the Pacific oyster (*Crassostrea gigas*) alive in culture, with two of the largest hatcheries reporting production rates down by as much as 80%. Moreover, there has been little or no "natural" recruitment for several years in areas where naturalized populations were previously established. In regions of upwelling along the continental shelf of western North America, Feely *et al.* (2008) have determined that the surface waters have a lower pH and a lower aragonite saturation than expected. At 40–120 m depth in many locations along the coast, but at the surface in the region near the California–Oregon border, pH was reported to be 7.75, with an aragonite saturation of 1.0. Whether or not the recent recruitment and aquaculture failures are linked to changes in carbonate chemistry is unknown.

Most mariculture currently occurs in relatively shallow coastal margins, which have two different and opposing characteristics that are important for future changes. Typically, coastal systems with low salinity will have lower total alkalinity than those with high salinity and, therefore, have less buffering to changes in pH. However, in semi-enclosed areas of high primary productivity (e.g. the Sète Lagoon in France and the Rias Baixas in Spain), pH will be high, often exceeding 8.1.

5.11 Effects on fisheries

The direct biological impacts of OA occur at the cellular level; however, it is the expression of these effects at population and ecosystem levels, and their interaction with the socio-economic status of fishing communities, that is of concern to society. To date, research on the effects of acidification have concentrated on physiological effects. The productivity of commercially important stocks depends upon both the physiological status of target species and the ecological setting within which they occur. This requires scaling-up from physiological experiments to the prediction of population- and ecosystem-level effects accompanied by consideration of ecology as well as physiology. Determining the resulting impact that this has on fishing businesses and communities will involve further socio-economic assessments of the status of fisheries and the capacity for adaptation, within fisheries and markets, to changes in resource productivity.

From an ecological perspective, two key questions can be asked about the potential impacts of OA on fisheries: (i) will the relative composition of the species making up a marine community be altered, and (ii) will overall system productivity or productivity at a given trophic level be altered? The drivers of these changes fall into two classes: direct and indirect effects. Direct effects are the result of the action of OA on the physiological condition of an organism. Indirect effects may result in changes in ecological interactions, such as reduced prey availability if a prey organism is directly affected.

The above discussion of the impacts of OA on higher trophic-level organisms suggests that many fish will be broadly insensitive to direct impacts of acidification, although some invertebrates, especially calcifiers, may suffer from direct impacts. A study on cod found that juveniles held at ca. 3000 ppmv CO_2 for 12 months did not show any change in swimming performance or resting and active metabolic rates compared with a control group (Melzner *et al.*, 2009a), supporting the contention that developed fish are robust to acidification effects. In contrast, a study of two species of reef cardinal fish (*Ostorhinchus doderleini* and *O. cyanosoma*) found that aerobic scope was reduced by 33 and 47%, respectively, at approximately 1000 ppmv CO_2, and that temperature and CO_2 had a synergistic effect on aerobic scope (Munday *et al.*, 2009a). A reduction in aerobic scope could lead to a smaller window of thermal tolerance and thus a more restricted geographic distribution (Pörtner, 2008). Furthermore, a change in aerobic scope indicates that there could be an underlying change in energy partitioning, possibly the result of the increased costs of maintaining internal ionic balance. Similarly, the work on calcifiers discussed above indicates that calcification under acidified conditions may incur greater energetic costs. The increased costs of maintenance or growth reduce the efficiency by which food is transformed into somatic growth and, likewise, trophic-transfer efficiency. The latter would progressively reduce production at higher trophic levels, with potentially important impacts for fisheries. The impact of acidification on the internal energy budgets of organisms is poorly understood and should be a priority for future research.

Direct effects on the physiology of organisms may lead to changes in behaviour, growth rates, or mortality rates. However, changes in physiological rate do not necessarily translate into an identical linear change at the population level, and any response may vary depending on its condition. This is illustrated and considered in more detail in terms of possible population-level effects of acidification-induced changes on reproduction and early development. Within fishery assessment and modelling, reproduction is normally considered within stock–recruitment (S–R) relationships. Standard S–R theory assumes that the maximum number of recruits that can enter a population each year is limited by the carrying capacity of the system, and that recruitment is limited to this level by competition for food or space (Beverton and Holt, 1957). The other key aspect of most S–R relationships is the maximum survival rate of developing larvae that is achieved at low population numbers in the absence of competition. Ocean acidification could affect the maximum survival rate if the development success of larvae is reduced. Alternatively, OA could affect the carrying capacity by altering either the availability of planktonic food for larvae or the energetic requirements of developing larvae such that limiting competition sets in at a different level. Similarly, a smaller thermal-tolerance window could reduce the availability of suitable habitat and thus carrying capacity.

So, what are the potential population-level impacts of acidification-induced changes in larval survival or carrying capacity? In the absence of exploitation, or under optimal management conditions, recruitment is likely to be highly density-dependent; thus the population is expected to be insensitive to moderate levels of variation in larval survival, but fishery production would be closely related to changes in carrying capacity (food availability). Conversely, if a population is reduced to low levels, it will be insensitive to changes in carrying capacity but very sensitive to changes in larval survival. A physiologically mediated reduction in larval survival would render a stock more susceptible to overfishing and could hinder the rebuilding of overexploited stocks. Mortality of the early life stages of broadcast-spawning species is typically high and highly variable, owing to natural match–mismatch and density-dependent processes in the planktonic stages (Hjort, 1914; Cushing, 1990; Goodwin *et al.*, 2006). Direct effects of acidification could be swamped by natural variability, and actually observing a reduction in recruitment caused by acidification would require a long time-series of data unless the effect is very large.

Indirect effects are likely to be more relevant than direct effects, but are even harder to quantify. Ocean acidification may influence the structure and productivity of primary and secondary benthic production, which in turn may indirectly affect the productivity of fish communities and higher trophic levels. Changes in food source (e.g. Barents Sea herring feeding on pteropods) may result in shifts in species distributions, lower species abundance, or diet shifts. However, predicting indirect foodweb effects is difficult because many marine organisms have broad and variable diets, and are able to switch diets depending on prey availability (Pinnegar *et al.*, 2003; Trenkel *et al.*, 2005; Pinnegar and Blanchard, 2008). The possible effects of acidification on the timing of appearance, abundance, and quality of larval-fish prey sources, such as phytoplankton and zooplankton, remain unknown (Edwards and Richardson, 2004). The gaps in knowledge that need to be addressed are extensive, but research could focus on key target fishery species, particularly those that depend heavily on calcifying taxa (e.g. pteropods) as prey. A key unknown in assessing the relative importance of acidification for fisheries is how physiological effects will scale-up to population and ecosystem levels. Acidification effects have yet to be observed in shelf seas, so direct effects in the next 50 years are likely to be relatively minor compared with the massive impacts of overexploitation over the past few decades (Jennings, 2004; Dulvy *et al.*, 2005). However, combined temperature and acidification effects could interact with fishing effects, especially if environmentally driven changes leave stocks less resilient to overexploitation (Planque *et al.*, 2010).

5.12 Conclusions

Since the beginning of the industrial age, surface ocean pH, carbonate ion concentrations, and aragonite and calcite saturation states have been decreasing because of the uptake of anthropogenic CO_2 by the oceans.

- By the end of this century, pH could decrease further by as much as 0.3–0.4 units.

- Aragonite and calcite saturation horizons ($\Omega = 1$) are rising at ca. 1–2 m year^{-1} and could reach the surface as soon as 2020 in the Arctic Ocean.
- Natural processes, such as freshwater input (e.g. Baltic) and coastal upwelling, may accelerate the shoaling of corrosive waters in shallow regions of the oceans.

Although the chemical change of the oceans is unambiguous, predicting the ecological impact of this change is not straightforward. Publications such as Iglesias-Rodriguez *et al.* (2008) and Wood *et al.* (2008) for coccolithophores, and Findlay *et al.* (2008) for mussel growth, have contradicted previous works (e.g. Riebsell *et al.*, 2000; Gazeau *et al.*, 2007). Recent review papers by Hendriks *et al.* (2010) and Kroeker *et al.* (2010), who used meta-analysis to synthesize a number of experiments, were inconclusive, with Kroeker *et al.* (2010) stating that there is evidence of strong negative responses associated with increasing CO_2, whereas Hendriks *et al.* (2010) concluded that the evidence is not clear. However, CO_2-rich, O_2-poor water has already affected shell fisheries off Oregon (Feely *et al.*, 2008).

One of the challenges of the many national and international ongoing programmes on OA (e.g. European Project on OCean Acidification (EPOCA); Biological Impacts of Ocean Acidification (BIOACID)) is to produce results that not only test a positive hypothesis (e.g. what happens at 680 ppmv), but are also robust enough to identify negative results (e.g. what happens at 680 ppmv but over a number of life cycles). Unfortunately, proving a negative usually takes substantially longer than proving a positive. Currently funded programmes, although extensive, are not sufficiently targeted at studying effects at higher trophic levels. Furthermore, at species level, experiments do not include multiple stressors, such as higher temperatures and potential anoxia, in addition to increased CO_2 concentrations.

Although a single-species approach to testing responses of organisms to CO_2 enrichment provides a logical starting place for the assessment of potential ecosystem impacts of acidification, more emphasis needs to be placed on scaling based on observed physiological and biological effects in order to predict population, community, and ecosystem responses. This requires the explicit incorporation of ecology into acidification studies because density-dependent processes and ecological feedbacks may variously buffer or amplify the manifestation of biological effects at the population and community levels, or may even lead to counterintuitive outcomes. Future work should focus on key environmental areas that sustain ecosystems as well as individual species, with cold-water coral reefs as a prime example of potentially affected ecosystems.

6 Chlorophyll and primary production in the North Atlantic

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6.1 Introduction

Marine plankton is a crucial component of life on Earth. The plants of the plankton (i.e. the phytoplankton, which include microalgae and photosynthetic bacteria) produce oxygen and change the composition of the air, as well as producing organic matter that sustains marine foodwebs. Annually, phytoplankton contributes approximately half of the net carbon fixation of the biosphere (Behrenfeld *et al.*, 2006). Some of this organic matter is produced in excess of local consumption and becomes incorporated in bottom sediment as a carbon sink by means of the biological pump (i.e. the transfer of CO_2, fixed by photosynthesis in the surface, to the deep oceans in the form of dead organisms, faeces, and carbonated skeletons; Reid *et al.*, 2009b). In a geological context, part of this sink has been transformed into fossil fuels, such as oil and gas. Through the rapid exploitation of fossil fuels, human beings are closing a cycle of millions of years in only a few centuries. Changing this pivotal process of Earth's ecology is likely to lead to imbalances that are difficult to foresee and may lead to pronounced effects on marine ecosystems (Denman *et al.*, 2007).

The importance of marine phytoplankton for the biosphere includes the fixation of inorganic carbon, thereby reducing the concentration of CO_2 in the atmosphere. Phytoplankton also affects the chemical composition of other gases and aerosols (e.g. N_2O, O_2, dimethyl sulphide and sulphate) in the atmosphere, which, in turn, affect climate (Charlson *et al.*, 1987). Increased atmospheric CO_2 has warmed the ocean through the greenhouse effect, but may also lead to shifts in ocean ecosystems because the acidification of marine waters may affect key processes of the biological pump, such as production, calcification, and sedimentation (Orr *et al.*, 2005; Doney *et al.*, 2009; Hofmann and Schellnhuber, 2009).

In addition to their large biogeochemical significance, marine phytoplankton also support foodwebs, including productive fisheries, worldwide. Spatial variation in fishery catch is significantly related to spatial variation in primary productivity (Ware and Thomson, 2005; Chassot *et al.*, 2007). Fishing, as a top–down pressure, also influences catch and affects the movement of energy through ecosystems although, in relatively high productivity areas, increased productivity is associated with increased fishery yields (Frank *et al.*, 2006; Chassot *et al.*, 2010). Improved estimation of the energy transferred to higher trophic levels requires constraints on phytoplankton biomass losses. Apart from cell lysis, losses of phytoplankton are attributed to grazing by zooplankton and to aggregation (the formation and sinking of marine snow), which is responsible for the vertical flux of biomass out of the upper ocean's layers. Thus, understanding the variability of the bottom–up supply of energy from phytoplankton productivity is critical for successful ecosystem-based fishery management in the long term.

Phytoplankton requires adequate levels of light and nutrients for photosynthesis, and is therefore restricted to the upper layers of the ocean, where sunlight penetrates and a supply of nutrients is provided by convective mixing. Temperature of oceanic waters is not, in general, a limiting factor for phytoplankton production (Fasham, 2002). Temperature, however, is one of the main environmental factors affecting the degree of stratification (or, conversely, of mixing) of the surface layers of the ocean. Warming of the ocean surface triggers the development of an upper layer with a reduced density that restricts both the dispersal of phytoplankton to the dark, deep ocean and the transfer of nutrients upwards from subsurface layers. The optimal environment for phytoplankton production requires some stratification near the surface and sufficient availability of nutrient-rich waters. For this reason, only a small fraction of the ocean displays high levels of primary production (Figure 6.1), but the large size of the less productive ocean explains its importance for global carbon uptake.

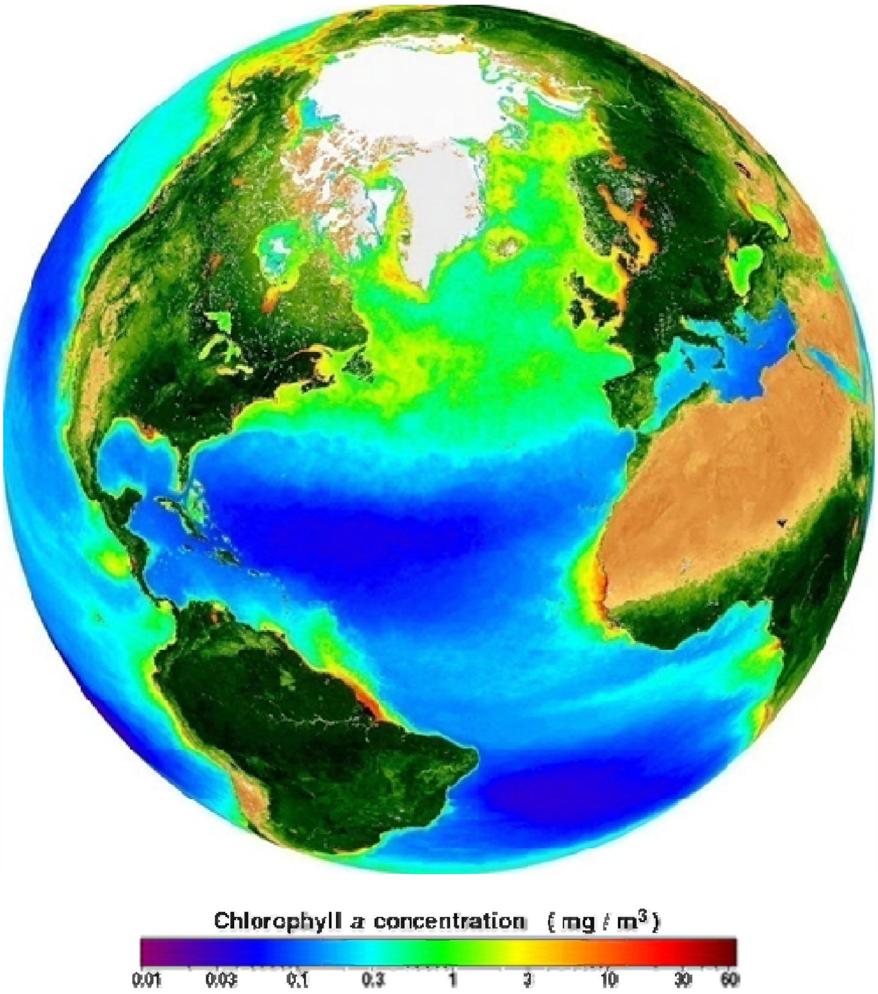

Figure 6.1. Composite image of annual mean surface chlorophyll in the North Atlantic as measured by the satellite-borne Sea-viewing Wide Field-of-view Sensor (SeaWiFS). Image obtained with the GES-DISC Interactive Online Visualization ANd aNalysis Infrastructure (GIOVANNI) of the Goddard Earth Sciences Data and Information Services Center (NASA).

Changes in climate are closely connected to variations in the productivity of the ocean. The warming trend of the atmosphere is already affecting the ocean surface (Revelle and Suess, 1957; Belkin, 2009) and deeper ocean layers, and contributing to modifications in currents and stratification (Bindoff *et al.*, 2007). In principle, higher temperature would favour an increase in primary production up to the optimal growth value and, therefore, greater removal of CO_2 from the atmosphere. Yet, at the same time, rising temperature forced from the surface will lead to the development of a more permanent stratification and a reduced supply of nutrients. The net result of these processes is predicted to be a reduction in global primary production (Behrenfeld *et al.*, 2006). However, the variability seen in data of satellite-derived phytoplankton concentrations appears to be greater than that of sea surface temperature (SST). This is attributed to advection and mixing processes operating at a mesoscale level and contributing to the supply of nutrients to the upper productive layers (Klein and Lapyere, 2009). In addition, decadal and longer cycles in primary production related to warming and cooling of the ocean are still poorly known, thus limiting the present ability to predict future changes (Chavez *et al.*, 2011).

Human activities are increasing the discharge of nutrients from land (and the atmosphere) into coastal waters, which can lead to excessive levels of primary production and eutrophication (Druon *et al.*, 2004). In coastal and continental shelf regions especially, but also in the open ocean, other direct anthropogenic effects, such as pollution (Cabeçadas *et al.*, 1999) and overfishing (Cury *et al.*, 2000), are increasingly modifying marine ecosystems. Increased UV radiation (Forster *et al.*, 2007) reduces survival and production rates of phytoplankton and affects the turnover of oceanic organic matter, particularly at high latitudes (Moran and Zepp, 2000). However, it is not clear whether or not the increasing radiation would also increase the production of aerosols derived from phytoplankton, and in turn cloud coverage together with a negative feedback on radiation levels in the surface ocean (Charlson *et al.*, 1987), or if this effect would be of minor importance (Woodhouse *et al.*, 2010).

A number of hypotheses on the direction of change (i.e. increase, decrease, or no change) in the production of phytoplankton in the oceans have been proposed and have been tested recently in studies at local, regional, and global scales, with the aim of providing predictive clues for the state of the biosphere in the near future. In this review we will focus on two effects directly related to warming of the ocean.

1) **Thermal stratification** of the surface layers of the ocean induced by warming of the atmosphere is likely to lead to a severe reduction in the supply of nutrients from deeper water to the productive photic layer, thus reducing the production and biomass of phytoplankton, especially in oligotrophic low-latitude regions (Sarmiento *et al.*, 2004). This is the most important negative effect expected for most of the open ocean, where primary production is mainly limited by the input of nutrients from mixing. Where the North Atlantic is strongly influenced by outflow from the Arctic Ocean, stratification by low-salinity waters is intensified by increased meltwater from sea ice and large run-off from circumpolar rivers (Greene and Pershing, 2007). Similarly, evaporation in tropical waters may cause shallower mixed layers than thermal gradients suggest (Foltz and McPhaden, 2009). The ensuing haline stratification, like thermal stratification, can be expected to reduce or enhance primary production according to whether or not the phytoplankton is limited by the fluctuation of nutrients or light, respectively.
2) An increased **thermal gradient** between the land and the ocean (as the ocean responds more slowly to warming than the land) is expected to reinforce alongshore winds and, in turn, increase coastal **upwelling** of deep, nutrient-rich waters near the coast. Such upwelling may increase phytoplankton production in some coastal areas, as was predicted for the major upwelling regions off the east coasts of continents (Bakun, 1990). Modelling studies, however, contend that warming will decrease upwelling on a global scale (Hsieh and Boer, 1992). The outcome of these two major opposing scenarios is difficult to foresee because of regional differences and interactions with other factors, particularly near the land–

sea interface, where atmospheric, terrestrial, and oceanic forcings intersect (Cloern and Jassby, 2008; Beardall *et al.*, 2009).

6.2 Regional approach and datasets

Given the large number and variety of regions within the oceans, phytoplankton is likely to show an equally diverse and complex response to changes in climate. In this section, we examine the evidence of change during recent decades in phytoplankton biomass and primary production, with special emphasis on the waters of the Atlantic Ocean north of 25°N. Studies reviewed include global scale analyses as per the United Nations Environment Programme (UNEP) Large Marine Ecosystem Report for the coastal ocean (Sherman and Hempel, 2009), and other analyses for deep ocean regions (e.g. McClain *et al.*, 2004; Antoine *et al.*, 2005; Gregg *et al.*, 2005; Behrenfeld *et al.*, 2006; Chavez *et al.*, 2011). Studies at regional or local scales, including long-term observations, were considered to display a variety of responses. The latter were illustrated by the contributions to the Theme Session on "Trends in Chlorophyll and Primary Production in a warmer North Atlantic" during ICES Annual Science Conference 2009 in Berlin. In addition, trends in phytoplankton biomass in North Atlantic waters were extracted from the time-series recorded in the ICES Zooplankton Status Report 2006/2007 (O'Brien *et al.*, 2008).

Phytoplankton biomass is represented in most studies by chlorophyll *a* concentrations, derived either from satellite measurements, as in global or regional studies (e.g. Behrenfeld *et al.*, 2006; Sherman and Hempel, 2009), or from direct determinations in field samples, the latter generally in local studies (e.g. Bode *et al.*, 2009b). Chlorophyll biomass is indicative of primary production over the past hours or days, reflecting the net result of production and losses through grazing, cell lysis, exudation of organic matter, and sedimentation. Primary production can be determined by several methods, but the most extended is ^{14}C-labelling in incubations of phytoplankton for a few hours. These measurements, however, are limited to a few depths and sites. As for chlorophyll, in global studies, primary production is computed from satellite data using models. These models are generally applied to weekly or monthly data, resulting in production estimates over large spatial scales that are less variable than *in situ* measurements. Temporal variability of chlorophyll and primary production is assessed using time-series. However, although ^{14}C measurements have been collected over the past 50 years, there are only a few *in situ* time-series that extend over ~2 decades. Such long-term data are needed to determine multivariate effects of the environment on primary production and biomass (see Chavez *et al.*, 2011). Global estimates of chlorophyll and production derived from satellites since 1997 are available (e.g. McClain *et al.*, 2004). Estimates of chlorophyll from satellite measurements are complicated by the presence of mineral particles, coloured dissolved organic matter, and other materials (Mobley *et al.*, 2004). These particles are more concentrated in coastal waters and can lead to errors in satellite estimates of chlorophyll compared with *in situ* measurements (Guðmundsson *et al.*, 2009). In this review, we use time-series of water-column integrated chlorophyll and primary production values derived from both satellites and *in situ* measurements, where available. In other cases, surface measurements are employed, because water column production is globally related to surface values (Chavez *et al.*, 2011).

Evidence of changes in phytoplankton biomass and primary production in ICES waters and in some additional areas to the west of Greenland are presented below. These geographic regions (Figure 6.2) have distinctive ecological characteristics. Linear trends in SST (1982–2007; Belkin, 2009) and phytoplankton biomass and production derived from satellite data in this region (1998–2006; Table 6.1) were obtained from the study by Sherman and Hempel (2009), although the time-series is very short for interpretation of links to climate. The descriptions were completed with additional time-series data from field studies (e.g. Barton *et al.*, 2003; O'Brien *et al.*, 2008). Recent global phenological analyses (Cloern and Jassby, 2008; Zingone *et al.*, 2010) describe the timing and amplitude of recurrent features in the annual cycle of phytoplankton at many coastal sites within the North Atlantic regions under consideration.

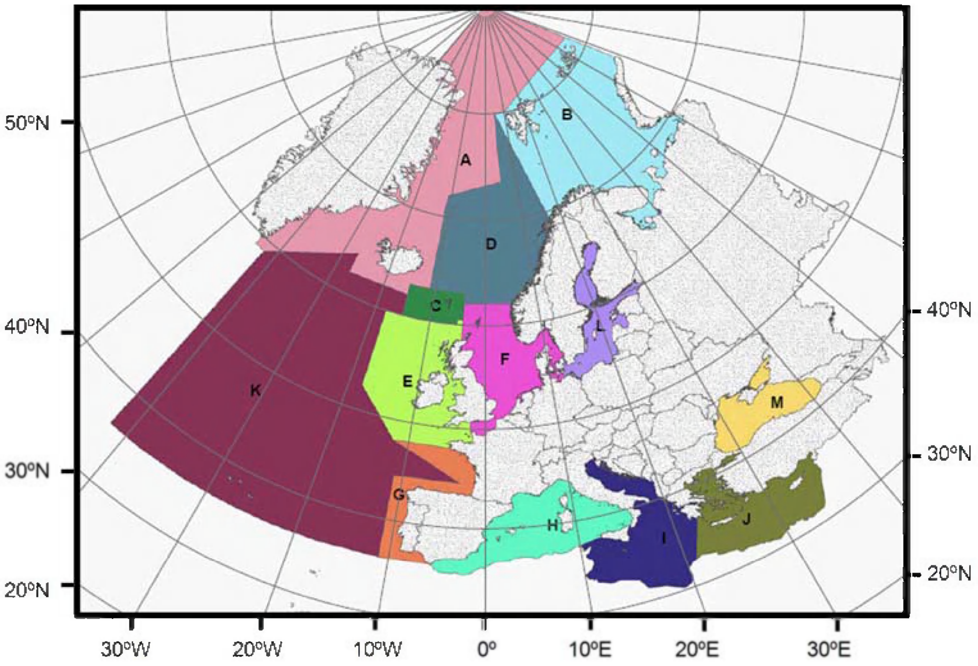

Figure 6.2. Ecoregions based on ICES Advice ACFM/ACE report (ICES, 2004a). A = Greenland and Iceland Seas, B = Barents Sea, C = Faroes, D = Norwegian Sea, E = Celtic Sea, F = North Sea, G = South European Atlantic Shelf, H = Western Mediterranean Sea, I = Adriatic-Ionian Seas, J = Aegean-Levantine Seas, K = Oceanic Northeast Atlantic, L = Baltic Sea, M = Black Sea. ICES Convention area (FAO area 27) includes regions A–G, L. Regions H–J, M are outside the ICES area.

Table 6.1. Linear trends in mean annual values of sea surface temperature (SST trend, °C $(10\text{year})^{-1}$), chlorophyll *a* (B trend, mg Chl *a* m^{-3} $year^{-1}$), and primary production (PP trend, mg C m^{-2} $year^{-1}$) with time between 1982 and 2007 (SST) or 1998 and 2006 (B and PP). Mean values for chlorophyll (B, mg Chl a m^{-3}) and primary production (PP, mg C m^{-2} $year^{-1}$) for the whole period are also indicated. Significance of trends is shown by asterisks: * = $p<0.05$, ** = $p<0.01$. (Data and trend analysis from Sherman and Hempel, 2009.)

Large Marine Ecosystem	SST trend	B trend	PP trend	B	PP
Iceland seas	0.86	0.031	0.589	1.19	203
East Greenland	0.73	0.028*	1.674	0.80	130
West Greenland	0.73	0.021	0.277	1.00	149
Barents Sea	0.12	0.091**	4.812	2.45	240
Faroe Islands	0.75	0.031	3.403	0.81	174
Norwegian Sea	0.85	–0.003	–1.627	1.21	204
Celtic Sea	0.72	–0.002	1.051	1.26	225
North Sea	1.31	–0.007	–0.030	2.26	294
Southeastern European Atlantic Shelf	0.68	0.003	–0.359	0.53	156

Baltic Sea	1.35	0.094	10.499	6.87	601
Northwestern Atlantic (Newfoundland–Labrador shelf)	1.04	0.014	-0.689	1.07	181
Northwestern Atlantic (Scotian Shelf)	0.89	0.026	0.916	1.75	257
Northwestern Atlantic (US Northeastern shelf)	0.23	0.019	0.690	2.38	345

6.3 Changes at a global scale

The spatial scale of the distribution of phytoplankton that is relevant to climate response studies varies from metres to entire ocean basins (Fasham, 2002). There is, therefore, a need for global assessments of phytoplankton biomass and production that are based on long time-series of observations to ascertain the impact of climate change on these variables. Information on the spectral colour of the ocean surface has been gathered by satellites since the early 1980s and has been used to produce comprehensive global estimates of phytoplankton biomass and, later, using models, of primary production. The first long-term analyses (Antoine *et al.*, 2005) estimated an overall increase of ca. 22% in the global average of oceanic chlorophyll concentration between the period 1979–1986, when the first observations were made by the Coastal Zone Colour Scanner (CZCS), and the more recent period, 1998–2002, measured by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS). The increment consisted of a large increase in the intertropical regions during spring and summer, a lower increase at higher latitudes, and a decrease in the oligotrophic gyres, and was not the result of the differences in methodology between the two periods. The Atlantic Ocean ranked second after the Indian Ocean in the level of increase (Antoine *et al.*, 2005). Later studies confirmed the global increase (estimated at 4.1% globally in the period 1998–2003) with the largest change (+10.4%) in coastal regions (Gregg *et al.*, 2005). Enhancement of coastal upwelling (Bakun, 1990) was considered a possible cause of the increase, although a direct effect of eutrophication by anthropogenic nutrient additions in most coastal regions could not be ignored.

More recent analyses, which considered water-column integrated production derived from satellite data, aligned the increases with cooling periods (including the *El Niño/La Niña* transition from 1997 to 1999), but demonstrated a general reduction in both phytoplankton biomass and production with warming at low latitudes and an increase at high latitudes (Behrenfeld *et al.*, 2006; Chavez *et al.*, 2011). This was attributed to increased stratification by surface warming that, in turn, would have reduced nutrient inputs by mixing and eventually primary production at low latitudes. In contrast, stratification would have increased the time for which phytoplankton cells were exposed to light at high latitudes, where primary production is limited by light (Figure 6.3). Oligotrophic gyres, characteristic of the subtropical areas of all oceans, were the most important regions for primary production and biomass, despite their low biomass of phytoplankton, because of their large size. The oligotrophic areas of the subtropical ocean have increased steadily in size since 1998 (McClain *et al.*, 2004; Behrenfeld *et al.*, 2006; Polovina *et al.*, 2008), probably as a consequence of a reduced input of nutrients caused by enhanced stratification. Even so, the input of nutrients caused by submesoscale processes is not well resolved in these areas (Klein and Lapyere, 2009). The changes in global primary production were correlated with variation in global climate, as indicated by the *El Niño*/Southern Oscillation index (Behrenfeld *et al.*, 2006; Chavez *et al.*, 2011), suggesting that global climate plays a major role in its variability. By extending the surface chlorophyll time-series back to 1899 using water transparency records, a general decreasing trend was found in most ocean basins (Boyce *et al.*, 2010), although this result has been contested (Mackas,2011; Rykaczewski and Dunne, 2011; McQuatters-Gollop *et al.*, 2011) The analysis by Boyce *et al.* also concluded that climatic oscillations (e.g. *El Niño*) accounted for most of the variability of surface chlorophyll. However, in these global studies, data from the productive continental shelves are generally outweighed by those from the larger oligotrophic areas of the ocean, where most of the production and chlorophyll is well below the surface layer, and does not include cyanobacteria and other small phytoplankton. Cyanobacteria (e.g. *Prochlorococcus*) and other small phytoplankton are found well below the surface layer in the larger oligotrophic areas. In any case, as corroborated by palaeoclimatic studies (see references in Chavez *et al.*, 2011), the computed linear trends in primary productivity are only indicative of the direction of change during a limited period when considering long-term oscillations in climate and primary productivity.

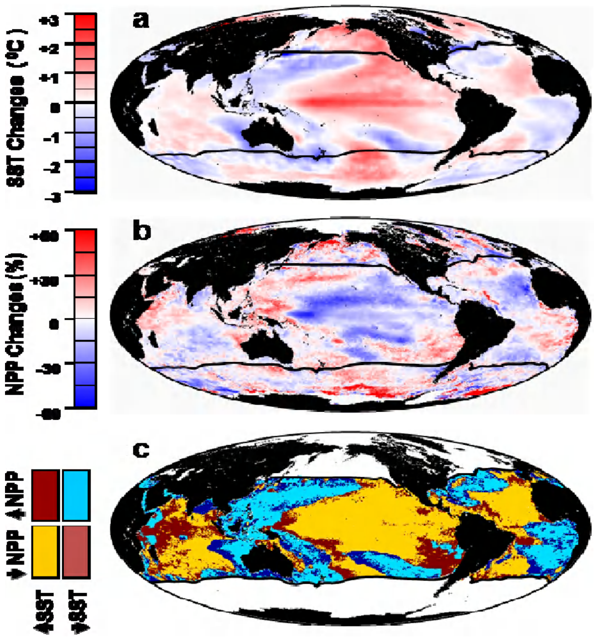

Figure 6.3. Climate controls on ocean productivity cause net primary production (NPP) to vary inversely with changes in sea surface temperature (SST). Global changes in: (a) annual average SST, and (b) NPP for the 1999–2004 warming period (c). For 74% of the permanently stratified oceans (i.e. regions between black contour lines), the NPP and SST changes were inversely related. Yellow = increase in SST, decrease in NPP; light blue = decrease in SST, increase in NPP; dark blue = decreases in SST and NPP; dark red = increases in SST and NPP. A similar inverse relationship is observed between SST and chlorophyll changes. (Source: Behrenfeld *et al.*, 2006, Figure 3. Courtesy of *Nature*.)

In contrast to the open ocean, an examination of variations in chlorophyll and primary production over the continental shelf did not reveal any consistent large-scale pattern of change between 1998 and 2006 (Sherman and Hempel, 2009). Out of 64 Large Marine Ecosystems (LMEs) analysed, only ten revealed statistically significant trends in mean annual chlorophyll and four in the case of primary production. Most of the trends, however, were positive, with significant decreases only in the eastern Siberian Sea (chlorophyll) and the Bay of Bengal (primary production). Such variability in coastal systems is to be expected, given the relative shortness of the time-series (9 years) and the multiple factors affecting primary production in the coastal ocean (e.g. stratification, nutrients, eutrophication, turbidity). Considering *in situ* time-series spanning the last 10–20 years, both chlorophyll and primary production increased at coastal sites, particularly at eastern boundary continental margins, and were associated with major climate anomalies (Chavez *et al.*, 2011). These results suggest that, in general, productivity in coastal ecosystems benefits from warming and increased nutrient inputs from both open ocean and coastal sources. In turn, fishery biomass yields were enhanced with increasing primary productivity in all LMEs, particularly in areas with moderate warming (Figure 6.4).

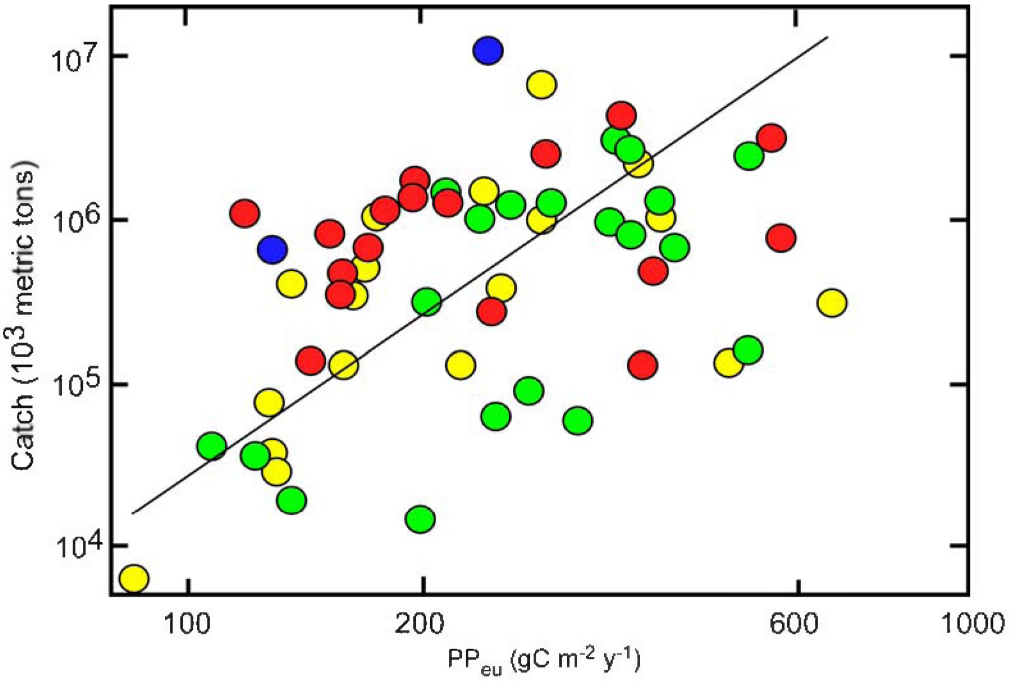

Figure 6.4. Positive correlation of 5-year mean annual fishery biomass yield with 9-year mean annual primary production in fast warming (red), moderately warming (yellow), slower warming (green), and cooling (blue) Large Marine Ecosystems (LMEs). Significance of regression line $p<0.001$. (Source: Sherman and Hempel, 2009, Figure 5a. Courtesy of UNESCO.)

From a biogeochemical perspective, however, the observed changes in phytoplankton biomass and production did not seem to have greatly influenced the capacity of the ocean to store carbon, which was estimated at 1.8 ± 0.8 Gt C $year^{-1}$ in the 1980s, 2.2 ± 0.4 Gt C $year^{-1}$ in the 1990s, and 2.2 ± 0.5 Gt C $year^{-1}$ between 2000 and 2005 Denman *et al.*, 2007). This suggests that major changes in physiology (e.g. increased respiration), foodwebs (e.g. increased predation), and biogeochemical processes (e.g. acidification and sedimentation rates) are occurring in parallel with the observed changes in phytoplankton production at the scale of the global ocean and affecting the carbon cycle on Earth (Figure 6.5).

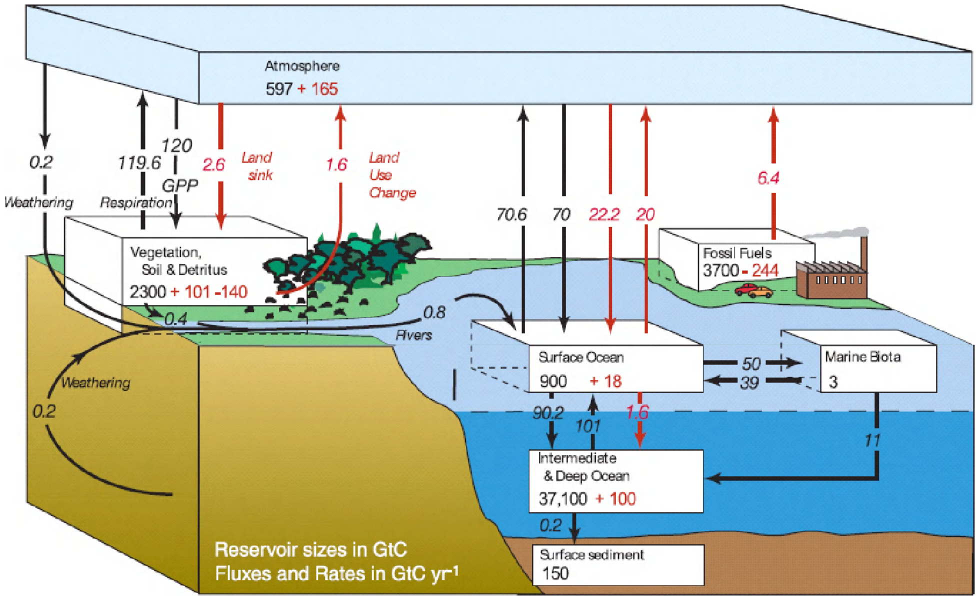

Figure 6.5. The global carbon cycle for the 1990s, showing the main annual fluxes in Gt C year^{-1}; black = pre-industrial "natural" fluxes; red = "anthropogenic" fluxes. Gross fluxes generally have uncertainties of more than ±20%, but fractional amounts have been retained to achieve overall balance when including estimates in fractions of Gt C year^{-1} for riverine transport, weathering, deep ocean burial, etc. GPP = annual gross (terrestrial) primary production. Atmospheric carbon content and all cumulative fluxes since 1750 are as of end 1994. (Source: Denman *et al.*, 2007, Figure 7.3.)

6.4 Changes in North Atlantic regions

The large heterogeneity in the distribution of phytoplankton (as shown in Figures 6.1 and 6.3) is well represented in the North Atlantic waters studied by ICES (Figure 6.2). In this region, marine ecosystems range from the Arctic to temperate, mid-latitude waters, and from the deep ocean to coastal and shelf seas. It also includes enclosed or semi-enclosed seas, such as the Baltic Sea. The physical characteristics of the various subregions constrain phytoplankton production, mainly by determining the area and period where blooms can be produced. For instance, parts of the Arctic are covered by seasonal sea ice for an extended period of the year, thus restricting bloom development in open waters to a relatively short period after the ice melts, when light levels in the surface layer and nutrients allow phytoplankton growth. Melting of sea ice favours local increases of stratification because of the input of freshwater and also provides microalgae, fostering a bloom over large areas, which follows the melting front as it recedes (Sakshaug and Slagstad, 1992; Niebauer *et al.*, 1995).

In contrast, in open waters at lower latitudes in the ICES region, phytoplankton production is concentrated in spring and autumn. In this case, as the annual cycle of sunlight progresses, spring stratification developed by the gradual warming of the surface leads to a rapid uptake of nutrients by the phytoplankton. These nutrients are soon exhausted in the upper layer and remain at low levels throughout summer. In these circumstances, the only input of nutrients for phytoplankton growth comes from deeper waters through the pycnocline (i.e. where the water density gradient in the mixing layer is maximum) via eddy diffusion and from physical instabilities that induce mixing. The result is the development of a characteristic deep chlorophyll maximum, closely related to the nitracline (i.e. the maximum subsurface nitrate gradient). The deep chlorophyll maximum occurs at depths where phytoplankton growth critically depends on light and nutrients, and its maintenance and magnitude is regulated by a close coupling of biological and physical processes (Varela *et al.*, 1992). Consumption by grazers is enhanced near this maximum, preventing further phytoplankton accumulation (Burkill *et al.*, 1993). The mixing of the surface and subsurface layers as the thermal gradient is disrupted during autumn results in new blooms in some areas, although the strong mixing and low light levels during winter restrict any further growth of phytoplankton. This seasonal pattern is modified over the continental shelf by the mixing effect of tides and by riverine and terrestrial inputs at intermediate (10–100 km) scales. In this way, coastal areas and semi-enclosed seas display a characteristically heterogeneous distribution of blooms for most of the year, although primary production is still maintained at low levels during winter (Smetacek, 1988).

Blooms are generally concentrated in the transitional periods between water-column mixing and stratification (i.e. winter–spring and summer–autumn) and the timing of changes in stratification, and bloom formation is crucial to many ecosystem processes, including the success of fish larvae (Cushing, 1990; Rodríguez, 2008). Increases in phytoplankton biomass during blooms and extension of the growing season were observed in the North Sea and in the Atlantic in the 1980s (Reid *et al.*, 1998; McQuaters-Gollop *et al.*, 2007). These changes also expanded to nearby regions and were related to changes in large-scale hydrometeorologic forcing (temperature and wind intensity and direction, and associated changes in the position of oceanic biogeographic boundaries) and reflect a pronounced change in climate (Beaugrand, 2004). A general trend in the North Atlantic, evident from global studies from 1979 to present, is an increase in phytoplankton biomass in shelf areas of both the Northeast and Northwest Atlantic, and to a decrease in phytoplankton biomass in the central North Atlantic Subtropical Gyre (Antoine *et al.*, 2005; Gregg *et al.*, 2005; Vantrepotte and Mélin, 2009).

Shelf systems also include ecosystems that are subject to seasonal coastal upwelling, induced by alongshore winds, which enhances primary production near the coast through the input of nutrients from deep waters. In this regard, the northwest Iberian coast represents the northern limit of the eastern boundary upwelling ecosystem of the North Atlantic (Alvarez *et al.*, 2008), which has a large impact on primary production and marine foodwebs in this region (Bode *et al.*, 1996; Alvarez-Salgado *et al.*, 2002; Valdés *et al.*, 2007; Bode *et al.*, 2009a, 2009b; Pérez, F. F., *et al.*, 2010). Local upwelling, caused by internal tides, also occurs along the shelf break, enhancing phytoplankton production (e.g. Pingree *et al.*, 1982).

6.4.1 Greenland and Icelandic seas

Warming of the sea surface has proceeded at a fast rate in this region since 1982 (Belkin, 2009), exceeding the global average of 0.2°C decade^{-1} (Bindoff *et al.*, 2007). The warming was accompanied by increases in both phytoplankton biomass and production (Table 6.1), although only trends in annual average chlorophyll for the period between 1998 and 2006 in the Eastern Greenland Shelf were significant ($P<0.05$). On the West Greenland Shelf, increases in spring chlorophyll from 1994 to 2005 (Li *et al.*, 2006) have continued throughout 2009 (Labrador Sea Monitoring Group, 2010). It is often presumed that annual primary production in these waters is linearly related to the duration of the ice-free period through cumulative exposure to solar irradiance. However, the regions with the longest ice-free periods are also those where advective and convective supply of nutrients are extensive. It appears that annual primary production per unit area in seasonally ice-free waters is controlled primarily by nitrogen supply and modulated by the light regime, which may affect phenology and species composition (Tremblay and Gagnon, 2009).

6.4.2 Barents Sea

In this region, there has been a minimal linear increase in SST, but average annual phytoplankton biomass (but not production) increased significantly (Table 6.1). These results are supported by a reduction in the oxygen saturation of bottom waters, as revealed by *in situ* measurements over the period 1957–2008 (Titov, 2009). The oxygen saturation of the near-bottom layers in the Barents Sea has decreased by ca. 1% in this period, and a prolonged period of low saturation was observed between 1998 and 2005 (Figure 6.6). The excess oxygen consumed can be considered a proxy for an increase in the degradation of organic matter produced by phytoplankton. As in the previous region, warming has favoured the melting of ice and enhanced the formation of hydrographic fronts with increased water column stability, allowing an expansion of areas that are suitable for the growth of phytoplankton populations.

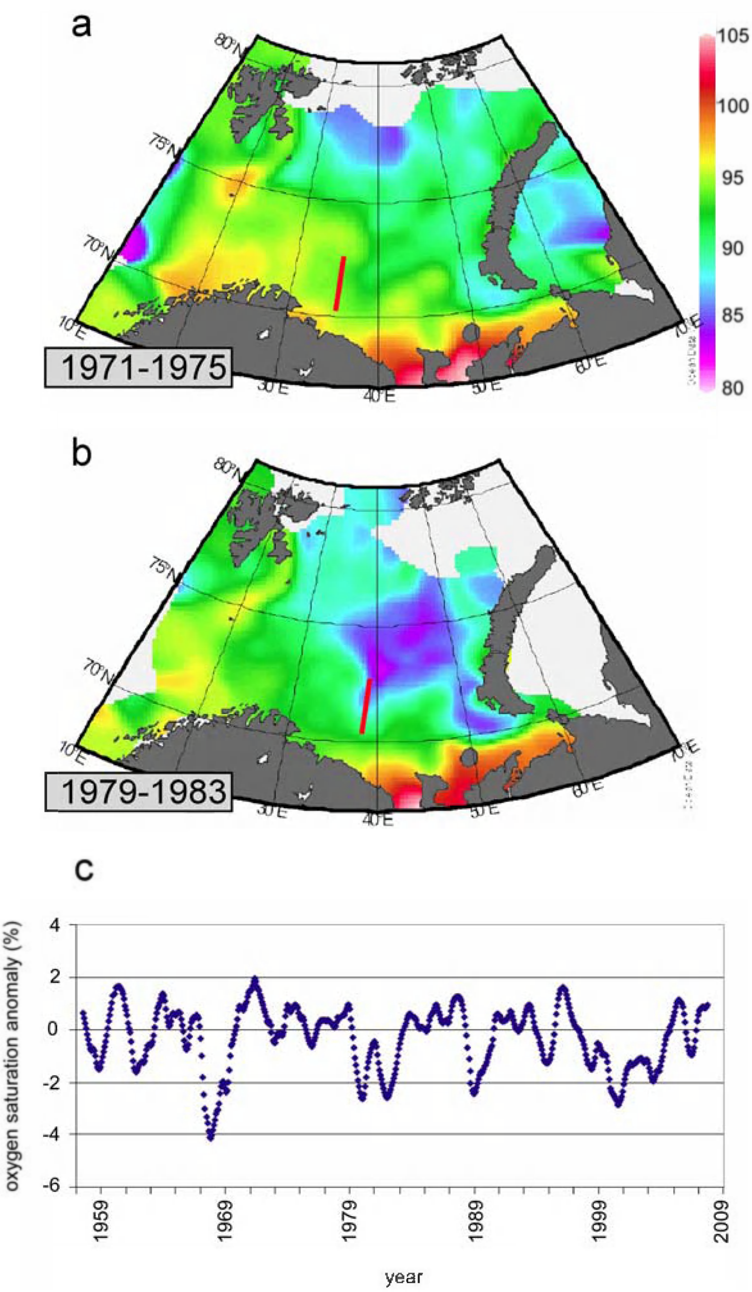

Figure 6.6. Oxygen saturation (%) of bottom layers in the Barents Sea averaged for periods of (a) high saturation (1971–1979) and (b) low saturation (1979–1983). The red line shows the position of the Kola section from where the mean anomalies smoothed by moving-average from the previous year are displayed (c). (Source: modified from Titov, 2009.)

6.4.3 Faroe Islands

As for other high-latitude regions, warming has proceeded at a fast rate in the sea around the Faroe Islands (Belkin, 2009), with SST values above the mean of the past century (O'Brien *et al.*, 2008). Satellite data since 1998 have revealed a small, but not significant, increase in both phytoplankton biomass and production (Table 6.1), although field data for the period 1990–2007 demonstrated no clear trend in chlorophyll values to the north or south of the Faroe Islands (O'Brien *et al.*, 2008).

6.4.4 Norwegian Sea

No significant trends in satellite-estimated phytoplankton biomass and production were measured in the Norwegian Sea, which is characterized by high warming rates (Table 6.1). Chlorophyll measurements during spring cruises in the area since 1991 reveal a significant positive relationship between chlorophyll and stratification, with values in the Arctic generally exceeding those found in Atlantic waters (Figure 6.7). Temporal trends, however, were inconclusive in these series (Debes *et al.*, 2009).

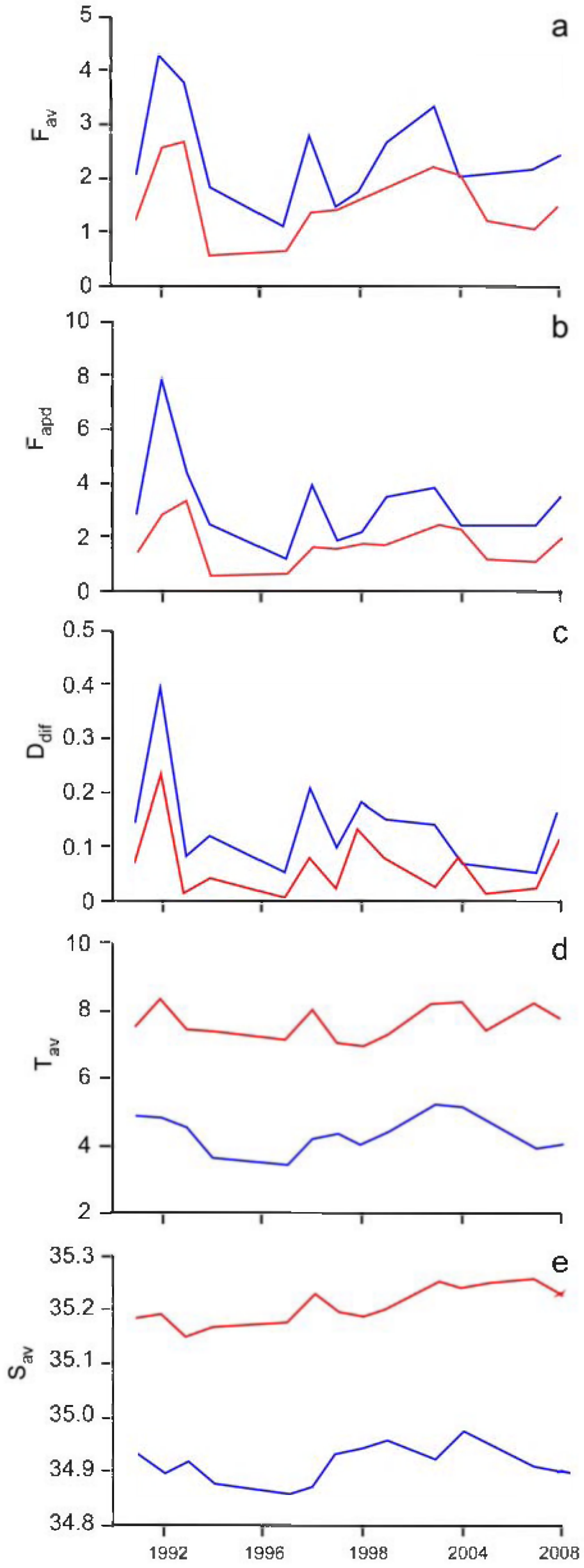

Figure 6.7. Time-series (from top to bottom) of: mean (±s.d.) chlorophyll *a* concentration (mg m^{-3}) in the upper 50 m (F_{av}); chlorophyll *a* concentration (mg m^{-3}) above the pycnocline (F_{apd}); density change (kg m^{-3}) through the upper 50 m (D_{dif}); temperature (°C) in the upper 50 m (T_{av}); and salinity in the upper 50 m (S_{av}); measured in a transect of 14 stations running along 6°05′W, from 62°20′N to 64°30′N in the Norwegian Sea during May. Blue lines = Arctic Water; Red lines = Atlantic Water. (Source: Debes *et al.*, 2009).

6.4.5 Celtic Sea

Changes similar to those in the Norwegian Sea were also observed in the Celtic Sea (Table 6.1), where phytoplankton biomass and production did not change significantly over time, despite the rapid warming of surface waters. A more detailed analysis of satellite data emphasized the large variability observed within this region (i.e. no change or a reduction in the oligotrophic areas in the north and central part of the region and an increase in the south), although field studies also indicated no clear trend in the period 1992–2007 (O'Brien *et al.*, 2008). Similarly, a study of a time-series of annual primary production, based on nutrient inputs by mixing and estimated from additive models, revealed no clear pattern between 1960 and 2003, but demonstrated high production periods in the early 1960s and 1990s (Heath and Beare, 2008). The study revealed that primary production in stratified oceanic areas was correlated with the North Atlantic Oscillation (NAO) index and explained the high production periods as a response to an enhanced flux of nitrate-rich oceanic water in the early 1990s (Figure 6.8). In contrast, nutrient inputs from rivers and the atmosphere were of lesser importance for primary production than oceanic inputs into the Celtic Sea (Heath and Beare, 2008). Other studies noticed a marked increase in the Phytoplankton Colour Index (PCI, a proxy for phytoplankton biomass determined from the greenness of Continuous Plankton Recorder (CPR) samples) between 1958 and 2002 in a region of the Northeast Atlantic that includes the Celtic and North seas (Leterme *et al.*, 2005). Such an increase cannot be attributed to the effects of eutrophication by anthropogenic nutrients near the coast but is mainly the result of warm winters increasing stratification and the input of oceanic waters, along with an improvement in water clarity resulting from reduced turbidity (Leterme *et al.*, 2005; McQuatters-Gollop *et al.*, 2007, 2009).

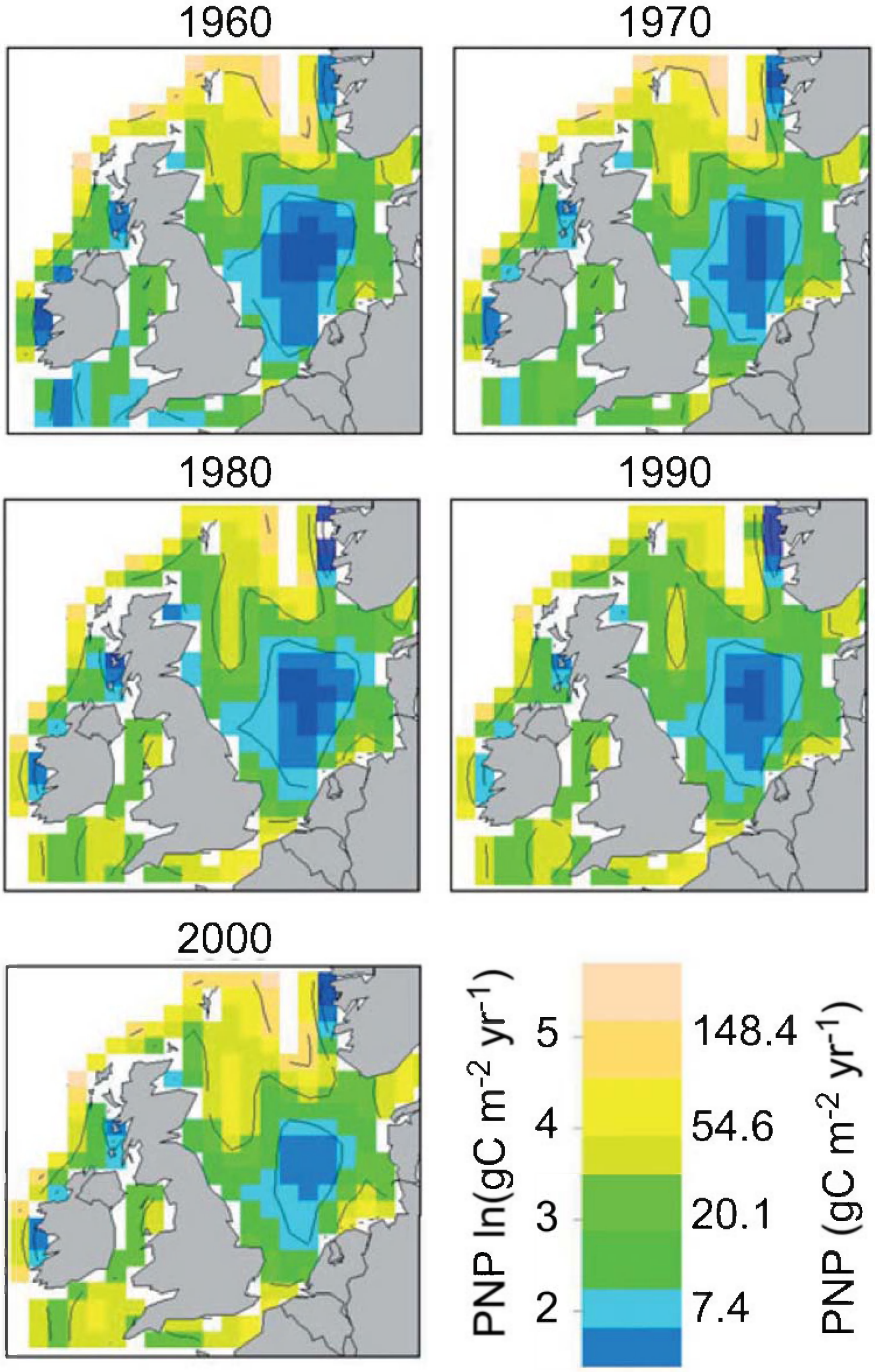

Figure 6.8. Spatial distributions of log$_e$-transformed annual potential new primary production (PNP, ln g C m^{-2} year^{-1}) at 10-year intervals from 1960, estimated from the draw-down of nitrate in the water column. Contours shown at log-PNP values of 3, 4, and 5. (Source: Heath and Beare, 2008, Figure 5. Courtesy of Inter-Research.)

6.4.6 North Sea

The North Sea is one of the most studied regions of the North Atlantic, displaying one of the fastest rates of warming in recent years (Belkin, 2009). When considering the whole region, average annual phytoplankton biomass and production demonstrated little change in the period 1998–2006 (Table 6.1). Studies of field data, however, indicate a large variability in observed responses. Phytoplankton chlorophyll decreased in the northeast of the region (Skagerrak), although no clear trend was found in the northwest (Stonehaven) in the period 1994–2007 (O'Brien *et al.*, 2008). Over a longer period (1946–2002), a stepwise increase in phytoplankton biomass, as deduced from PCI values, occurred after the major late phase-shift of the 1980s (regime shift) in oceanography that affected many physical and ecosystem variables in the North Sea (Reid *et al.*, 2001a; Beaugrand, 2004; Leterme *et al.*, 2005; Weijerman *et al.*, 2005). This increase in phytoplankton biomass has been largely attributed to the climatic effect of warm winters that increased water column stratification, reduced turbidity (McQuatters Gollop *et al.*, 2007), enhanced the nutrient input from oceanic waters (Reid *et al.*, 2003a), and favoured phytoplankton production.

Like the Celtic Sea, the estimated production during the period 1960–2003 revealed no clear pattern (Figure 6.8), with a high production period in the early 1990s (Heath and Beare, 2008). Although the influence of nutrients provided by riverine and atmospheric sources was, on average, larger than that calculated for the Celtic Sea, the concentration of nitrate in the water appeared to be determined more by the concentration in ocean source waters than in river inputs (Hydes *et al.*, 2004). The production maximum in the early 1990s was attributed mainly to oceanic inputs driven by climate (Reid *et al.*, 2003a; Heath and Beare, 2008). At local scales, field data also revealed frequent periods of increase and decrease. For instance, Lindahl (1995) reported an increase in phytoplankton biomass and annual primary production at a coastal site in the Skagerrak in the period 1985–1994, caused in part by large blooms in 1987–1988. The changes were attributed to an increase in nutrient inputs but their source (oceanic or terrestrial) was not identified. However, an extension of the dataset to 1996 and new analyses revealed that the increasing trend in primary production was not significant and that climate-driven oceanographic changes may have triggered a lagged response of the phytoplankton (Lindahl *et al.*, 1998).

Similarly, Cadée and Hegeman (2002) found an increase of phytoplankton biomass in the coastal Wadden Sea from 1973 to 1985, then a small decrease until 2000. Primary production also increased, in this case from 1964 to 1974, and then decreased as reported for biomass. Coastal eutrophication has been invoked to explain earlier increases, with subsequent reductions in both biomass and production attributed to improvements in the removal of excess (anthropogenic) nutrients in river waters (e.g. Hickel *et al.*, 1993), but recent interpretations assign a major role to changes in the nutrient inputs from oceanic waters (Carstensen *et al.*, 2005; McQuatters-Gollop *et al.*, 2007, 2009; Schlüter *et al.*, 2009). However, coastal (<10 km offshore), estuarine, and isolated areas, which are not being monitored by the CPR programme, are likely to be affected by nutrient discharges from the continent.

6.4.7 Southeastern European Atlantic Shelf

This region is characterized by a transition between open ocean and shallow coastal waters on the one hand, and south–north and east–west reducing gradients in the intensity of upwelling (Lavín *et al.*, 2004) on the other. As a consequence, multiple fronts and alternating extremes influence the photic zone where phytoplankton production occurs (Bode *et al.*, 1996; Alvarez-Salgado *et al.*, 2002). This may explain why overall trends in phytoplankton biomass and production were small and insignificant (Table 6.1), even when sea-surface warming proceeded at a relatively high rate. Annual mean values of phytoplankton biomass appeared to increase in the period 1958–2002, considering the whole region and the changes observed in PCI (Leterme *et al.*, 2005), but such changes were not significant when considering only the upwelling-influenced southwest of the region and extending the data period to 2006 (Bode *et al.*, 2009a). For coastal and offshore waters located farther south, in the vicinity of the Galician Rías Baixas, a significant decrease in net primary production, estimated from new nutrient inputs and accompanied by shifts in phytoplankton dominant groups, was associated with weakened upwelling over a 40-year period (Pérez, F.F., *et al.*, 2010).

Analysis of local time-series of *in situ* measurements in the southern Bay of Biscay also revealed years of high and low phytoplankton biomass over the period 1989–2007 (O'Brien *et al.*, 2008). An extended analysis of two coastal time-series with updated datasets (Figure 6.9) revealed a lack of clear patterns in annual mean phytoplankton biomass at the site that was influenced by upwelling, although maximum values occurred at both ends of the series at the site that was only marginally affected by upwelling (Bode *et al.*, 2009b, In press). These changes can be related to parallel variations in the input of nutrients, particularly phosphate, owing to changes in the origin of the intermediate water masses, related in turn to atmospheric forcing in winter at the formation area and the advection of western waters (van Aken, 2001). High nutrient inputs, such as those found in 2005, could be the result of deep mixing of the water column during extremely cold winters which reduced the stratification of the upper layers for several years (Somavilla *et al.*, 2009). An apparent linear reduction in primary production measured *in situ* in the southern Bay of Biscay between 1993 and 2003 was attributed to a decrease in surface nutrients (Llope *et al.*, 2007) and enhanced thermal stratification induced by the warming of the sea surface (Valdés *et al.*, 2007).

These patterns are part of the variability of response by coastal sites to the influence of upwelling and annual variations in the input of nutrients from the ocean (Bode *et al.*, 2009b, In press). In this way, mean annual primary production increased fourfold at the coastal upwelling site between 1989 and 2006, whereas in the southern Bay of Biscay it first decreased until the early 2000s but increased thereafter (Figure 6.9). Analysis of *in situ* chlorophyll data from the southeast of the Bay of Biscay also revealed no evidence of change in the period 1986–2008 (Revilla *et al.*, 2009), although winds that are favourable to upwelling have reduced in this region since the 1960s (Alvarez *et al.*, 2008). The inconclusive changes, or even the increases observed in total primary production, could be the consequence of an increase in the input of regenerated nutrients (Pérez, F. F., *et al.*, 2010).

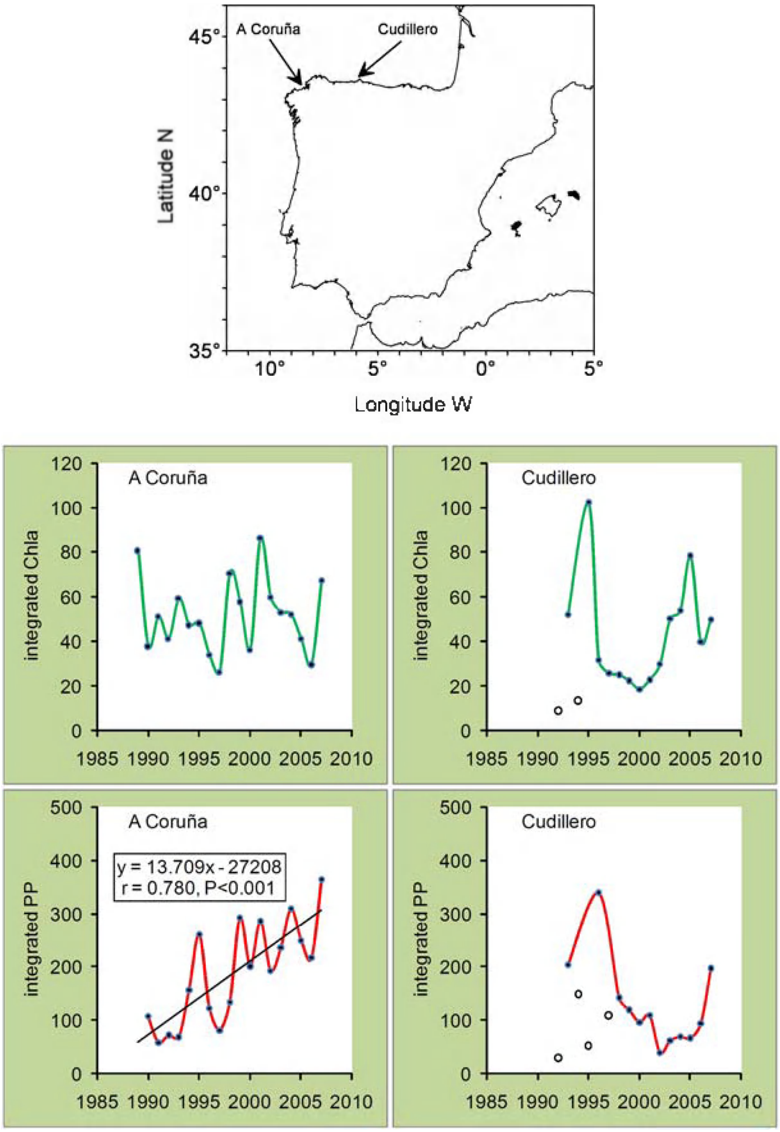

Figure 6.9. Annual mean water-column integrated chlorophyll *a* concentrations (mg m^{-2}) and primary production (PP, ^{14}C uptake, mg C m^{-2} h^{-1}) measured at two coastal stations in the southern Bay of Biscay. Open circles represent mean values computed from <8 monthly observations and not used in the estimation of trends by linear regression. (Source: modified from Bode *et al.*, 2009b).

6.4.8 The oceanic Northeast Atlantic

Evidence of changes in phytoplankton in the oceanic North Atlantic areas comes mostly from satellite data. Behrenfeld *et al.* (2006) and O'Brien *et al.* (2008) demonstrated contrasting trends of change in primary production in this region, ranging from net increases in southern areas to net reductions in the north during the 1999–2004 warming period. Data based on the PCI also indicate a decrease in biomass to the south of Iceland to ca. 1997 (Figure 6.10); since then, there has been a large increase (Leterme *et al.*, 2005; Reid, 2005) that has been linked to the westward retreat of the Subpolar Gyre (Hátún *et al.*, 2009a). The convergence and mixing of subtropical and subpolar waters west of Ireland causes a transition zone where the mixing layer depth attains optimal conditions of light and nutrient for phytoplankton production. This transition zone shifts west and north as the Subpolar Gyre weakens, as observed in the period post-1995 (Hátún *et al.*, 2009a).

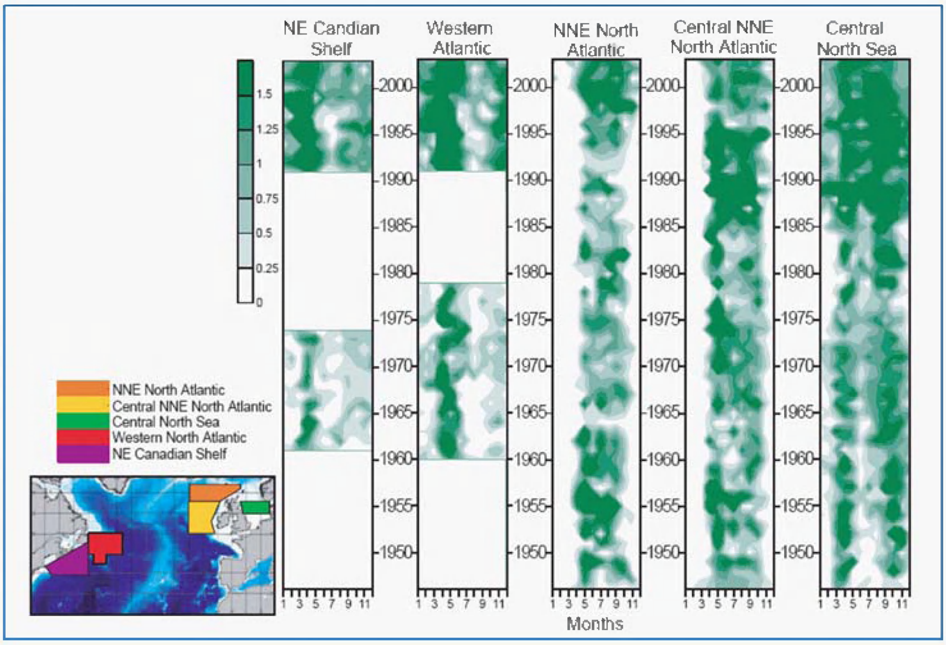

Figure 6.10. Contour plots of the mean monthly Phytoplankton Colour Index (PCI) from the Continuous Plankton Recorder for the northeastern Canadian Shelf, Western Atlantic, NNE North Atlantic, Central NNE North Atlantic, and Central North Sea. (Source: Reid, 2005, Figure 1. Courtesy of GLOBEC).

6.4.9 Baltic Sea

The Baltic Sea displayed one of the highest linear trend values in recent sea surface warming of all world regions, equivalent to the trend found in the North Sea (Belkin, 2009). No clear patterns, however, were found in mean annual phytoplankton biomass and production (Table 6.1). Increased freshwater inputs, along with warming, may have caused the large values in primary production estimated for recent years (Sherman and Hempel, 2009). Analysis of *in situ* chlorophyll measurements from local time-series (O'Brien *et al.*, 2008) revealed an increase in mean values for the Gulf of Finland (1993–2007) and in the Southern Baltic (1979–2007), although no clear trend was found in other areas, such as the Gulf of Riga (1993–2007) and the northern Skagerrak (1994–2007). The changes in the areas with increases in the concentration of chlorophyll were attributed to higher levels of nutrient caused by enhanced mixing of bottom waters in spring during years of warm winters, producing earlier and longer spring blooms than those years with cold winters (O'Brien *et al.*, 2008). A recent analysis using open and coastal water data, including all seasons and stations from the Baltic Proper demonstrated a very slowly decreasing trend for median chlorophyll *a* from 1974 until 2005 (Håkansson and Lindgren, 2008). The time-series of primary production data reveal a change in the annual maxima in recent years, with one in March and another between July and September, that were not recorded in the 1950s and 1960s (Rydberg *et al.*, 2006). The results also indicate that annual primary production has clearly increased between the 1950s and 1980. Intensive anthropogenic influence in this enclosed sea, however, makes it difficult to separate the effects of eutrophication from those of climate-driven changes.

6.4.10 Northwest Atlantic

The rate of increase in SST was highest in the Newfoundland–Labrador region, moderately high in the Scotian Shelf, and equivalent to the global ocean average in the northeastern shelf of the US (Belkin, 2009). Phytoplankton biomass and production estimated from satellite data revealed small but positive increases in all three areas except for the Newfoundland–Labrador region, which displayed an apparent reduction (Table 6.1). Further examination of these data, extending the time-series from 1987 to 2007 and considering more subareas, indicated positive increases in biomass in all areas, except for Georges Bank (Figure 6.11), where tidal currents are considered a more important contributor to phytoplankton biomass than climate forcing (Hyde *et al.*, 2009). The tidal contribution, however, should even out and not affect interannual changes. In the Mid-Atlantic Bight phytoplankton blooms (particularly those of autumn and winter) have declined from the 1970s and 1980s to the last decade (Schofield *et al.*, 2008). The decrease in autumn blooms was attributed to a late erosion of surface stratification, whereas that of winter blooms may be associated with an increase in winter winds that enhance winter mixing, thus increasing light limitation of the phytoplankton. Field studies covering large areas are generally consistent with recent increases in biomass. For instance, Leterme *et al.* (2005), analysing PCI data in mostly off-shelf areas, found a marked increase in biomass between 1958 and 2002 that was attributed to the production of earlier and larger blooms in years with a positive NAO index; this situation would have enhanced water column mixing and the input of nutrients from below the photic layer. Time-series of chlorophyll and primary production rates measured in the Sargasso Sea between 1988 and 1998 did not reveal any clear pattern of change (Steinberg *et al.*, 2001). The lack of variation is considered to be a consequence of the dominance of mesoscale over climatic factors in determining primary production in this oceanic area. High primary production rates, however, were related to positive anomalies of the NAO index.

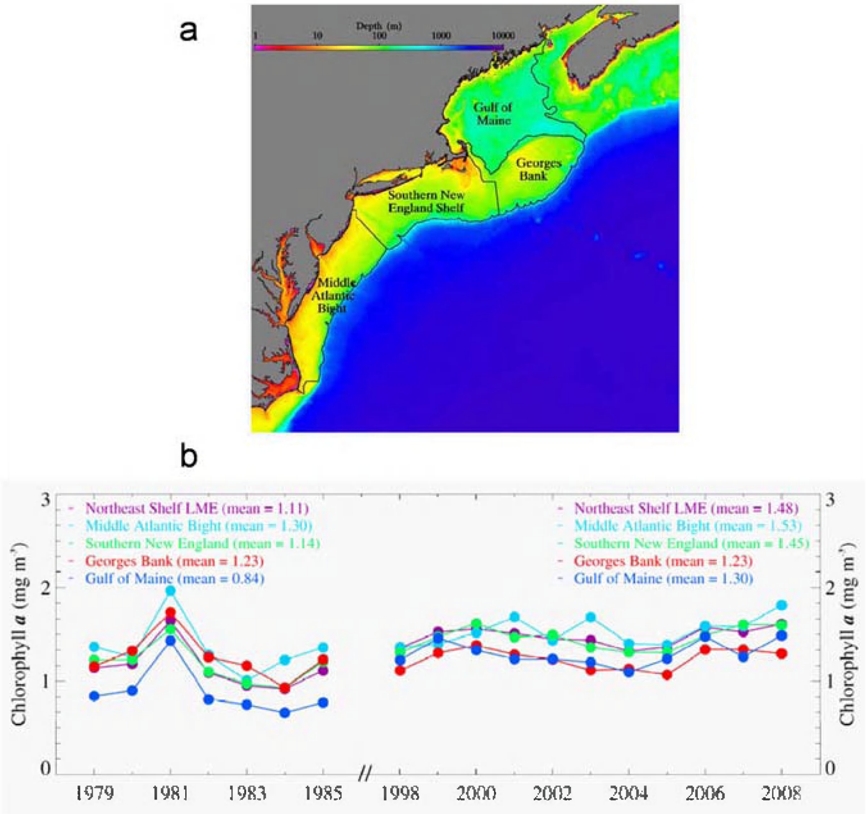

Figure 6.11. Subregions of the US Northeastern Atlantic Shelf (a) and annual chlorophyll *a* means (b) from 1979–1985 (estimated from the Coastal Zone Color Scanner) and from 1998–2008 (estimated from SeaWiFS; Source: modified from Hyde *et al.*, 2009).

Over the Scotian Shelf, an increase in mean chlorophyll in spring and a decrease in autumn was detected for the period 1997–2009 (Li *et al.*, 2006; Li, 2009). Both trends were balanced out at an annual level, with no net change in biomass but a potential impact on foodweb dynamics (Ji *et al.*, 2010). Nevertheless, at a local scale in Bedford Basin adjoining the Scotian Shelf, and using a frequently sampled long time-series, it is possible to discern multidecadal change in chlorophyll associated with nutrient enrichment (Li *et al.*, 2008), as well as interannual phytoplankton variability associated with climate-driven stratification (Li and Harrison, 2008).

In the Labrador Sea, the situation is complicated by the variability of the modes of phytoplankton regulation (light or nutrient limitation) at different times of the year and in different regions of the sea (Harrison and Li, 2008). Earlier analysis of a 12-year time-series indicated chlorophyll decreases in the Labrador Basin and on the Labrador Shelf (Li *et al.*, 2006), but the interannual trends have flattened with additional observation in more recent years (Labrador Sea Monitoring Group, 2009, 2010). In Labrador waters, a net reduction in primary production was found (Li, 2009) and attributed to changes in the availability of nutrients caused by an increase in thermal stratification. In contrast, average chlorophyll concentrations were reduced in most time-series obtained at coastal sites, except for the St Lawrence Estuary (O'Brien *et al.*, 2008). A detailed analysis of satellite data revealed large spatial heterogeneity in local responses, despite the trends observed in their core or averages within a given region (Devred *et al.*, 2009).

6.5 Phytoplankton productivity, foodwebs, and biogeochemistry in the North Atlantic

6.5.1 Biomass and production

Despite the marked differences between the mean values of chlorophyll *a* and primary production between the different areas, there is no clear relationship between the variability of SST, as an index of changes in stratification, and trends in chlorophyll or primary production when considering the whole region. In some cases (e.g. Subarctic waters) the increase in water column stratification induced by moderate warming seems to stimulate phytoplankton production and the accumulation of biomass. However, the stratification leads to reductions in primary production and biomass in other areas (e.g. subtropical waters). An independent study using time-series of chlorophyll from both eastern and western regions of the North Atlantic (Morán *et al.*, 2010) also established a significant negative relationship between average water column chlorophyll and temperature (Figure 6.12a). Century-scale trends also point to a global reduction in surface chlorophyll (Boyce *et al.*, 2010), although this remains contentious. Model simulations and the available high-resolution palaeorecord suggest that plankton biomass is highly sensitive to changes in the meridional overturning circulation of the North Atlantic (Schmittner, 2005). A severe disruption of the overturning circulation would lead to a collapse of plankton biomass owing to increased shoaling of the winter mixed layer, which becomes isolated from the reservoir of nutrients in deep waters. In turn, the amount of biogenically fixed carbon would decline as integrated export production declines.

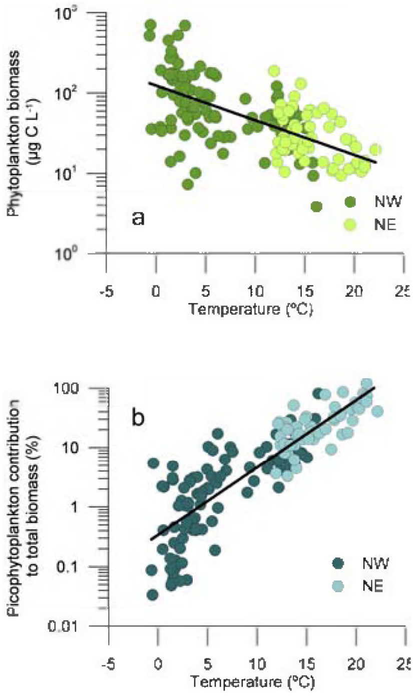

Figure 6.12. Relationship between temperature and: (a) phytoplankton biomass (estimated from chlorophyll), and (b) percentage contribution of picophytoplankton to total phytoplankton biomass in two regions of the North Atlantic. Fitted lines are least-squares linear regressions for the pooled datasets (p<0.001). (Source: Morán *et al.*, 2010, Figures 1 and 4. Courtesy of Wiley-Blackwell.)

Primary production includes a particulate and a dissolved fraction. The latter is frequently not measured, contributing less to total rates (10–30%), but it is especially important for heterotrophic bacteria. Knowledge of the effect of ocean warming on primary production partitioning is still scarce, but results from perturbation experiments suggest higher fluxes of dissolved organic carbon (DOC) with increasing temperatures (Morán *et al.*, 2006; Wohlers *et al.*, 2009). It is unclear how these extra inputs of dissolved compounds will affect bacterial metabolism in the long term, but some studies point to an increase in microbial loop processes in parallel with a weakening of the strength of the biological pump (Hoppe *et al.*, 2008; Wohlers *et al.*, 2009; Kirchman *et al.*, 2009). Different temperature sensitivities of phytoplankton and heterotrophs also underlie predictions of a shift in planktonic metabolism towards net heterotrophy in a warmer ocean (López-Urrutia *et al.*, 2006; O'Connor *et al.*, 2009).

6.5.2 Shift to smaller species

The study by Morán *et al.* (2010) revealed that a reduction in total phytoplankton biomass was accompanied by an increase of picoplankton (<2 µm of equivalent spherical diameter) cells with temperature (Figure 6.12b). According to their analysis, picoplankton constituted >50% of the phytoplankton biomass as water temperatures approach 20°C. This dominance of picoplankton at higher temperatures may be explained by a combination of the temperature–size rule, predicting lower cell sizes at high temperatures, and the inverse relationship found between total cell abundance and individual cell size. In warmer conditions, the average size of organisms in a community would reduce and, because smaller organisms have lower absolute energy requirements than their larger equivalents, the number of phytoplankton cells that can be hosted will be higher. A shift to smaller cells is also favoured under strong stratification because small cells are more effective in acquiring nutrients and less susceptible to gravitational settling than large cells. An increasing abundance of picoplankton in freshening Arctic waters (Li *et al.*, 2009) may be propagated to parts of the North Atlantic that are influenced by Arctic outflow. Although nutrients undoubtedly play a role in determining organism size (e.g. Finkel *et al.*, 2010), consistent observations within various phytoplanktonic groups of a decrease in mean cell size with increasing temperature (Atkinson *et al.*, 2003; Daufresne *et al.*, 2009; Finkel *et al.*, 2010) support the prediction that, on average, phytoplankton cells will be smaller in the next few decades.

6.5.3 Foodwebs

Notwithstanding changes in species composition (e.g. Richardson and Schoeman, 2004; Schlüter *et al.*, 2009), a general reduction in the rates of primary production and in the size of phytoplankton cells as a consequence of severe warming imply profound transformations in the foodweb. Export rates of biologically fixed carbon to the sediments, for instance, are likely to be greatly reduced, as small cells are rapidly degraded in the water column (Bopp *et al.*, 2001), further reducing the capacity of the ocean to remove CO_2 from the atmosphere (Denman *et al.*, 2007). In addition, regional studies demonstrated changes in bacterioplankton abundance that were coherent in direction and magnitude with those of phytoplankton biomass (Li *et al.*, 2006; Li, 2009) in agreement with the idea of changes at the ecosystem level directed by climate variations. Foodwebs based on progressively smaller primary producers and having lower absolute rates of primary production will not be able to sustain current fish populations, implying that pronounced changes will take place in the size and composition of fish catches as temperatures rise as a result of climate change (Sherman and Hempel, 2009). As fish catches have been increasingly limited by primary production for the past 60 years (Chassot *et al.*, 2010), this effect will exacerbate problems arising from increasing pressure from the fishery, with unpredictable consequences for ecosystems.

6.5.4 CO_2 uptake

The increase in ocean CO_2 concentration may not have large direct effects on photosynthetic rates, but some phytoplankton species (e.g. coccolithophorids) are likely to show significant stimulation of growth (Orr *et al.*, 2005; Iglesias-Rodríguez *et al.*, 2008; Beardall *et al.*, 2009). Interactions between temperature rise, CO_2 levels and sensitivity of phytoplankton to UV radiation may modify primary productivity and the assemblage composition of phytoplankton. The results of simulation models indicate that the fraction of anthropogenic CO_2 taken up by the ocean (from 42 ± 7% during 1750 to 1994 to 37 ± 7% during 1980 to 2005) will decline if atmospheric CO_2 continues to increase (Denman *et al.*, 2007). At the same time, ocean CO_2 uptake has lowered the average ocean pH by approximately 0.1 units. The consequences for marine ecosystems may include reduced calcification by shell-forming organisms (Orr *et al.*, 2005), and in the longer term, the dissolution of carbonate sediments (Doney *et al.*, 2009). Other effects of rising CO_2 levels include an increase in DOC exudation by phytoplankton, enhancing the formation of transparent exopolymer particles (Engel, 2002), and possibly affecting carbon export (Arrigo, 2007; Riebesell *et al.*, 2007). Laboratory experiments suggest that increasing CO_2 concentrations will affect phytoplankton carbon fixation rates, but its importance in modifying oceanic primary production remains uncertain (Riebesell, 2004; Riebesell *et al.*, 2007; Beardall *et al.*, 2009). Nevertheless, nitrogen-fixing cyanobacteria may enhance productivity in oligotrophic areas because of their sensitive response to high CO_2–low dissolved-nutrient conditions (Barcelos e Ramos *et al.*, 2007).

6.6 Conclusions

Available observations show an overall increase in global oceanic phytoplankton biomass since the 1970s. Regional changes, however, vary from increases in Subpolar and large upwelling regions to net decreases in the Subtropical Gyres. Alleviation of light limitation for phytoplankton growth by enhanced stratification provided by surface warming is likely the cause for the increases in chlorophyll found in areas typically characterized by well mixed waters. On the contrary, a reduction in mixing exacerbates nutrient limitation in areas with near permanent stratification. In the northern North Atlantic, the available evidence also supports a general increase in the average biomass and primary production of phytoplankton that is associated with rising SST. The observed changes, however, are not uniform either spatially or temporally. The increase in biomass and production in subpolar (and probably also in temperate shelf waters) can be related to warming and wind patterns but also to shifts in the position of the Subpolar and Subtropical Gyres, causing marked shifts in nutrient inputs and ecosystem composition and production. An example of the interactions between different factors is the large regime shift displayed by the North Sea in the late 1980s, which was attributed to the joint effect of warming, change in wind intensity and direction, and an increase in the inflow of oceanic waters. In these ocean and shelf areas, the effect of anthropogenic nutrient enrichment on primary production is in general of minor importance compared with climatic and large-scale oceanographic factors. However, along most of the temperate and tropical margins of the Atlantic, although primary production is largely regulated by the flux of nutrient from below the nutricline, additional factors such as high frequency perturbations from tides to storms, run-off, and agricultural eutrophication can make it difficult to discern the effects of climate in these regions.

Increases in total primary production in the upwelling region off the northwestern Iberian peninsula can be related to variations in the input of nutrients caused by mixing during the formation of intermediate waters. Near the southern Galician coast, a 40-year reduction in upwelling intensity and frequency has led to a reduction in the input of new nutrients so that total primary production depended increasingly on nutrient regeneration. In contrast, reductions in phytoplankton biomass in the southeastern Bay of Biscay were attributed to increasing stratification by warming and a reduced influence of upwelling, but the trend may be reversed in years of high mixing of the water column during winter. Changes in the Baltic and other enclosed coastal areas, however, are difficult to ascertain owing to the interaction of climate and eutrophication, as the observations generally indicate larger values of primary production and biomass in recent years compared with historical records. Variability of trends on both sides of the Atlantic is similar, with a general increase in phytoplankton biomass and production in most shelf waters but with large local variability. Blooms have reduced in intensity and changed timing in some regions of the western Atlantic (e.g. Mid-Atlantic Bight and Labrador waters) although no clear pattern of change was found for the eastern Atlantic. Climate-driven changes in the position of oceanic gyres and in the mixing depth of waters during winter interact with stratification caused by surface warming thus affecting the availability of nutrients and light for phytoplankton production in the whole area, but particularly in the transition region between subpolar and subtropical waters. Because of interactions between direct (e.g. CO_2 and temperature increases) and indirect effects (e.g. nutrient inputs) of climate change, the exact nature and direction of future changes in phytoplankton production is difficult to establish without having long-term (i.e. >30 year) time-series of observations as reliable baselines against which to interpret the effects of abrupt or gradual changes. These series must be methodologically consistent and representative of the main ecosystem types.

Acknowledgements

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7 Overview of trends in plankton communities

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7.1 Introduction

Phytoplankton and zooplankton occupy pivotal positions within marine ecosystems. These small organisms fuel and support the foodwebs upon which almost all higher organisms depend. Fisheries and related economic activities are highly dependent on the production, size, and composition of zooplankton which, in turn, rely on primary production by phytoplankton. In addition to their role as prey for herbivorous zooplankton, phytoplankton absorb enormous quantities of dissolved CO_2 via photosynthesis. Zooplankton then plays an essential role in the biological pump by consuming phytoplankton and transporting carbon from the upper ocean to the deep ocean, where it is sequestered for hundreds to thousands of years (Ducklow *et al.*, 2002).

Given the ecological and economic importance of phyto- and zooplankton, it is essential to understand and predict how they are likely to respond to climate change. This is a complex problem, but recent research suggests that both groups are especially sensitive to climate-induced change in the physical and chemical properties of the upper ocean, and that their responses have implications for fish stocks and fisheries (Edwards, 2009).

In addition to light, the concentration of nutrients in the euphotic zone is the major factor controlling phytoplankton production in the oceans. This process is believed to be affected by warming of ocean water, with different responses in the cold and warm regions of the Northeast Atlantic (Reid *et al.*, 1998; Richardson and Schoeman, 2004). Thus, in the colder regions (north of approximately 50°N), sea surface warming is accompanied by increasing phytoplankton abundance, whereas the opposite is true in the warmer regions (south of 50°N). This apparent contradiction is thought to arise because colder waters tend to be strongly mixed and nutrient-rich, whereas warmer waters farther south are more stratified and nutrient-poor. Warming in the relatively well-mixed waters in the north will thus lead to only moderate stratification that will be beneficial to phytoplankton growth, whereas, in the south, the increased warming will enhance the already existing stratification, thus limiting admixture of nutrients into the euphotic zone even further and leading to a reduction in phytoplankton growth. Evidence that the climate impact on growth of phytoplankton depends on the physical structure of the water column is seen off the north and northwest coasts of Spain (Valdés *et al.*, 2007). There, primary production is predicted to decline over the long term in the more stratified regions while increasing in regions where upwelling is relatively intensive (Valdés *et al.*, 2007).

Climate-related hydrographic changes may also directly affect the abundance and composition of zooplankton, shifting the distribution of dominant species (Beaugrand *et al.*, 2002; Möllmann *et al.*, 2005), changing the structure of the zooplankton community (Reid *et al.*, 2001b; Beaugrand, 2004), and altering the timing, duration, and efficiency of zooplankton reproductive cycles (Bunker and Hirst, 2004; Edwards and Richardson, 2004).

Superimposed on these climatic factors, ocean acidification through increased carbon dioxide dissolution in the upper ocean is lowering the pH in surface waters (Makarow *et al.*, 2009). A lower pH could impair the physiology and ultimately the abundance of many phytoplankton and zooplankton species, especially those that produce calcareous structures.

Recruitment success of fish stocks depends to a large extent on whether or not spawning occurs in close spatial and temporal proximity to blooms of phytoplankton and zooplankton prey. If young fish cannot secure sufficient food, they will starve, and few will survive to adulthood. Changes in the temperature of the upper ocean are likely to alter the timing and intensity of phytoplankton blooms and zooplankton peak abundance, and when, where, and how they occur, thus altering the availability of plankton to fish larvae and juveniles. Shifts in temperature and other hydrographic properties can result in pronounced changes in the distributional range of zooplankton. As warm-water species of zooplankton tend to be smaller than species from higher latitudes, changes in temperature can alter the size distribution, life-history pattern, and nutritional value of zooplankton assemblages. Consequently, these changes may have major effects on fish stocks that depend on zooplankton (Cushing, 1990; Platt *et al.*, 2003; Head *et al.*, 2005).

For all of these and other reasons, it is important to understand how phytoplankton and zooplankton are likely to respond to climate-induced changes in the ocean. This section explores what is known about the sensitivity of phytoplankton and zooplankton to climate change and summarizes the trends that are evident in plankton communities within the ICES Area.

7.2 Plankton time-series: indicators of change

The distribution and abundance of phytoplankton and zooplankton are highly variable in time and space at both small and large scales. Seasonal and interannual changes reflect the recurrent variability of their milieu from season to season and from year to year. Longer-term trends and patterns in abundance, species composition, and spatial distribution can only be identified by examining patterns that emerge over long time-series. By researching such changes in the context of hydrographic shifts, hypotheses regarding cause and effect can be developed and tested. There are currently 39 time-series (including some from the Mediterranean) whose data are summarized by ICES through the Working Group on Zooplankton Ecology (WGZE; Figure 7.1 and Table 7.1; O'Brien *et al.*, 2008). In these time-series, zooplankton are collected using a variety of sampling nets (with mesh sizes of between 90 and 333 μm), and at various sampling frequencies (mostly only a few times a year), for a minimum of 10 to a maximum of more than 70 years. Generally, the sampling methods are targeted to monitor the mesozooplankton (i.e. planktonic organisms between 0.2 and 20 mm in length) and provide only limited information on plankton outside this size range. The Continuous Plankton Recorder (CPR) survey is the monitoring programme that covers the greatest spatial (tens to thousands of kilometres) and temporal (monthly to multidecadal) scales, providing data on plankton near the surface of the ocean. Of the 31 North Atlantic time-series, 12 are within the area covered by the CPR and are thus available for comparison with the results of this survey. These time-series and the patterns described by the CPR were generally in agreement for total copepod abundance (O'Brien *et al.*, 2008). Comparisons between phytoplankton time-series and CPR results have not yet been made.

The CPR surveys began in the North Sea in 1931, but have only been extended over much of the ICES region since 1960 (Figure 7.1). Phytoplankton and zooplankton are collected between continuously advancing rolls of silk gauze as the CPRs are towed behind ships of opportunity (Batten *et al.*, 2003; Reid *et al.*, 2003a), and they are counted and identified to species/taxa once the samples are returned to the laboratory. The Phytoplankton Colour Index (PCI) is derived from the greenness of the silk mesh and is used as a proxy for phytoplankton biomass. Comparison of this visual assessment with SeaWiFS (Sea-viewing Wide Field-of-view Sensor) satellite measurements has demonstrated that the PCI is a good indicator of phytoplankton standing stock (Raitsos *et al.*, 2005).

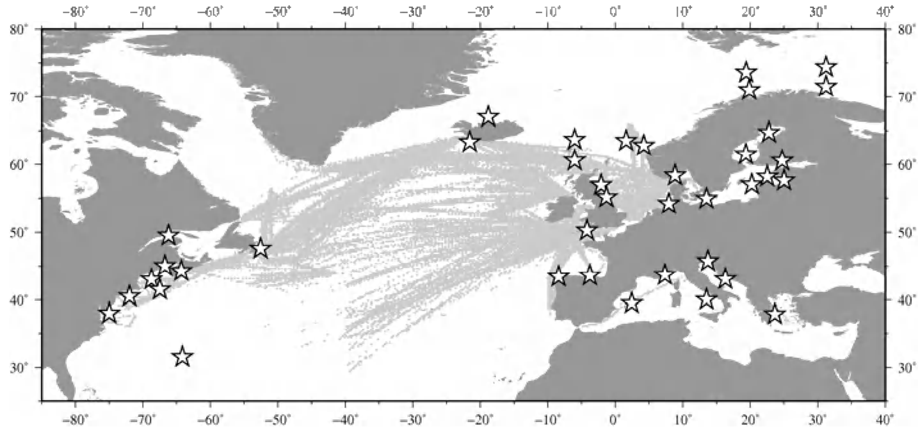

Figure 7.1. Locations of zooplankton time-series (☆) and sample positions as dots (pale grey) for the Continuous Plankton Recorder (CPR) survey (1931–2008). (Source: O'Brien *et al.*, 2008.)

7.3 Changes in phytoplankton

7.3.1 Distribution and abundance

A large increase in phytoplankton biomass (i.e. annual mean PCI) has been recorded in the Northeast Atlantic since the mid-1980s, particularly in the North Sea and in the area west of the British Isles (Figure 7.2), which appears in part to be related to increasing sea surface temperatures (SSTs; Reid *et al.*, 1998; Edwards, 2000; Edwards *et al.*, 2001b, 2007). In the same area, an extension of the duration of the seasonal maximum of the PCI has also been observed.

In contrast to previous observations, Boyce *et al.* (2010) have recently indicated a global decline in phytoplankton standing stock of up to 1% of the median phytoplankton biomass per year. However, the validity of this study is currently under debate because the heterogeneities of the data and the methodology used are considered to have biased the results presented by Boyce and co-authors (Mackas, 2011; McQuatters-Gollop *et al.*, 2011; Rykaczewski and Dunne, 2011).

Table 7.1. Summary of available time-series data on zooplankton compiled by the ICES Working Group on Zooplankton Ecology (WGZE). Data summarized by O'Brien *et al.* (2008) and table courtesy of Todd O'Brien, National Oceanic and Atmospheric Administration–National Marine Fisheries Service (NOAA–NMFS).

Ocean Region	Western North Atlantic								
Country	USA				Canada				
Sampling / Monitoring Programme	NMFS-NEFSC				AZMP				
Sampling Site Name	MAB	SNE	GOM	GBK	Prince 5	Halifax Line 2	Gaspé Current	Anticosti Gyre	Station 27
Sampling Location	Mid-Atlantic Bight	Southern New England	Gulf of Maine	Georges Bank	Bay of Fundy	Scotian Shelf	Gulf of St. Lawrence	Gulf of St. Lawrence	Newfoundland Shelf
Sampling Duration	1977 - present	1977 - present	1977 - present	1977 - present	1999 - present	1999 - present	1999 - present	1999 - present	1999 - present
Sampling Frequency	Cross monthly surveys six times per year.				Monthly / Biweekly				
Sampling Gear (diameter)	Bongo Net				Ring Net (75 cm)				
Sampling Mesh (µm)	333 µm				200 µm				
Samping Depth (m)	0 to 200 (or bottom)				0 to bottom				

Ocean Region	Icelandic-Norwegian Basin						Barents Sea			
Country	Iceland		Faroe Islands		Norway		Norway			
Sampling / Monitoring Programme	MRI-Iceland		FFI-Faroe Islands		IMR-Bergen		IMR-Bergen			
Sampling Site Name	Selvogsbanki Transect	Siglunes Transect	Northern Transect	Faroe Shelf	Svinøy Transect West	Svinøy Transect East	Fugløya-Bjørnøya Transect North	Fugløya-Bjørnøya Transect South	Vardø-Nord North	Vardø-Nord South
Sampling Location	South Iceland	North Iceland	North Faroe Islands	South Faroe Islands	Norwegian Sea		Western Barents Sea		Eastern Barents Sea	
Sampling Duration	1971 - present	1961 - present	1990 - present	1990 - present	1996 - present	1996 - present	1994 - present	1994 - present	1994 - present	1994 - present
Sampling Frequency	Annually (May–June)		Annually (late May)		4 - 6 times per year		3 - 6 times per year		3 -4 times per year	
Sampling Gear (diameter)	1971–91: Hensen Net; 1992–present: WP-2 Net		1990–1991: Hensen Net; 1992–present: WP 2 Net		WP-2 Net (56 cm)		WP 2 Net (56 cm)			
Sampling Mesh (µm)	200 µm		200 µm		180 µm		180 µm			
Samping Depth (m)	0 to 50		0 to 50		0 to 200		0 to 100			

Ocean Region	Baltic Sea						
Country	Finland		Estonia		Latvia		Germany
Sampling / Monitoring Programme	HELCOM Monitoring				National monitoring programme of Latvia	LatFRA-monitoring	IOW
Sampling Site Name	Bothnian Bay	Bothnian Sea	Tallinn Bay	Pärnu Bay	Station 121	Eastern Gotland Basin	Arkona Basin
Sampling Location	Northern Baltic Sea		Gulf of Finland	Gulf of Riga		Central Baltic Sea	Southern Baltic
Sampling Duration	1979 - present	1979 - present	1993 - present	1957 - present	1993 - present	1960 - present	1979 - present
Sampling Frequency	August		up to 10 times per year	monthly to weekly in non-ice months	at least 3 times per year	seasonally	seasonally
Sampling Gear (diameter)	WP 2 Net (56 cm)		Juday Net (36 cm)		WP-2 Net	Juday Net (36 cm)	WP-2 Net
Sampling Mesh (µm)	100 µm		90 µm		100 µm	160 µm	100 µm
Samping Depth (m)	0 to bottom		0 to bottom		0 to 50	0 to 100	0 to 25

Ocean Region	North Sea / English Channel				Bay of Biscay / Iberian Coast	
Country	Norway	Germany	UK	UK	Spain	Spain
Sampling / Monitoring Programme	IMR	BSH and DZMB	FRS-MLA	L4-PML/UK	IEO-Spain	
Sampling Site Name	Arendal Station 2	Helgoland Roads	Stonehaven	Plymouth L4	Santander	A Coruña
Sampling Location	Northern Skagerrak	Southeast North Sea	Northwest North Sea	English Channel	Southern Bay of Biscay	Northwest Iberian Peninsula
Sampling Duration	1994 - present	1975 - present	1997 - present	1988 - present	1991 - present	1990 - present
Sampling Frequency	twice per month	Every Monday, Wednesday, and Friday	Weekly (52 weeks per year)	Weekly (~40 weeks per year)	Monthly	Monthly
Sampling Gear (diameter)	WP-2 Net	Hydrobios and Calcofi	Bongo Net (40 cm)	WP 2 Net	Juday Net (50 cm)	Juday Net (50 cm)
Sampling Mesh (µm)	180 µm	150 µm, 500 µm	200 µm	200 µm	250 µm	1971–96: 250 µm; 1996–present 200 µm
Samping Depth (m)	0 to 50	0 to bottom	0 to 50	0 to 50	0 to 50	0 to 50

Ocean Region	Mediterranean						North Atlantic
Country	Spain	France	Italy	Italy	Croatia	Greece	UK
Sampling / Monitoring Programme	IEO-Spain	LOV-France	SZN-Italy	UNITS-Italy	IZOR-Croatia	HCMR-Greece	Continuous Plankton Recorder
Sampling Site Name	Baleares Station	Villefranche Point B	Gulf of Naples	Gulf of Trieste	Stončica	Saronikos-S11	CPR Surveys
Sampling Location	Balearic Sea	Cote d'Azur	Tyrrhenian Sea	Northern Adriatic	Middle Adriatic Sea	Aegean Sea	Continuous Plankton Recorder Surveys
Sampling Duration	1994 - present	1974 - present	1984 - present	1970 - present	1959 - 1991; 1995 - present (unprocessed)	1987 - present	1946 - present
Sampling Frequency	monthly (up until 2006)	monthly	monthly	monthly	monthly (with gaps)	seasonally (1987–1998); monthly after 1999	Monthly (with gaps)
Sampling Gear (diameter)	Bongo Net (20 cm)	Juday-Bogorov Net	Nansen Net (113 cm)	WP-2 Net	Hensen Net (73 cm)	WP-2 Net	CPR (1.24 cm)
Sampling Mesh (µm)	100/250 µm	330 µm	200 µm	200 µm	330 µm	200 µm	280 µm
Samping Depth (m)	0 - 100	0 - 75	0 - 50	0 - 18	0 to 100	0 to 75	sub-surface (7-10 m)

In the North Sea a pronounced increase in SST and windspeed after the 1980s resulted in an extension of the season favourable for phytoplankton growth, particularly in the southern North Sea. However, McQuatters-Gollop *et al.* (2007) and Llope *et al.* (2009) found that nutrient concentrations were not an important contributory factor to the observed changes in phytoplankton standing stock.

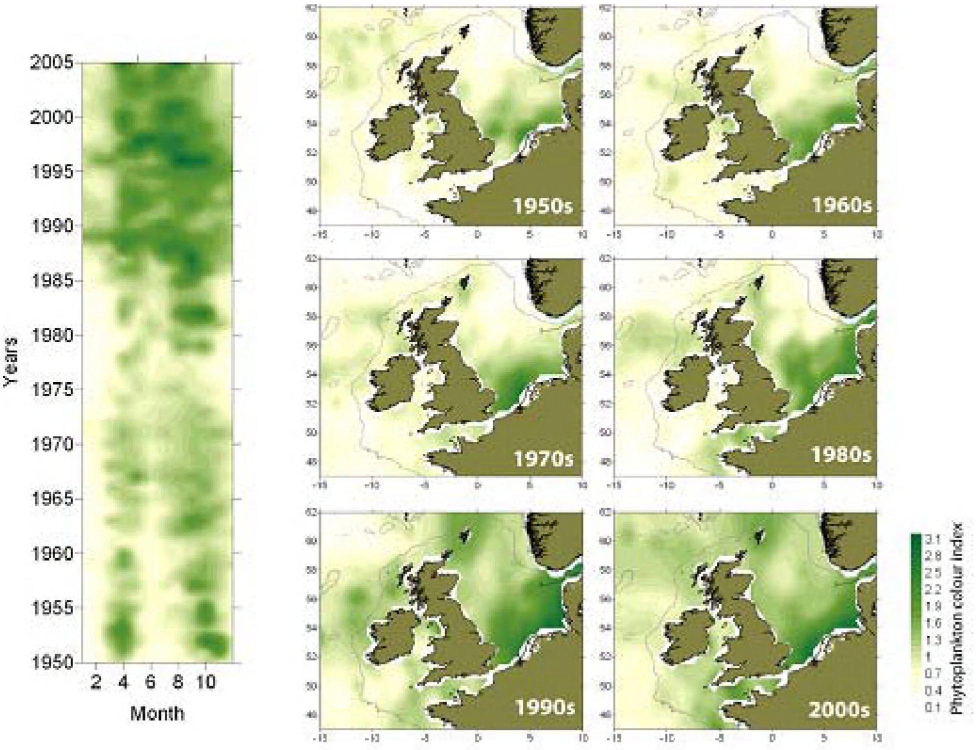

Figure 7.2. Mean spatial distribution of phytoplankton standing stock (Phytoplankton Colour Index, or PCI) per decade from the 1950s to the present. A considerable increase in PCI has been recorded since the mid-1980s, particularly in the North Sea and in the area west of the British Isles in relation to increasing sea surface temperature (SST). (Source: Edwards, 2009.)

In the waters around Iceland, particularly in the north–northeastern region, hydrographic changes (i.e. changes in currents and hydrography related to large-scale climate variability) may have an important influence on annual mean spring productivity. Primary production tends to be higher in years with a high inflow of relatively warm Atlantic Water than in years when this inflow is not so pronounced (Gudmundsson, 1998). A model developed by Ellingsen *et al.* (2008) demonstrates that primary production is likely to increase in a similar way in the Barents Sea under a warming scenario.

In the Northwest Atlantic, an increase in phytoplankton standing stock has been recorded in the past decade in both shelf and deep-ocean regions. The observed changes on the continental shelf and in the Gulf of Maine have been related to changes in the circulation and freshwater export from the Arctic Ocean, which are considered to be a consequence of climate warming (Greene and Pershing, 2007; Head and Sameoto, 2007), whereas, in the Subpolar Gyre, they are thought to be the direct result of increasing stratification caused by rising temperature (Head and Pepin, 2010).

In the Baltic Sea, it is difficult to distinguish the effects of changing climate, fishing, and eutrophication on phytoplankton biomass and species composition (Casini *et al.*, 2008). Wasmund *et al.*, (1998) consider that the spring increase in chlorophyll *a* in the

Bornholm and southern Gotland basins is related to eutrophication, whereas the reduction in diatoms in favour of the dinoflagellates is related to mild winters. The intensity of surface blooms of cyanobacteria is regulated by a combination of climatic factors, such as water temperature, solar radiation, and windspeed (Kahru *et al.*, 1994; Wasmund, 1997; Stal *et al.*, 2003).

7.3.2 Community structure

Regional climate variability has been related to changes in phytoplankton community structure observed in data from the CPR survey since the 1960s in the North Sea, with an increase in dinoflagellate abundance and a decrease in diatom abundance in response to warmer sea temperature (Leterme *et al.*, 2005; Edwards *et al.*, 2006a). The abundance of dinoflagellates is positively correlated with the North Atlantic Oscillation (NAO) and SST, whereas diatom abundance is negatively correlated with the NAO and SST (Edwards *et al.*, 2001a, 2006a). The marked hydrographic changes that have occurred in the North Sea since the late 1980s, and which have continued to the present, have resulted in an environment that appears to favour the growth and earlier succession of dinoflagellates (Edwards and Richardson, 2004; Edwards *et al.*, 2006b). In the North Sea, studies based on long-term phytoplankton dataseries other than the CPR have noted similar ecological changes in the Northeast Atlantic in the late 1980s or in more recent years and, in particular, an increase in the ratio of dinoflagellates to diatoms in the southern North Sea (Hickel, 1998) and the western English Channel (Widdicombe *et al.*, 2010). Against this background of change, the abundance of the most common species of the armoured dinoflagellate *Ceratium* (e.g. *C. furca*, *C. fusus*, and *C. horridum*) has decreased markedly in the North Sea since the early 2000s (Edwards *et al.*, 2009).

In recent decades, in parallel with the rise in dinoflagellates, increasing records of harmful algal bloom (HAB) taxa have been reported in some regions of the North Sea. Anomalously high frequencies of HABs were recorded in the late 1980s in the Norwegian coastal region and in the Skagerrak, and HABs continued to be common in the Norwegian coastal region thereafter (Figure 7.3; Edwards *et al.*, 2006a). These modifications, which could merely be a consequence of a change in the centre of the distribution of HABs, are thought to be related to regional climate change, particularly to changes in temperature, salinity, and the NAO. In Gullmar Fjord on the Swedish coast, a possible link between the occurrence of toxin-producing *Dinophysis* spp., primary production, and the NAO index was hypothesized by Belgrano *et al.*, (1999).

Warming temperatures at higher latitudes appear to be providing conditions conducive to the northward expansion of warm-water plankton and possibly some HAB species. For instance, fossil records collected over the past few thousand years have revealed increased densities of *Lingulodinium polyedrum* and species similar to toxic *Gymnodinium catenatum* during periods of relatively warm temperatures in Scandinavian waters (Dale and Nordberg, 1993; Thorsen and Dale, 1997).

Blooms of *L. polyedrum* have been described from off the Portuguese coast since the 1940s, and the toxic autotrophic dinoflagellate *G. catenatum* has been associated with upwelling events along the Iberian coast since 1976 and farther off the Portuguese coast since 1986 (Pinto, 1949; Margalef, 1956; Moita *et al.*, 1998; Amorim and Dale, 2006; Ribeiro and Amorim, 2008).

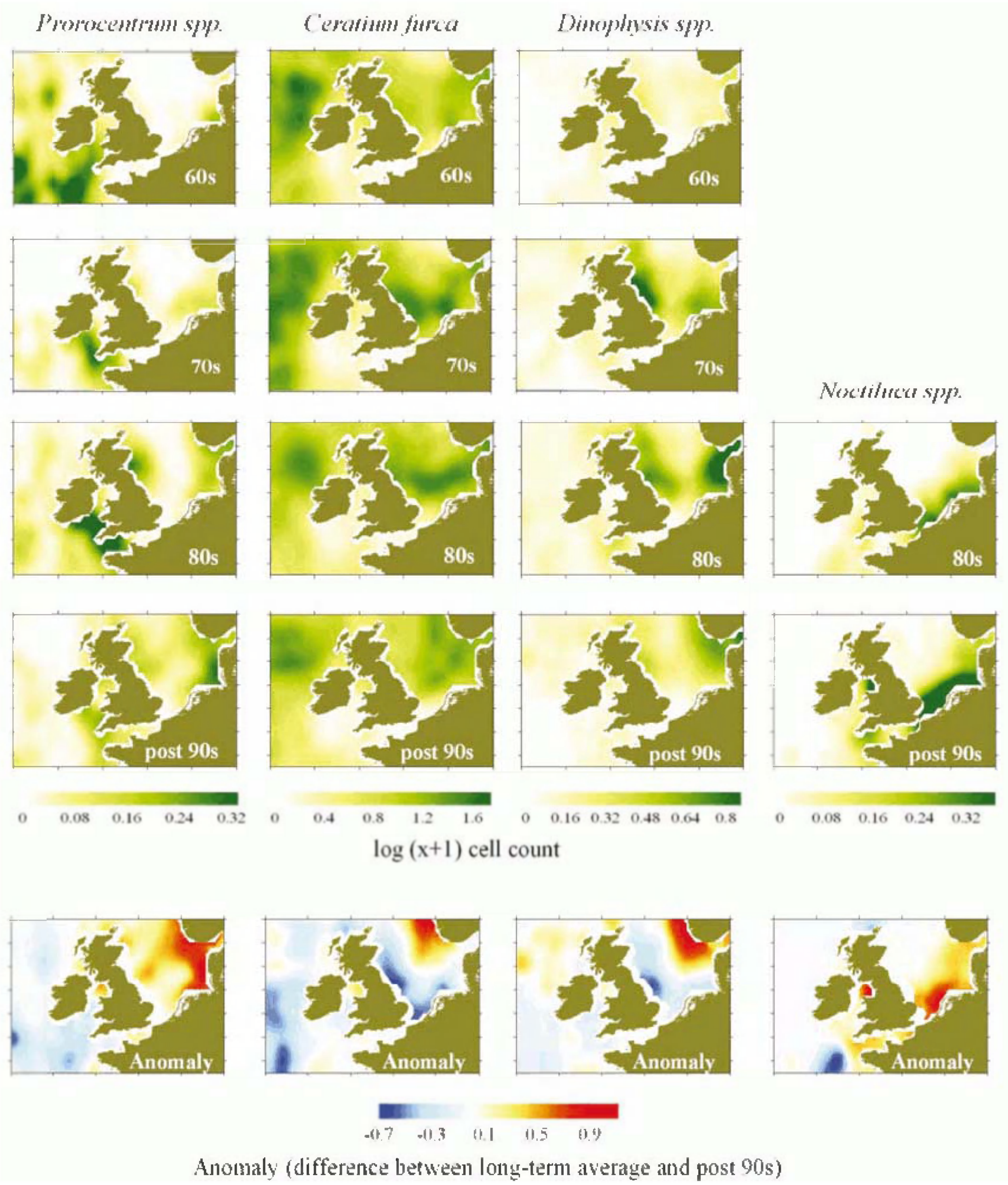

Figure 7.3. Top: mean spatial distribution of four dinoflagellate taxa in the Northeast Atlantic derived from Continuous Plankton Recorder (CPR) data. Estimated cell counts were $\log_{(x+1)}$ transformed. Bottom: anomaly maps showing the difference between the long-term mean (1960–1989) and the post-1990s period (1990–2002). Red = values above the long-term mean; blue = values below the long-term mean; white = mean values. (Source: Edwards *et al.*, 2006a.)

Within species-specific physiological limits, the metabolic and growth rates of many phytoplankton species increase with rising temperature. The balance between metabolism (respiration) and growth (via photosynthesis) may not change with increases of the order of 1–2°C, but greater changes could lead to a decline in primary production. Changes will depend on the geographical location and the type of phytoplankton species (cold- or warm-adapted). For most of the phytoplankton species in the Baltic Sea, temperature has had only a limited impact on algal growth (Dippner *et al.*, 2008), but some of the species have their own preferred temperature ranges, so that the community composition may change as temperature rises further (Wasmund, 1994). Here and elsewhere, however, direct effects of temperature will be in addition to those caused by processes contributing to stratification (Wasmund *et al.*, 1998).

Increases in the intensity and frequency of winter storms, and increased rainfall, have been predicted for certain areas of the North Atlantic as consequences of global warming (McGrath and Lynch, 2008). These conditions will lead to increases in both the depth of deep winter mixing in the ocean and in freshwater run-off, with secondary effects on phytoplankton abundance and composition. On one hand, higher freshwater run-off will increase estuarine circulation and the dilution rate of many coastal regions, thereby constraining the accumulation of biomass. Freshwater can also create a shallow surface mixed layer in which irradiance is sufficient for net production, despite the water column as a whole being turbid. On the other hand, the large amounts of dissolved organic matter (*gelbstoft*) contained in some river outflows will reduce the depth to which photosynthetically active radiation can penetrate, thus confining photosynthetic cells to an upper shallow layer and limiting primary production (Heath *et al.*, 2009). Under these circumstances, species adapted to low light will have a competitive advantage in both oceanic and coastal regions. Moreover, an earlier stratification of the water column, evidence for which has been already reported in the Northeast Atlantic (MCCIP, 2008), may advance the onset of the phytoplankton bloom in spring.

River run-off normally contains high concentrations of dissolved nutrients derived from the weathering of soils, agriculture, and other human sources. Increased precipitation may lead to eutrophication and/or an increase in contaminant loads. An increase in the number of flash floods in summer could result in a pulsed supply of nutrients to nutrient-depleted coastal water, which could influence the timing and abundance of summer phytoplankton blooms. The HABs are also often triggered by events associated with loading from local rivers after heavy rainfall (Smayda, 2006). Local wind patterns can also affect water-column stability and nutrient availability below the pycnocline. This is particularly evident in regions where upwelling occurs (e.g. off the Iberian Peninsula). Changes in the intensity and frequency of local prevailing winds will affect the amount of fresh nutrient input to the euphotic zone and new primary production. The increased warming of the sea surface and thermal stratification should mitigate against wind-mixing events, if it were not for the expected movement towards a more variable climate with more extreme weather events.

7.3.3 New or non-native species

In recent years, an increasing expansion to new areas and abundance of warm-water phytoplankton species has been reported in the Northeast Atlantic. For instance, warm-water *Ceratium* spp. (e.g. *C. hexacanthum*) has been recorded in the North Sea (Edwards and Richardson, 2004).

The non-indigenous diatom *Coscinodiscus wailesii*, originally native to the Pacific Ocean, was first reported in the English Channel in the late 1970s. This species has subsequently spread to other European shelf seas and, since the mid-1980s, has become well established and abundant in the North Sea and around the British Isles (Edwards *et al.*, 2001b; Wiltshire *et al.*, 2010).

As summarized by Dippner *et al.*, (2008), several phytoplankton species that have invaded the Baltic Sea are thermophilic (e.g. *Alexandrium minutum* and *Gymnodinium catenatum*). Large blooms of diatoms (*Cerataulina pelagica, Chaetoceros brevis, Dactyliosolen fragilissimus*) that have recently formed massive blooms in Lithuanian waters, are believed to have been introduced by warm-water inflow from the Kattegat (Hajdu *et al.*, 2006).

The first records in the North Atlantic of the Pacific subpolar diatom *Neodenticula seminae* have been related to the melting of sea ice in the Arctic caused by climate warming. This species was first found in CPR samples from the central Irminger Sea south of Greenland during spring, following the ice-free period in 1998 (Reid *et al.*, 2007). The progressive spread of *N. seminae* in the Northwest Atlantic was confirmed by the presence of large numbers in the Gulf of St Lawrence in 2001 (Starr *et al.*, 2002).

Although many studies increasingly report new occurrences of species of non-native dinoflagellates (including some that are potentially harmful) and diatoms, it has been argued that they are cosmopolitan species that have been misidentified in the past (Goméz, 2008).

7.4 Changes in zooplankton

7.4.1 Distribution and abundance

Hydrographic variability in the North Atlantic has been related to changes in the population dynamics of key zooplankton species. Several studies have noted changes in the distribution of relatively large copepods (e.g. *Calanus* spp.) that have had an important effect on total zooplankton abundance and biomass. For example, the abundance of the cold-water species *C. finmarchicus*, a key component of the planktonic ecosystem of the North Atlantic, has changed in several regions since the 1950s, and this has been associated with increases in sea temperature (Planque and Fromentin, 1996; Pershing *et al.*, 2004).

The decrease in *C. finmarchicus* in the North Sea over recent decades has led to a significant reduction in total zooplankton standing stock, namely 70% in total biomass between the 1960s and post-1990s (Edwards *et al.*, 2006b, 2007). In the Northwest Atlantic, changes in the circulation patterns of slope water in the 1990s led to an apparent decrease in the abundance of *C. finmarchicus* and in zooplankton biomass in the Gulf of Maine and on Georges Bank (Greene and Pershing, 2003), although *C. finmarchicus* abundance increased again in the 2000s (Pershing *et al.*, 2010).

In the North Sea, warmer temperature conditions and increased phytoplankton abundance earlier in the year since the late 1980s have been accompanied by an increasing abundance of meroplankton (i.e. temporary planktonic larvae of benthic species), particularly echinoderm larvae, which may now control the trophodynamics of the pelagic ecosystem by competitive exclusion of the holozooplankton (i.e. permanent planktonic species; Kirby *et al.*, 2007). This change in foodweb structure may have had an important effect by rerouting energy flow from the pelagic ecosystem to the benthos.

Dippner *et al.* (2008) have reviewed climatic and environmental effects on mesozooplankton based on long-term observations in the Baltic Sea. Salinity, eutrophication, temperature, predation by pelagic fish, and non-indigenous planktonic invertebrates are all considered to have contributed to changes in zooplankton abundance. These and other authors have concluded that expected future increases in water temperature will have a secondary effect on mesozooplankton standing stock, mostly affecting winter survival and summer growth/reproduction (Viitasalo *et al.*, 1995; Möllmann *et al.*, 2000, 2005; Dippner *et al.*, 2001).

Data collected during the ICES-coordinated surveys in the Norwegian Sea, which have been conducted annually in May since 1995, have demonstrated a progressive reduction (by 80%) in zooplankton biomass since 2002, especially in Atlantic waters, which is probably related to hydrographic variability (Figure 7.4). In this region, the average biomass of zooplankton in Atlantic waters in May was formerly significantly correlated with the average NAO for the March–April period in the previous year, but the relationship broke down in 2003 (Figure 7.4). It has been suggested that the drop in zooplankton biomass in the Norwegian Sea may be the consequence of higher predation pressure, because the planktivorous fish stock abundance has increased markedly in recent years in that region, although no clear conclusion has been drawn as yet (ICES, 2010a).

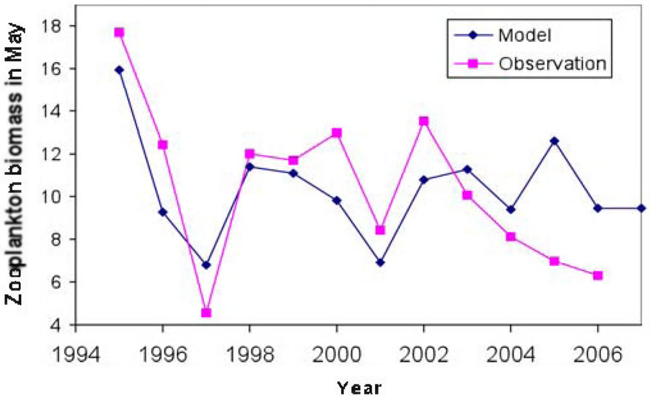

Figure 7.4. Observed and modelled zooplankton biomass (dry weight, g m^{-2}) in May for the upper 200 m of the Atlantic sector of the Norwegian Sea. Model: biomass ($year_{n+1}$)=2.3*NAO$year_n$+10.1; $r^2 = 0.44$, $p = 0.02$. (Source: Melle, 2008.)

Other studies confirm a connection between hydrographic variability and plankton in different subregions of the Nordic seas. For instance, the zooplankton biomass north of Iceland is influenced by the inflow of warm Atlantic Water into the area. Thus, in warm years, when the flow of higher salinity Atlantic Water onto the northern shelf is enhanced, the zooplankton biomass can be almost twice as high as in cold years, when this inflow is not as evident (Astthorsson and Gislason, 1995). This is probably related to better feeding conditions for the zooplankton, not only because of higher levels of primary production in warm years, but also because the incoming Atlantic waters have higher levels of zooplankton. There is a marked year-to-year variability in the community structure of zooplankton in the waters around Iceland, which again is largely determined by hydrography (Gislason *et al.*, 2009). In the Barents Sea, both field studies (Dalpadado *et al.*, 2003) and simulation exercises (Ellingsen *et al.*, 2008) demonstrated an increase in zooplankton productivity with increasing temperature.

Variability has also been observed in the plankton over the shelf and in open-ocean regions of the Northwest Atlantic. The Scotian and Newfoundland shelf regions are influenced by the outflow of water from the Arctic, whose contribution to the total flux increased in the 1990s. This change probably contributed to increased stratification in the water column, earlier and more intensive phytoplankton blooms, and changes in the zooplankton community. For example, although the abundance of the boreal–temperate species *C. finmarchicus* decreased on the Newfoundland Shelf, two species of Arctic *Calanus* (*C. glacialis* and *C. hyperboreus*), which had previously been relatively rare, increased in numbers in the 1990s and remained abundant in the 2000s. In the Northwest Atlantic Subpolar Gyre, temperature may have had a more direct effect, contributing, in recent years, to increased levels of phytoplankton and primary production (via increased stratification), and to increased production/survival of young *Calanus* copepodites and small copepods (Head and Pepin, 2007, 2010). In contrast, over the North Atlantic as a whole, Reygondeau and Beaugrand (2011) have demonstrated that the frequency of occurrence of *C. finmarchicus* (particularly early copepodites) decreases with increasing stratification.

There are indications that pelagic cnidarians and ctenophores (i.e. gelatinous zooplankton predators, or "jellyfish") have increased in abundance throughout the world in recent years (Mills, 2001). Jellyfish outbreaks appear to be more frequent (Purcell *et al.*, 2007), although much uncertainty surrounds the issue because of the scarcity of reliable baseline data. Many species of jellyfish are difficult to sample and to culture; consequently, there is a lack of information concerning their ecological impact on zooplankton communities and especially on fish larvae. An increase in the frequency of occurrence of some jellyfish has been related to hydroclimatic changes in the Northeast Atlantic during the last decade (Lynam *et al.*, 2004; Attrill *et al.*, 2007). Such increases are not limited to shelf areas but have also been observed in oceanic waters (Figure 7.5; Gibbons and Richardson, 2009; Licandro *et al.*, 2010). Notwithstanding our still limited understanding, increasing temperature appears to be one of the main triggering mechanisms for exceptional outbreaks of these gelatinous carnivores (CIESM, 2001; Purcell, 2005). The timing of jellyfish seasonal peaks over the shelf and in oceanic waters appears to be regulated by temperature rather than food (Gibbons and Richardson, 2009), which may explain why swarms of warm-temperate species have been observed more frequently in the Northeast Atlantic in recent years (Licandro *et al.*, 2010). Improved and systematic monitoring of marine and coastal areas for jellyfish needs to be implemented in order to obtain a comprehensive overview of their spatial, vertical, and temporal distribution.

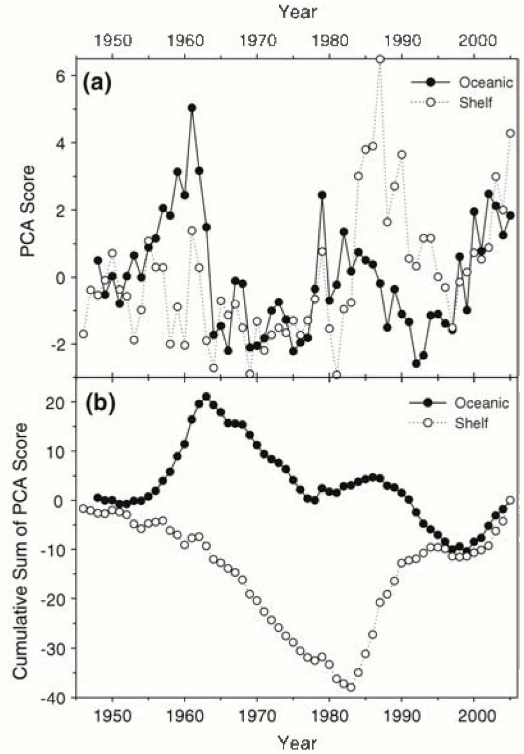

Figure 7.5. (a) First principal components of interannual variation in oceanic and shelf jellyfish from 1946 to 2005 derived from Continuous Plankton Recorder (CPR) data. (b) Cumulative sums of (a), highlighting the major step changes in the time-series. (Source: Gibbons and Richardson, 2009.)

7.4.2 Community structure

Pronounced biogeographic shifts or translocations have been recorded for zooplankton species over the entire North Atlantic by means of CPR sampling. These have been attributed to increasing regional sea temperatures. Calanoid species with warmer-water affinities have moved north by as much as 10° latitude in the Northeast Atlantic over the past few decades, and northward movement has continued to the present (Figure 7.6; Beaugrand, 2005; Edwards *et al.*, 2006b; Beaugrand *et al.*, 2009). In some North Atlantic regions, latitudinal changes have led to an increase in zooplankton diversity and parallel reductions in the mean size of the dominant zooplankton species (Beaugrand *et al.*, 2010).

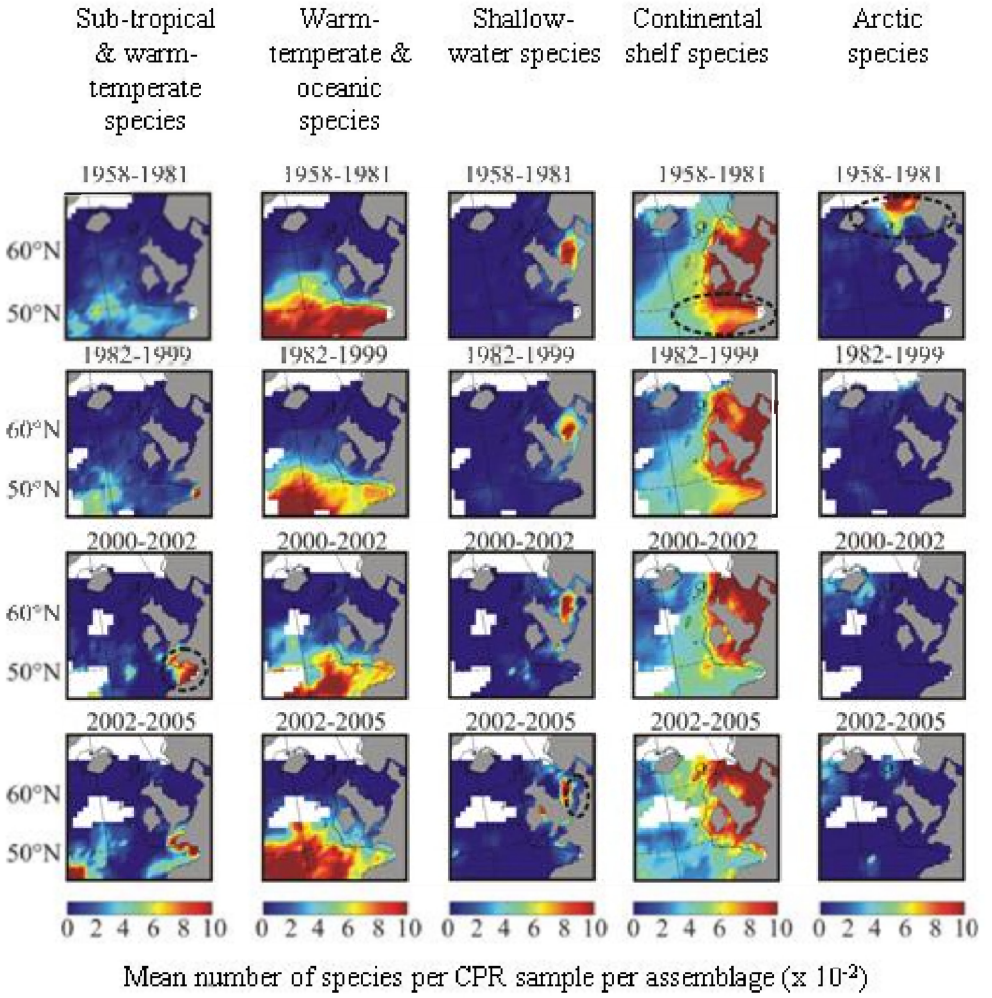

Figure 7.6. Maps showing biogeographic shifts of calanoid copepod communities in recent decades based on Continuous Plankton Recorder (CPR) data, with warm-water species shifting north by more than 10° of latitude and cold-water species retracting to the north. (Source: Beaugrand *et al.*, 2009.)

Examples of warm-water species/groups that have undergone changes in distribution include: increasing densities of *Calanus helgolandicus* in the North Sea and Bay of Biscay (Bonnet *et al.*, 2005; Helaouët and Beaugrand, 2007); the positive relationship between temperature and change in the abundance of *Centropages typicus* in the seas around the UK (Beaugrand *et al.*, 2007); the increase in species richness related to warmer waters in the western English Channel (Eloire *et al.*, 2010); and the northward shift of *Temora stylifera* into the Bay of Biscay (Figure 7.7; Valdés *et al.*, 2007) and of *Penilia avirostris* into the North Sea (Johns *et al.*, 2005). In Fram Strait (west of

Spitsbergen), northward shifts of the Atlantic hyperiid amphipods *Themisto abyssorum* and *T. compressa* have been observed since 2000, and are thought to be related to the increased influence of warm Atlantic waters (Kraft *et al.*, 2010). Euphausiids form a significant part of the zooplankton biomass in the North Atlantic, where they may play an important role as conveyors of energy between trophic levels. In the Barents Sea, euphausiid biomass (mainly *Thysanoessa inermis* and *T. raschii*) has increased since 2000, probably as a result of the recent warming, which provides favourable conditions for growth and survival of these species (Eriksen and Dalpadado, In press).

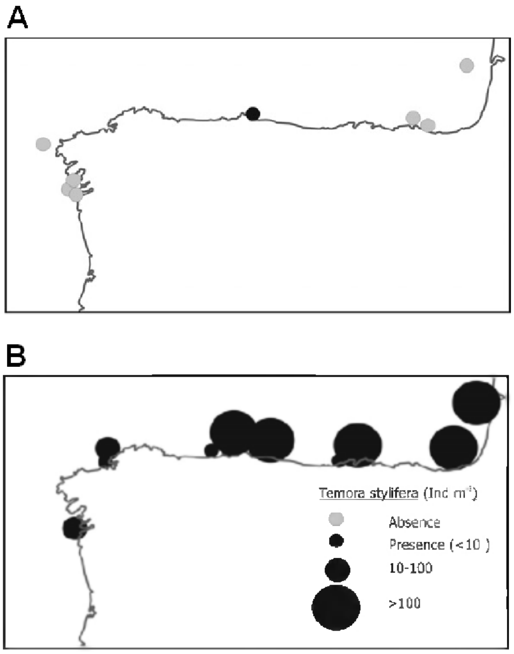

Figure 7.7. Abundance of the warm-water calanoid copepod *Temora stylifera* in transects off Vigo, Coruña, and Santander: (a) before 1982 and b) after 1982 (sampling by the Radiales project). Based on historical monitoring in the North–Northwest Iberian peninsula, *T. stylifera* was absent before 1978. Since the first record in the Cantabrian Sea in 1980, this species has become progressively more abundant in the Santander region, and a marked increase has been observed since the mid-1990s (Valdés *et al.*, 2007).

In the Baltic Sea, changes in temperature have had their greatest effect on organisms living in near-surface waters (Möllmann *et al.*, 2000, 2003, 2005), whereas those located deeper in the water column have been mostly affected by changes in salinity (Hansen, F., *et al.*, 2006). As a consequence, projected longer periods of higher water temperature and lower salinity during summer may strongly influence the pelagic foodweb, benefiting the growth of cladocerans, rotifers, and copepods, such as *Acartia* spp. (Viitasalo *et al.*, 1995; Möllmann *et al.*, 2000). In winter, higher temperatures may affect the survival of overwintering resting stages of copepods, cladocerans, and rotifers in sediment.

On the western side of the North Atlantic basin, in contrast to the Northeast Atlantic, a substantial movement south of Arctic species has occurred in areas where outflow from the Arctic has increased (Head and Sameoto, 2007; Head and Pepin, 2010). For example, on the Newfoundland Shelf, the abundance of the boreal–temperate species *C. finmarchicus* decreased in the 1990s, whereas abundance of two species of Arctic *Calanus*, which had previously been rare, increased and remained relatively abundant in the early 2000s (Head and Pepin, 2010). Similarly, the Arctic hyperiid amphipod

Themisto libellula increased in abundance in the 1990s in the Gulf of St Lawrence, where it has since become an abundant, full-time resident (Harvey *et al.*, 2009).

7.4.3 New or non-native species

As mentioned in Section 7.4.2, the calanoid copepod *Temora stylifera* has been recorded moving north into the Bay of Biscay from more southern waters (Valdés *et al.*, 2007). It was only observed north of the Iberian peninsula after 1978, and it has been cited as an example of a species that has shifted its distribution as a result of global warming (Villate *et al.*, 1997).

Penilia avirostris, a marine cladoceran typically found in subtropical and Mediterranean waters, was recorded at the Helgoland Roads time-series sampling station in 1990 and has increased in CPR samples collected in the North Sea since 1999 (Johns *et al.*, 2005). The increase in abundance is thought to be caused by higher SSTs, particularly during autumn. This species may have arrived in the North Sea by northward advection of adults in warmer waters or as resting eggs in the ballast water of ships (Johns *et al.*, 2005).

The ctenophore *Mnemiopsis leidyi* is a gelatinous predator originating on the American east coast. This species is believed to have been accidentally introduced into the Black Sea in the early 1980s via the ballast water of merchant ships (Shiganova, 1998). From the Black Sea, *M. leidyi* expanded into the Azov, Marmara, Mediterranean, and Caspian seas, and it is now increasingly being found in the Baltic Sea and in coastal waters of the North Sea from Bergen to the Netherlands (Leppäkoski *et al.*, 2002; Faasse and Bayha, 2006; Javidpour *et al.*, 2006). A persistent and increasing abundance of *M. leidyi* in the Northwest Atlantic has been related to warming water temperature (Purcell, 2005).

In the Baltic Sea, the first observations of *M. leidy*i were in the southwest in October 2006 (Javidpour *et al.*, 2006). Several publications have indicated a progressive eastward spread (Javidpour *et al.*, 2006; Janas and Zgrundo, 2007; Kube *et al.*, 2007; Lehtiniemi *et al.*, 2007). It should be noted here, however, that the invasive ctenophore *Mertensia ovum* has been wrongly identified as *M. leidyi* in the northern Baltic (Gorokhova *et al.*, 2009). As pointed out by these workers, further studies using molecular techniques are needed to elucidate the extent of invasion into European waters by *M. leidyi*. As stated by Javidpour *et al.* (2006), in the particular case of the Baltic Sea, it is not yet clear whether *M. leidyi* can severely affect zooplankton and fish populations directly, by feeding on fish larvae and eggs, or indirectly by competing for zooplankton food. However, taking into account the expected increase in water temperature and the remarkable ability of this invader to double its population size in a short time, it is a matter of concern and a challenge in predicting future risks to Baltic Sea ecosystems.

Unprecedented changes in the Arctic (including increased precipitation, river discharge, glacial and sea-ice melting) related to climate warming have led to changes in the plankton populations of the Northwest Atlantic, including marked increases in the abundance of Arctic species. Thus, the Arctic hyperiid amphipod *Themisto libellula* has been recorded since the early 1990s in the Gulf of St Lawrence (Figure 7.8; Harvey and Devine, 2008), where its abundance was positively correlated with the volume of Labrador Shelf Water advected into the Gulf through the Strait of Belle Isle during winter in the early 2000s, although not since 2006. The geographic expansion of *T. libellula* coincides with observations made by Drinkwater and Gilbert (2004) that the core temperature in the cold intermediate layer in the Gulf of St Lawrence in the

1990s was, on average, the coldest seen in the previous five decades. In addition, an increased contribution of Arctic Water to the Canadian continental shelf regions and the Gulf of St Lawrence in the 1990s led to increases in the abundance of cold-water copepods, such as *C. glacialis* and *C. hyperboreus*, on the Scotian Shelf in the early 2000s (Head and Pepin, 2010). In the past few years, however, the relative importance of some of these cold-water species has diminished in some regions (e.g. *C. glacialis* off Halifax and on the Grand Banks, *T. libellula* in the lower St Lawrence Estuary, northwest Gulf of St Lawrence, and Grand Banks), perhaps as a result of warming ocean temperatures and a reduction in the volume and extent of the cold intermediate layer.

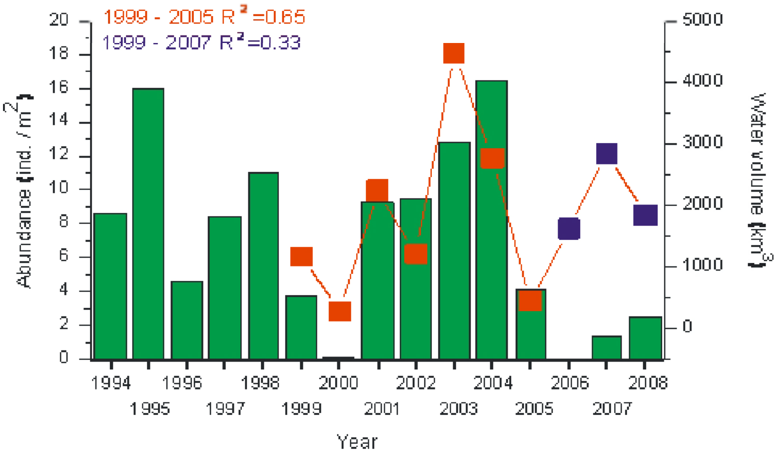

Figure 7.8. Relationship between the annual volumes of Labrador Shelf Water advected into the St Lawrence Estuary in winter (■) and the annual mean abundance of the hyperiid amphipod *Themisto libellula* (bars) in the lower St Lawrence Estuary and northwest Gulf of St Lawrence. (Source: Harvey and Devine, 2008.)

7.4.4 Phenology and life history

Climate-induced warming has triggered changes in the timing of occurrence (phenology) of many zooplankton taxa (Figure 7.9; Greve *et al.*, 2001; Edwards and Richardson, 2004; Edwards *et al.*, 2006b). The changes in phenology have varied among species, functional groups, and trophic levels, leading to potential mismatches in prey–predator relationships (Edwards and Richardson, 2004; ICES, 2006). In addition, recent investigations have demonstrated that winter temperature influences the time of spawning of some commercially important North Sea fish species, with warmer sea temperature being associated with earlier fish recruitment (Greve *et al.*, 2005).

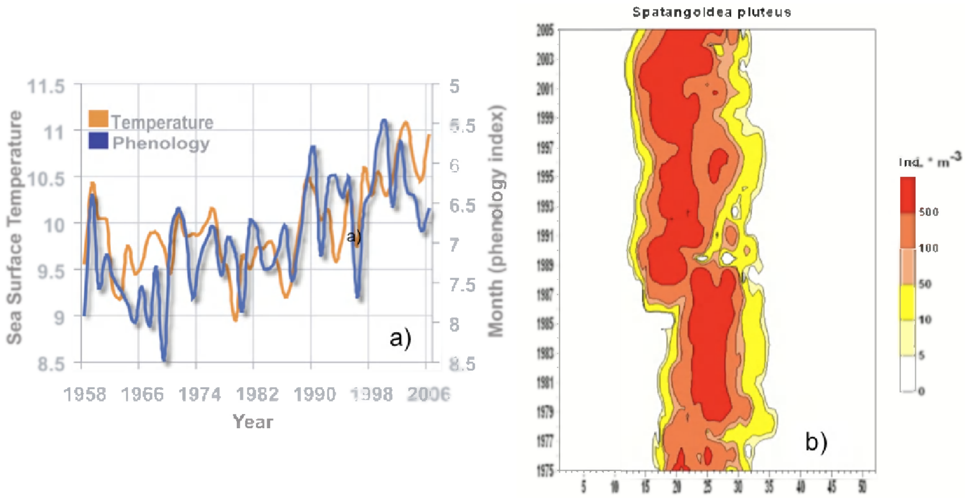

Figure 7.9. (a) Plot of the timing of the seasonal cycle (phenology) of echinoderm larvae from the Continuous Plankton Recorder (CPR) survey against sea surface temperature (SST) from 1958 to 2004, showing a close correlation between the larvae and SST (Edwards *et al.*, 2006b). (b) Contour plot showing abundance and seasonality of spatangoid plutei (i.e. echinoderm larvae) from 1975 to 2005, also showing a shift to an earlier timing. Data from the Helgoland time-series, southeastern North Sea. (Source: Greve *et al.*, 2001.)

In the central Labrador Sea, a key population centre for *Calanus finmarchicus*, there has been an increase in late winter–spring (and annual) average SST of ca. 1 °C since the mid-1990s (Figure 7.10). Over the same period, the start of the spring bloom has occurred earlier, and the percentage of young *C. finmarchicus* found during annual sampling cruises in late May has increased. The inference is that increasing temperatures and earlier blooms are leading to earlier reproduction and enhanced population development rates of *C. finmarchicus*. Future temperature increases will probably maintain this trend.

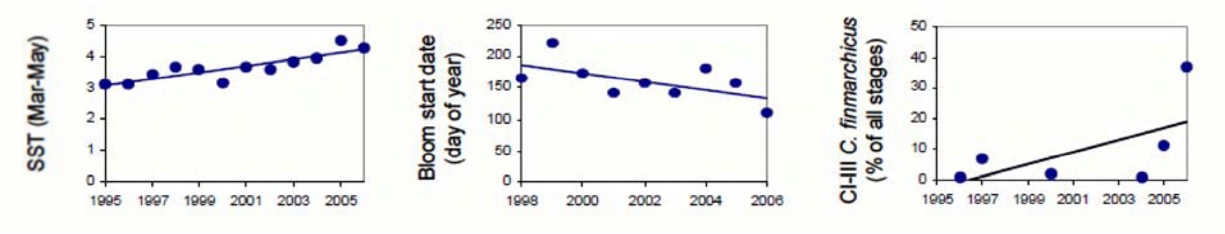

Figure 7.10. (a) Changes in late winter–spring temperatures; (b) the timing of the start of the spring bloom; and (c) the percentage of young *Calanus* (CI–CIII) present in late May in the central Labrador Sea. (Based on Department of Fisheries and Oceans (DFO), Canada time-series.)

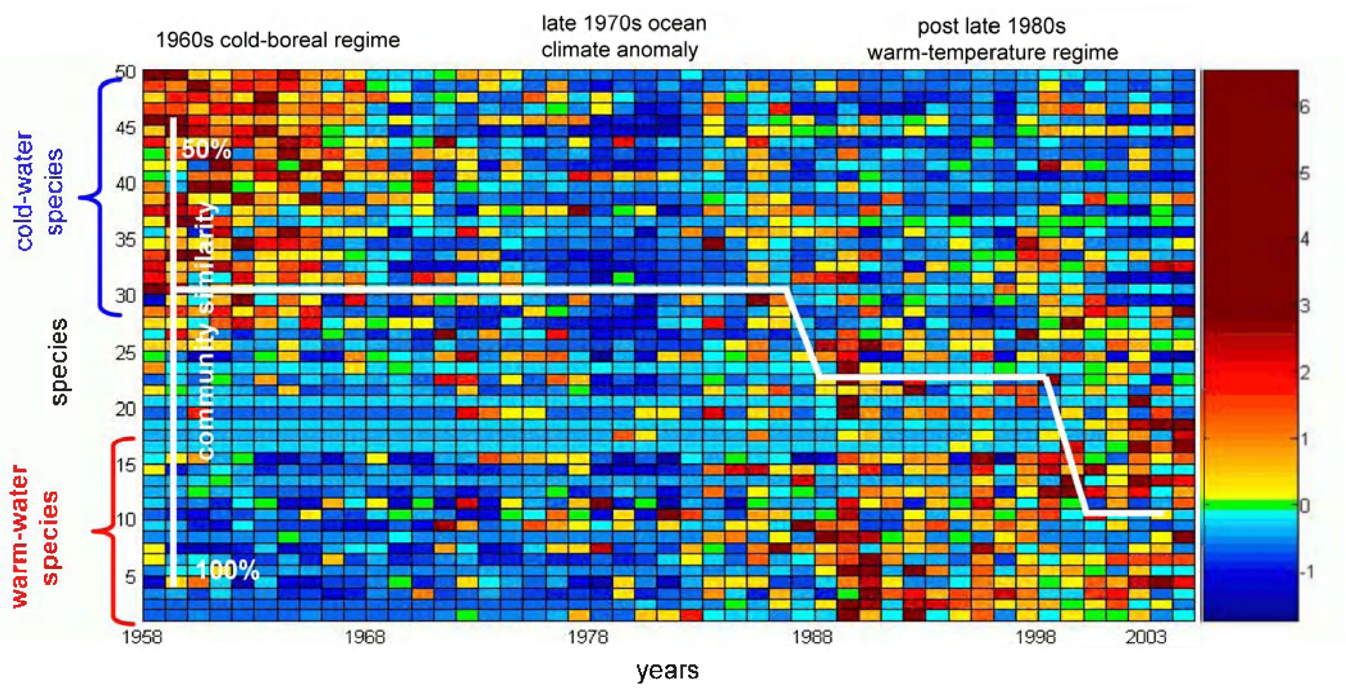

Figure 7.11. Continuous Plankton Recorder (CPR) data showing the results of a meta-analysis of 50 plankton species in the central North Sea (standardized abundance). The white line shows the community regime-shift index based on percentage similarity between 2006 and preceding years, calculated using displacement sequential regime detection (minimum regime shift = 10 years). (Modified from Edwards *et al.*, 2008.)

In the North Atlantic, substantial ecosystem changes seen across multiple trophic levels were demonstrated to be associated with temperature increases above a critical thermal boundary (Beaugrand *et al.*, 2008). This thermal threshold of 9–10 °C, if crossed, will lead to changes in community structure, biodiversity, and carrying capacity. Such changes, especially when combined with fishing, may initiate a marked reduction in some fish stocks (e.g. the North Sea cod (*Gadus morhua*) stock).

Synchronous ecological regime shifts occurred in the central Baltic and North Sea in the late 1980s (Alheit *et al.*, 2005). The NAO index changed in the late 1980s (1987–1989) from a negative to a positive phase, which may have contributed to these regime shifts. Increasing SSTs were the main direct and indirect driving forces, however. After 1987, phytoplankton biomass in both systems increased, and the growing season was prolonged. The composition of phyto- and zooplankton communities in both seas changed conspicuously; for example, dinoflagellate abundance increased and diatom abundance decreased, whereas key copepod species, which are essential in fish diets, experienced pronounced changes in biomass (abundance of *Calanus finmarchicus* in the North Sea and of *Pseudocalanus sp.* in the Central Baltic fell to low levels, whereas *C. helgolandicus* in the North Sea and *Temora longicornis* and *Acartia spp.* in the Central Baltic were persistently abundant). The changes in biomass of these copepods had important consequences for the biomass, fisheries, and landings of key fish species.

The regime shift in the Baltic Sea was evident in all trophic levels, but zooplankton and fish were especially affected (Möllmann *et al.*, 2008). A copepod community dominated by *Pseudocalanus acuspes* changed to one dominated by *Acartia* spp., which was attributed to lowered salinity and increased temperature. Although a link between hydrographic variability and changes in zooplankton and fish was recognized, it was noted that overfishing had probably amplified the climate-induced changes at both trophic levels. This study indicated that (i) climatic and anthropogenic pressures may propagate through the foodweb via multiple pathways; (ii) both effects can act synergistically to cause and stabilize regime changes; and (iii) zooplankton play a crucial role in mediating these ecosystem changes.

In the Northwest Atlantic, a regime shift occurred in the early 1990s in response to changes in the freshwater export and circulation patterns in the Arctic Ocean (Pershing *et al.*, 2004; Greene *et al.*, 2008). This regime shift was associated with a freshening and stratification of shelf waters, which in turn led to changes in the abundance and seasonal cycles of phytoplankton, zooplankton, and organisms at higher trophic levels. On the other hand, it has been suggested that removal of top predators by overfishing would alter the plankton through a cascading effect (Frank *et al.*, 2005). It is likely that the recently observed ecological responses to Arctic climate change in the North Atlantic will continue into the near future if current trends in sea ice, freshwater export, and surface ocean salinity continue.

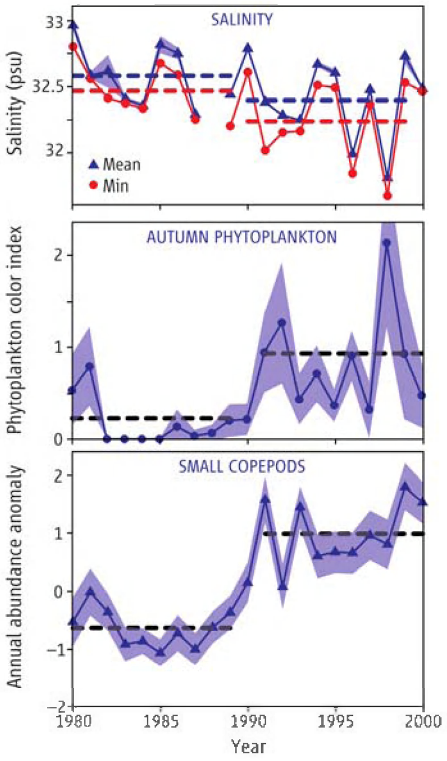

Figure 7.12. Salinity, phytoplankton, and zooplankton data from the Gulf of Maine and Georges Bank illustrate ecosystem changes associated with a regime shift. Dashed lines = mean values during 1980–1989 and 1990–1999; shaded areas = 95% confidence intervals. (a) Decadal mean salinities, based on annual mean (blue) and annual minimum (red) salinities (reported in Mountain, 2003): reduction after the regime shift. (b) Decadal mean autumn phytoplankton abundance, based on values of the annual mean Phytoplankton Colour Index (PCI; reported in Frank *et al.*, 2006): increase after the regime shift. (c) Decadal mean copepod abundance anomaly, based on the annual mean abundance of small copepods (reported in Durbin *et al.*, 2003): increase after the regime shift. (Source: Greene and Pershing, 2007.)

7.5 Effects on higher trophic levels: implications for fisheries

Given the importance of many zooplankton taxa as prey for larval and juvenile fish, the relative timing of zooplankton blooms and fish spawning is critical. This theory of the importance of trophic synchrony has been termed the "match–mismatch" hypothesis (Cushing, 1975). Climate change has the potential to alter the timing of fish spawning and egg development rates, as well as that of phytoplankton and zooplankton blooms. Thus, poor "recruitment" in traditional fishery target species, such as cod, plaice (*Pleuronectes platessa*), and herring (*Clupea harengus*), is a potential consequence of climate change.

There is evidence that the seasonal timing of phyto- and zooplankton production has altered in response to recent climate change, and that this may have influenced predator species, including fish (Edwards and Richardson, 2004; Richardson and Schoeman, 2004; ICES, 2010a). In the Northeast Atlantic, warmer conditions now prevail earlier in the year; this appears to have led to changes in plankton biomass and in the seasonal timing of plankton production, and thus to poor recruitment of several commercially important fish species and low seabird breeding success, particularly in the North Sea (Beaugrand and Reid, 2003; Beaugrand *et al.*, 2003; Frederiksen *et al.*, 2006; Payne *et al.*, 2009). In the Baltic Sea, the change in hydrography has affected the reproductive success of several fish species, resulting in a change in dominance from the piscivorous cod to the planktivorous sprat (*Sprattus sprattus*; Möllmann *et al.*, 2008). Changes in hydrological conditions influenced fish recruitment both directly (e.g. by reducing the areas of cod reproduction) and indirectly (by altering feeding conditions).

Further future warming is likely to alter the geographic distributions of primary and secondary pelagic production, with indirect effects on oxygen production, carbon sequestration, and biogeochemical cycling. Changes in pH are also inevitable, with the lowest values mainly occurring in colder waters. All of these changes may place additional stresses on already-depleted fish stocks and have consequences for dependent species, such as mammals and seabirds.

Climate-induced change could also alter the relative abundance of permanent (holoplanktonic) and temporary (meroplanktonic) zooplankton species. In the North Sea, for example, a stepwise increase in sea temperature has coincided with an increase in the abundance of phytoplankton and meroplankton (particularly the larvae of the sea urchin (*Echinocardium cordatum*)) since the late 1980s (Kirby *et al.*, 2007). This change in foodweb structure, hypothesized to be the result of the competitive exclusion of the holozooplankton by the meroplankton, may have significantly diminished the transfer of energy towards top pelagic predators (e.g. fish) and increased the transfer to the benthos.

There are indications of an increase in the occurrence of jellyfish swarms in the Northeast Atlantic (Licandro *et al.*, 2010). Jellyfish feed on the eggs and larvae of commercially important fish (Greve, 1994; Bamstedt *et al.*, 1998), so outbreaks of jellyfish may ultimately lead to a reduction in the fish biomass available to fisheries. The introduction and continued presence of the ctenophore *Mnemiopsis leidyi* in the Baltic and North seas is of concern because this non-native species has had a pronounced negative impact on ecosystems in the southern seas of Europe (Javidpour *et al.*, 2006). The distribution pattern of *M. leidyi* in the Bornholm Basin has a substantial overlap with that of cod eggs. Predation of *M. leidyi* on cod eggs has the potential to alter recruitment success in this species, which is the top predator in the system, and thus to change the foodweb structure of the Baltic (Haslob *et al.*, 2007).

Although most studies demonstrate that hydrographic variability is the main factor controlling long-term changes in the plankton, recent research has suggested that removal of top predators from an ecosystem may also affect the trophic levels below by what is known as a "trophic cascade". Studies in both the eastern and western North Atlantic suggest that climate and fishing may have synergistic effects on the community composition and abundance of phytoplankton, zooplankton, and fish (Frank *et al.*, 2005; Casini *et al.*, 2008; Baum and Worm, 2009; Kirby *et al.*, 2009).

7.6 Conclusions

- An analysis of plankton time-series reveals that, in the North Atlantic, important changes have occurred in the abundance, distribution, community structure, and population dynamics of phytoplankton and zooplankton.
- These planktonic events appear to be responding to changes in regional climate, caused predominately by the warming of air and SSTs, and associated changes in hydrodynamics. Anthropogenic pressures (e.g. fishing) may also affect the community composition and abundance of plankton and may act synergistically with the climate.
- Changes in phytoplankton and zooplankton communities at the bottom of the marine pelagic foodweb may affect higher trophic levels (e.g. fish, seabirds), because the synchrony between predator and prey (match–mismatch) plays an important role (bottom–up control of the marine pelagic environment) in the successful recruitment of top predators, such as fish, seabirds, and mammals.
- The poor recruitment of several fish species of commercial interest and the low seabird breeding productivity recorded in recent years in some North Atlantic regions are associated with changes in plankton biomass and in the seasonal timing of plankton production.

7.6.1 Recommendations

- Long-term funding needs to be guaranteed in order to maintain the few time-series that exist at single sites and along transects, and to expand the CPR survey to cover unsampled and poorly sampled areas in the North Atlantic.
- Improved and systematic monitoring of jellyfish in coastal and offshore areas needs to be implemented in order to obtain a comprehensive overview of their spatial, vertical, and temporal distribution.
- Zooplankton should be included as a mandatory biological variable in the management of marine resources in different North Atlantic regions. In particular, abundance, biodiversity, and population dynamics (e.g. phenology) of zooplankton, as well as species that act as indicators of ecological status, should be monitored regularly.
- Anthropogenic activities (e.g. fishing) combined with climatic effects may put additional pressure on marine ecosystems. This possibility should be considered in the management of marine resources.

Acknowledgements

We thank the members of the ICES/IOC working groups on Zooplankton Ecology (WGZE) and Harmful Algal Bloom Dynamics (WGHAB) for assistance in preparing this report. Thanks are also due to A. Amorim and B. Dale for their helpful suggestions.

8 Responses of marine benthos to climate change

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8.1 Introduction

Benthic communities are especially suited for long-term comparative investigations because many of the constituent species are sessile or have low mobility, are relatively long–lived, and integrate the effects of environmental change over time (e.g. dredged material, organic enrichment, aggregate extraction, and climate change; Rachor, 1990; Frid *et al.*, 1999; Birchenough *et al.*, 2006; Rees *et al.*, 2006; Foden *et al.*, 2009; Birchenough *et al.*, 2010). Furthermore, the macrobenthos has an important functional role in the reworking of sediments (i.e. bioturbation and bio-irrigation activities), provides nutrients/food to other higher trophic groups, and also creates habitats through habitat-engineering species (Figure 8.1; e.g. Tsuchiya and Nishihira, 1986; Ragnarsson and Raffaelli, 1999; Callaway, 2006; Hendrick and Foster-Smith, 2006; Van Hoey *et al.*, 2008).

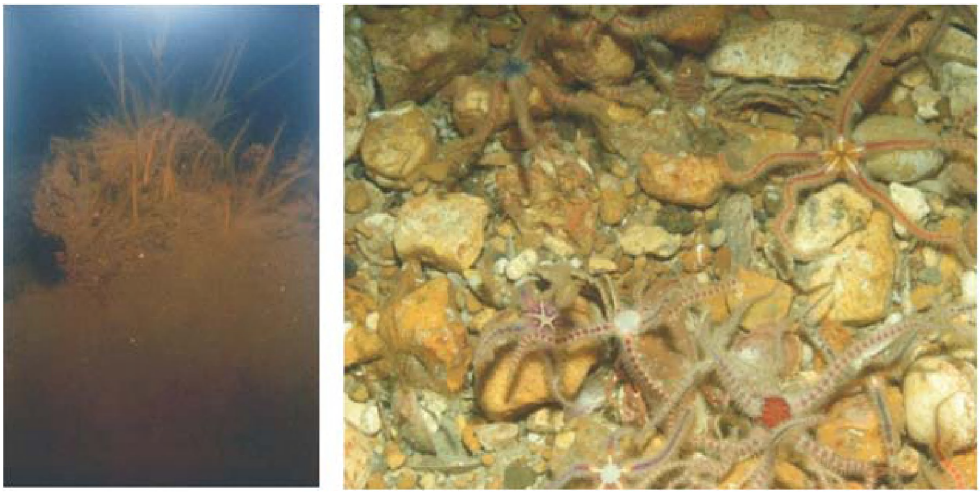

Figure 8.1. Examples of different benthic habitat types: (left) image of reefs formed by the tube polychaete *Sabellaria spinulosa* collected with Sediment Profile Imagery (SPI), and (right) photo of *Ophiothrix fragilis* beds over coarse substratum. Images are used to show the different types of benthic habitat with high levels of biodiversity in marine ecosystems. (Images courtesy of Cefas.)

Descriptions of benthic variability and its relation to climate change and other effects are subjects that are still evolving as more evidence and time-series observations become available. Climate change may modify population dynamics over time and space, phenology, and the geographical distribution of communities (and species; Dulvy *et al.*, 2008). These modifications could result in habitat loss and species extinctions over time, with repercussions for biogeochemical fluxes, ecosystem functioning, and biodiversity.

The need to assess and monitor benthic changes in relation to a wide range of stressors, including climate change, has prompted researchers to collect information over a long time-scale. Long-term studies of the macrobenthos have been carried out at a number of sites in the ICES region over the past 100 years (ICES, 2009a). For the eastern Atlantic, these sites include the North Sea (Rees *et al.*, 2002), western English Channel (Southward *et al.*, 1995, 2005), Bay of Biscay (Alcock, 2003), Bristol Channel (Henderson *et al.*, 2006) and the Wadden Sea (Beukema, 1992; Beukema *et al.*, 2009), and, for the western Atlantic, Chesapeake Bay (Seitz *et al.*, 2009) and Boston Harbor (Diaz *et al.*, 2008).

Assessment of effects over larger areas (i.e. the North Sea) in relation to climate change is based on localized studies, with some exceptions (e.g. Bay of Biscay and the UK; Alcock, 2003). Efforts to document the status and change of the benthos have involved collaboration, via ICES, in a number of initiatives: the North Sea Benthos Project (NSBP), Benthic Ecology Working Group (BEWG) and Study Group on Climate-related Benthic Processes in the North Sea (SGCBNS). These collaborative projects have allowed scientists to assess the structure and dynamics of the benthic assemblages inhabiting the North Sea between the 1980s and 2000s.

Current requirements under international legislation (Water Framework Directive (WFD), Habitats and Bird Directives, EU Marine Strategy Framework Directive (MSFD), US Clean Water Act (CWA), US Oceans Act, etc.) focus on the quality and status of the marine environment (see Borja *et al.*, 2008, 2010, for an overview). However, under the new MSFD, climate change is included under Descriptor 1. Possible effects are, at present, an unquantified pressure on species and ecosystems. Little is known about the robustness and sensitivity of the proposed "Good Environmental Status" (GES) descriptors that will be used to support future assessments (see also additional information provided in Borja *et al.*, In press). Benthic systems have been studied by employing a suite of indices as tools to characterize community status (e.g. Borja *et al.*, 2000; Rosenberg *et al.*, 2004; Muxika *et al.*, 2007). Although there is merit in these approaches, there is still a need to fully understand the function and mechanisms that are altering these processes; such studies will lead to a better knowledge of benthic responses and a more targeted tool for the environmental management of marine systems (Birchenough *et al.*, In press).

Climate change and variation could affect all components of marine and coastal ecosystems, including habitats, benthos, plankton, fish, mammals, seabirds, and the presence of non-native species. Such effects have implications for physiological responses, biogeochemical processes, and higher trophic groups, with repercussion for overall ecosystem biodiversity and function. Some examples of complex interactions within the benthic–pelagic environment in relation to climate change are summarized in a conceptual model (Figure 8.2). The model illustrates the complex linkages between various environmental factors (effects of storms, sea-level rise, turbidity, currents, stratification, and salinity) and biotic effects (e.g. benthos and pelagic systems). The left panel shows the influence of increased CO_2 and temperature, and how these factors could directly affect biotic and abiotic components.

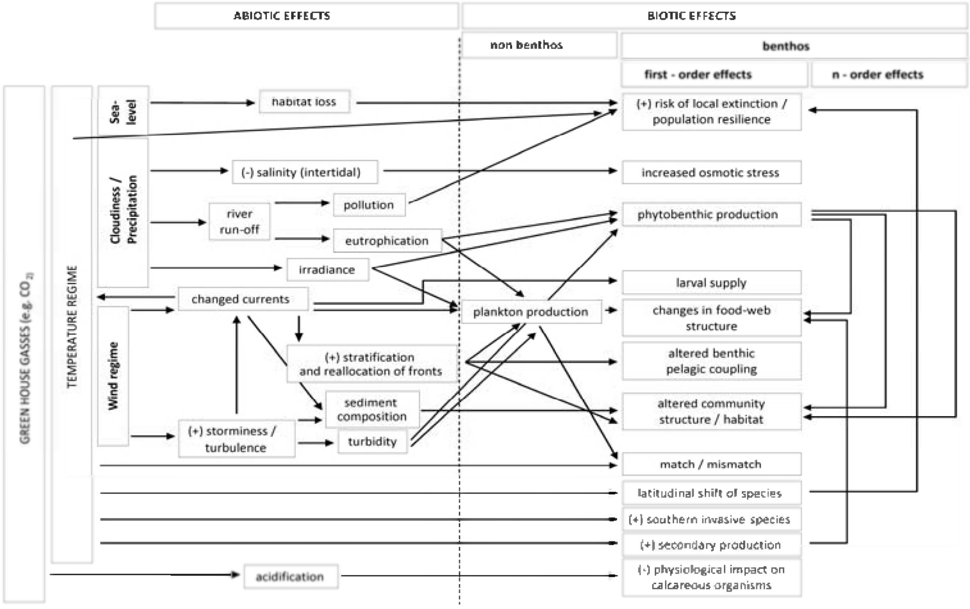

Figure 8.2. Conceptual diagram of the effects of climate change and benthic interactions (taken from ICES, 2008b), illustrating the influence of increased CO_2 and temperature (left panel) and how these factors could directly affect biotic and abiotic components (Further explanation is provided in the text.)

8.2 The impacts of climate change on the benthos

This review attempts to provide an assessment of the effects and mechanisms causing changes to the benthos (benthos, by definition, encompasses all organisms living in or on the seabed; epifauna, and infauna), which may be interlinked with climate change. It also reports on the current peer-reviewed literature and considers areas where research gaps exist.

Direct evidence of climate-change-related impacts on the marine benthos is still largely lacking, but information from other research areas, relevant in a context of climate change and variability, provides circumstantial evidence of climate-change effects. In the following sections, three main issues are addressed:

i) **The relationship between physical aspects of climate change and the marine benthos (Section 8.3).** This investigation focuses on (i) responses to changes in seawater temperature (biogeographic shifts, phenology, parasites); (ii) altered hydrodynamics; (iii) ocean acidification; and (iv) sea-level rise–coastal squeeze (Figure 8.2).

ii) **The possible integrated impact of climate change on the benthos, based on relationships with proxies for climate variability (Section 8.4).** Lessons learned from the relationship between the North Atlantic Oscillation (NAO) index, as a proxy for climate variability, and the marine benthos provide further insight into the possible integrated impact of climate change on the benthos.

iii) **The interaction between climate-change- and human-activity-induced impacts on the marine benthos (Section 8.5).** As climate change may also modify human activities in the marine environment, indirect effects on the benthos are also to be expected. This section details interactions between climate change and impacts induced by human activities.

8.3 Physical aspects of climate change and marine benthos

8.3.1 Change in seawater temperature

8.3.1.1 Latitudinal distribution shifts

Biogeographic studies dating back to the 1700s have long established a link between the distribution of marine species and mean sea surface isotherms (e.g. Van den Hoek, 1982; Breeman, 1988); a change in the latitudinal distribution of species might be expected when the temperature of the oceans increases. Distribution shifts of marine species in the Northeast Atlantic – possibly linked to temperature change – have been found for several components of the ecosystem: fish (e.g. O'Brien *et al.*, 2000; Perry *et al.*, 2005; Poulard and Blanchard, 2005; Rose, 2005), phytoplankton (e.g. Beaugrand *et al.*, 2008; Leterme *et al.*, 2008), zooplankton (e.g. Lindley *et al.*, 1995; Pitois and Fox, 2006; Beaugrand, 2009), and benthos (e.g. Southward *et al.*, 2004; Eggleton *et al.*, 2007).

The relationship between temperature change and modifications to the distribution of species is, however, complicated by the effects of other environmental parameters, physical barriers to movement, and human usage of the coastal zone. Differences in life cycles, dispersal ability, and habitat connectivity may also influence the vectors of spread or retreat of coastal benthic species. All of these factors complicate the process of attributing causal mechanisms and may result in the actual distribution lying within the potential range of a species. As such, between 1986 and 2000, some evidence of change in the distribution of North Sea benthic species was detected that may be attributable to natural variation in the recruitment process of relatively short-lived species; however, there was little indication of a consistent directional trend that could be linked to temperature change (Eggleton *et al.*, 2007).

To date, clear evidence of change in the distribution and abundance of benthic species in response to temperature change has been recorded in the North Atlantic (Alcock, 2003; Southward *et al.*, 2004; Beukema *et al.*, 2009; Jones *et al.*, 2010; Wiltshire *et al.*, 2010). Most changes are initially observed at the edge of ranges, where organisms are more likely to be physiologically stressed, but there is also evidence of local and regional heterogeneity within biogeographic ranges, with infilling of gaps or loss of site occupancy away from range limits. Living close to their physiological tolerance limits, being sessile or sedentary, having typically short lifespans, and being from lower trophic levels, intertidal organisms have demonstrated some of the fastest responses to climate change.

As such, a strong climatic signal is observed in the relative abundance of the co-occurring intertidal Lusitanian barnacles *Chthamalus montagui* and *Chthamalus stellatus*, and the Boreal species *Semibalanus balanoides* over the past 50 years in the UK. Numbers of *S. balanoides*, the dominant competitor, increased during cooler periods but have declined significantly as temperatures have increased in recent years (Poloczanska *et al.*, 2008). The southern range limit of *S. balanoides* has also shifted north within the Bay of Biscay (Wethey and Woodin, 2008), whereas the northern range edges of the chthamalids have extended to Scotland (Mieszkowska *et al.*, 2006). Models based on a 50-year time-series forecast a total disappearance of *S. balanoides* from shores in southwest England by 2050 (Poloczanska *et al.*, 2008). Similarly, latitudinal shifts were observed in two intertidal and shallow subtidal barnacle species: *Solidobalanus fallax*, a West African warm-water species, not known from the European coasts until 1994 (Southward, 1998), has extended its range along the English Channel in recent decades (Southward *et al.*, 2004); *Balanus perforatus*, a

Lusitanian species, has extended its range through the eastern English Channel (Herbert *et al.*, 2003) and has now also expanded into the southern North Sea (Kerckhof, 2002; Kerckhof *et al.*, 2009). Hence, many changes in northern Europe have occurred in the breakpoint region between cooler Boreal waters to the north and warmer Lusitanian waters to the south, where many species reach their distributional limits and congeneric species from different provinces co-occur (see Alcock, 2003, for the Northeast Atlantic).

Other examples of intertidal, hard-substratum fauna distribution changes linked to changes in temperature include: the gastropods *Osilinus lineatus* (Mieszkowska *et al.*, 2006., 2007), *Gibbula umbilicalis* (Kendall, 1985; Kendall and Lewis, 1986; Mieszkowska *et al.*, 2006, 2007) and *Testudinalis* spp. (Mieszkowska *et al.*, 2006), as well as the blue mussel (*Mytilus edulis*; Europe: Berge *et al.* 2005; US Atlantic: Jones *et al.*, 2010). An example of infilling within a biogeographic range is observed for the Lusitanian intertidal, hard-substratum limpet *Patella rustica*, which has colonized a break in the distribution in northern Portugal during a period of warmer sea temperatures caused by a possible climate-driven reduction in upwelling in the southern Biscay region and a weakening of the western Iberian Shelf Current (Lima *et al.*, 2007). In fact, rates of change of up to 50 km decade^{-1} are much greater than the average rate of range-edge shift of 6.1 km decade^{-1} documented for terrestrial species (Parmesan and Yohe, 2003), but an order of magnitude less than those seen in plankton in the Northeast Atlantic and North Sea (Beaugrand and Reid, 2003). These different rates may arise from the difference in the degree of connectivity between pelagic, benthic, and terrestrial systems.

Though less well documented, examples of changes in geographic distribution because of temperature change also exist for subtidal, soft-substratum organisms. For example, several Lusitanian benthic species, such as the decapods *Diogenes pugilator*, *Goneplax rhomboides*, and *Liocarcinus vernalis*, have extended their range farther into the North Sea during recent decades. These southern species tend to thrive off the Belgian coast during warmer years (e.g. Laporte *et al.*, 1985; d'Udekem d'Acoz, 1991; 1997; Doeksen, 2003), but have now extended their range farther north into Dutch and German waters (e.g. Doeksen, 2003; Franke and Gutow, 2004; Van Peursen, 2008; Neumann *et al.*, 2010). Since Barnett (1972) demonstrated that the gastropod *Nassarius reticulatus* has an earlier and faster development in warmer waters, the sudden appearance of this species in the 1980s (e.g. Craeymeersch and Rietveld, 2005) can also be attributed to the temperature increase in coastal waters.

A change in the geographic distribution of habitat-forming or habitat-engineering species, such as various macroalgae (Vance, 2004; Mieszkowska *et al.*, 2006), by definition, means a change in habitat type, and hence assemblage and functioning (M. T. Burrows, pers. comm.). It might, as such, have important consequences for the ecosystem goods and services provided to mankind.

A shift in the distribution of species might also trigger a change in species richness in certain areas. As a consequence of the greater benthic species richness in southern waters of northwest Europe compared with those to the north, an increase in species richness is to be expected in the North Sea as the climate warms: namely, more species will probably enter the area from the south than will leave it to the north (Hawkins *et al.*, 2009; Beukema and Dekker, In press).

8.3.1.2 Phenology

Phenology is the study of periodic recurring life-cycle events of species and how they are influenced by changes in climate regime. These life-cycle events include (i) reproductive output, (ii) larval transport and settlement, and (iii) recruitment and post-recruitment development of benthic organisms. Recruitment and development play important roles in benthic community structure, diversity, and functioning. A variety of biotic and abiotic factors modulate these life-cycle processes, of which some are direct (e.g. physiological responses) and others are more indirect (e.g. changes in trophic interactions), and are likely to be influenced by climate change.

Many macrobenthic organisms have pelagic larvae and are planktonic (meroplankton) for a short time during their life cycle. Studying the timing of these recurring life-cycle events and how they are influenced by seasonal and interannual variability (phenology) may reveal sensitive indicators of the effects of climate change. Indeed, recent studies have revealed that meroplankton are more sensitive to increases in sea temperature than holoplankton. Edwards and Richardson (2004) demonstrated that the timing of the seasonal peak of meroplankton occurred 27 days earlier (echinoderm larvae 47 days) in the North Atlantic, based on a 45-year study period (Figure 8.3; see also Lindley *et al.*, 1993). The abundance of meroplankton also changed, revealing an increase in decapod and echinoderm larvae and a decrease in bivalve larvae caused by rising sea surface temperature (SST) in the North Sea from 1958 to 2005 (Kirby *et al.*, 2008). Similar changes were also found for holoplankton and fish larvae (e.g. Southward *et al.*, 1995; Lindley and Batten, 2002; Greve *et al.*, 2005).

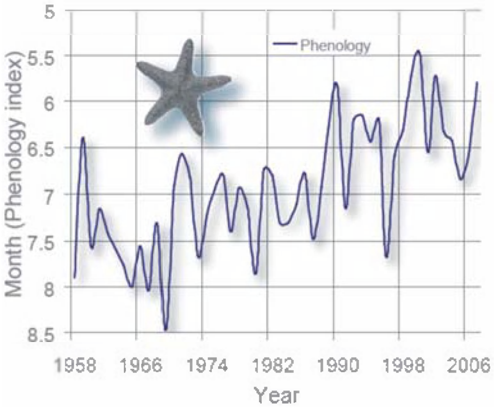

Figure 8.3. Interannual variability in the peak seasonal development of echinoderm larvae (an indicator of plankton phenology) in the North Sea. The general trend through time is towards an earlier seasonal cycle (Source: Edwards *et al.*, 2009).

Changes in temperature may directly influence mortality, reproduction, onset of spawning, and the embryonic and gonad development of benthic species, and thus may change phenological processes. For example, rising sea temperature affects the gametogenesis and spawning of *Echinocardium cordatum*, an abundant echinoderm species in the North Sea (Kirby *et al.*, 2007). In coastal waters of northern Europe, severe winters are often followed by high densities of intertidal bivalve recruits (Beukema *et al.*, 1998; Strasser *et al.*, 2003). This was partly attributed to lower metabolism during cold winters resulting in higher biomass and production of more eggs in spring (Beukema *et al.*, 1998). Indeed, rising sea temperature was found to reduce reproductive output and advance the spawning of intertidal bivalves (Honkoop and van der Meer, 1998; Philippart *et al.*, 2003), but recruit density was highly variable and only a minor part was explained by the effects of temperature on reproductive output (Honkoop *et al.*, 1998). Several other environmental factors related to climate change and temperature rise may have influenced recruitment, such as changes in predation pressure or food availability (Hiddink *et al.*, 2002; Philippart *et al.*, 2003). These examples demonstrate the complex interactions and species-specific responses in benthic systems in relation to climate change. It is unlikely that changes in the abundance of meroplankton can be related directly to changes in adult populations because post-recruitment and juvenile dynamics are not well understood for most benthic organisms.

The shift in timing of meroplankton peaks described above seems to be a direct effect of sea temperature rise, but differences in the response between ecosystem components may also lead to indirect effects, such as altered competitive interactions or changes in foodwebs. The timing of the spring bloom remained fairly constant in the North Atlantic and the North Sea when compared with earlier cycles of meroplankton (and holoplankton; Edwards and Richardson, 2004; Wiltshire *et al.*, 2008). Other factors, independent of changes in temperature, such as photoperiod, seem to trigger the timing of the phytoplankton bloom (Eilertsen *et al.*, 1995). In contrast, phytoplankton biomass increased in several areas of the Northeast Atlantic during recent decades (Reid *et al.*, 1998; Raitsos *et al.*, 2005; McQuatters-Gollop *et al.*, 2007). However, the temporal mismatch between primary producers and consumers can have cascading effects on higher trophic levels, as already demonstrated for fish and bird populations (Conover *et al.*, 1995; Beaugrand *et al.*, 2003; Hipfner, 2008), with repercussions for foodweb structure. For benthic organisms, possible mismatch scenarios are most significant during the planktonic phase (at least for planktotrophic larvae) or during the post-recruitment phase on the sediment. Juvenile benthic organisms especially, which lack energy reserves and have a higher weight-specific metabolic demand, are supposed to depend much more on an adequate food supply than adults; therefore, they are more susceptible to starvation during times of food deprivation, possibly caused by climate-change effects (Òlafsson *et al.*, 1994).

The match–mismatch hypothesis (MMH; Cushing, 1990) provides a general and plausible framework for understanding variations in recruitment by means of species phenology, but it is difficult to test and has mainly been applied and debated in fishery science (Beaugrand *et al.*, 2003; Durant *et al.*, 2007). The mismatch between phytoplankton blooms and benthos dynamics has been little studied by either correlative approaches or experimental work. One exception is the study by Bos *et al.* (2006), who tested the MMH experimentally for the bivalve *Macoma balthica* against phytoplankton concentration. Although they found a clear effect of the timing of spawning on the growth and development of larvae, this was not related to changes in phytoplankton concentration, and the underlying mechanisms remain unclear. Also, Philippart *et al.* (2003) gained empirical evidence for the MMH and demonstrated that mortality of *M. balthica* juveniles became more density-dependent with an increase in the degree of mismatch. However, further experimental studies of the effects of temperature on the biology of benthic species and possible mismatch based on food availability are needed to clarify this situation. The response to climate change is often species-specific and may be determined by the timing (phenology) of particular processes. This suggests that a better knowledge of the life history of benthic organisms is needed for an adequate explanation of population changes and prediction of ecosystem responses (Richardson, 2008).

8.3.1.3 Parasites

Environmental change, such as higher temperature, and changing precipitation and currents, attributable to climate change, may alter parasite–host interactions (viral, bacterial, protozoan, and metazoan; Mouritsen and Poulin, 2002a) and, as such, adjust the structure and composition of natural animal communities. In intertidal communities, the most common parasites are trematodes, gastropods, and to a lesser extent bivalves, are the first intermediate host, and molluscs, crustaceans, polychaetes, or fish are the second intermediate host, with shorebirds or fish often as the definitive host. Parasitic nematodes use benthic invertebrates as the intermediate or only hosts. Cestodes and acanthocephalans use crustaceans as intermediate hosts, whereas decapods are often infected by nematomorphs, nemertean egg parasites, rhizocephalans, and parasitic isopods (Mouritsen and Poulin, 2002b). Parasites alter the survival, reproductive success, growth, and behaviour of their host (Mouritsen and Poulin, 2002b).

Parasites may also invade new areas, as illustrated by the protozoan *Perkinsus marinus*, which infects the eastern oyster (*Crassostrea virginica*). The parasite was originally found in Chesapeake Bay and the Gulf of Mexico, but in the early 1990s, an apparent range extension led to an epizootic outbreak over a 500-km range north of Chesapeake Bay (Ford, 1996; Cook *et al.*, 1998). The outbreaks coincided with increasing water temperatures during winter (Cook *et al.*, 1998; Ford and Chintala, 2006), with salinity also positively related to infection intensities (Ragone and Burreson, 1993; Powell *et al.*, 1996; Mouritsen and Poulin, 2002a).

Mud snails and corophiid amphipods often co-occur in high densities in coastal areas of the temperate North Atlantic, where they act as first and second intermediate hosts for a number of trematodes. Snails often show decreased resistance to extreme abiotic conditions when infected by trematodes, and they are often castrated (Mouritsen and Poulin, 2002b). Infestation of amphipods may cause anaemia, which is the most probable cause of increased surface activity observed among infected specimens. This parasite-induced behaviour may facilitate transmission of infective stages to shorebird hosts feeding on the amphipod (Mouritsen and Jensen, 1997). In the Danish Wadden Sea, a dense field of *Corophium volutator* disappeared completely, and the density of the mud snail *Hydrobia ulvae* declined by 40% during spring 1990 as a result of an epizootic by trematodes. High spring temperature accelerated both the development rate and the release of infective larval stages of an infectious trematode from the snail. This event coincided with a high positive NAO index, high temperatures, strong winds, and increased precipitation in northern Europe (Mouritsen and Poulin, 2002a, and references therein). The transmission rates of larval parasites from snail to amphipods and the rate of parasite-induced amphipod mortality are both strong positive functions of temperature (Jensen, K., and Mouritsen, 1992; Mouritsen and Jensen, 1997; Mouritsen, 2002). Using a simulation model, Mouritsen *et al.* (2005) demonstrated that a 3.8°C increase in ambient temperature would probably result in a parasite-induced collapse of the amphipod population in the Wadden Sea. This temperature increase is within the range predicted to prevail by the year 2075. As *C. volutator* builds tubes in sediment, the collapse of its population led to drastic changes in erosion patterns, sediment characteristics, and microtopography, as well as marked changes in the abundance of other macrofaunal species in the mudflat (Poulin and Mouritsen, 2006).

Marine bivalves harbour a diversity of trematode parasites that affect the population and community dynamics of their hosts (Thieltges *et al.*, 2006). The parasites may lead to a reduction in condition, make the bivalves more vulnerable to predation or, in the case of *Mytilus edulis*, reduce the production of byssal threads. Infection leads eventually to partial or complete castration and may induce behavioural changes that facilitate transmission of the parasite to the final host (Mouritsen and Poulin, 2002b). Thieltges and Rick (2006) demonstrated that, for the trematode *Renicola roscovita*, a major parasite in North Sea bivalves, the optimum temperature for transmission is 20°C. Similar observations were made for another trematode, *Himasthla elongata*, indicating that transmission to second intermediate bivalve hosts may peak during years with warm summers (≥20°C) in the variable climate regime of the North Sea.

A clear example of the effects of temperature on bacterial- or viral-induced diseases was observed on sea fans around the southwest UK (ukbars.defra.gov.uk). During 2003–2006, Hall-Spencer *et al.* (2007) observed widespread incidence of disease outbreaks in the pink sea fan (*Eunicella verrucosa*) around Lundy and from Lyme Bay to Plymouth. Laboratory analysis of specimens revealed water temperatures of 15°C had no effects, whereas temperatures of 20°C induced disease symptoms (Figure 8.4).

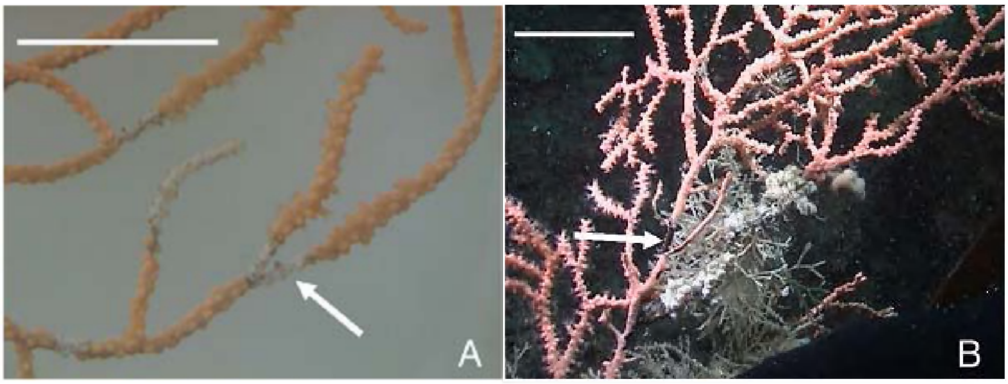

Figure 8.4. *Eunicella verrucosa*at 21m depth at Knoll Pins, Lundy, on 16 May 2003. (A) early onset of coenchyme necrosis (arrow), and (B) post-necrotic exposure of gorgonian skeleton (arrow) with fouling community of hydroids, barnacles *Solidobalanus fallax*, and bryozoans *Cellaria* sp. Scale bars = 40 mm. Source: Hall-Spencer *et al.*, 2007.)

8.3.2 Altered hydrodynamics

The hydrodynamic regime of the North Atlantic is characterized by a number of physical properties and circulation patterns that undergo substantial variability at seasonal–decadal time-scales. This variability can be affected by climate change, but it is rarely possible to separate these effects from natural variation in the system. Climate change may affect *inter alia* the mixed-layer depth, position of frontal regions, frequency and pathways of storms, and the occurrence of convection events, but these climate-change effects are not comprehensively understood (see Sections 2 and 3).

But how can changes in the physical properties of the water column affect benthic communities on the seabed? The hydrodynamic regime influences the benthos in various direct and indirect ways. Hydrodynamics can directly influence the benthos via the transport and dispersal of larvae, juveniles, and even adults, with important consequences for population dynamics (e.g. Palmer *et al.*, 1996; Todd, 1998; Levin, 2006) and can increase mortality caused by oxygen depletion (stratification) or storm events. The physical and chemical properties of the water column, especially of the upper layers, determine productivity in the ocean. Thus, among indirect effects, the influences of hydrodynamics on primary and secondary production in the water column and on the transport pathways of these food sources to the benthic system are probably most important (Rosenberg, 1995).

These effects are not restricted to shallow waters with a tight coupling of pelagic and benthic processes. Changes in surface-water hydrodynamics can also have implications for deep-sea benthic ecosystems (Davies *et al.*, 2007). Analyses of sediment cores from the Nordic seas also demonstrate a tight bentho-pelagic coupling for deep basins below 1200 m throughout the past 25 000 years (Bauch *et al.*, 2001). In the Northeast Atlantic, up to 4% of the surface production of the spring bloom reaches the seabed (Gooday, 2002), resulting in a response of the deep-sea benthic biota ranging from bacteria to megabenthos (Davies *et al.*, 2007). However, observed effects on benthic communities can rarely be related to a single hydrodynamic property, because they are often interrelated, and benthic communities are affected by a multitude of different environmental and anthropogenic drivers. Therefore, the following examples of climate-change effects on benthos via changes in hydrodynamics are somewhat uncertain and reflect the complexity in the coupling of benthic and water-column processes.

Oxygen depletion (i.e. hypoxia and anoxia) caused by high bottom-water temperature, reduced water circulation (enhanced by thermal stratification), and coastal eutrophication is considered among the most widespread deleterious influences on estuarine and marine benthic environments (Halpern *et al.*, 2007). Predicted global climate change is expected to expand hypoxic zones by (i) increased water-column stratification and warming that inhibits water exchange and (ii) changes in precipitation patterns that enhance discharges of freshwater and agricultural nutrients. At present, ca. 500 000 tonnes of benthic biomass are missing worldwide over a total area of 245 000 km^2 as a result of hypoxia (i.e. $<2 \text{ mg l}^{-1}$ dissolved O_2; Diaz and Rosenberg, 2008). Levin *et al.* (2009) demonstrated that oxygen depletion causes a reduction in the diversity of the benthos through loss of less-tolerant species and increased dominance of tolerant opportunists (e.g. nematodes, foraminifera, and small soft-bodied invertebrates with short generation times and elaborate branchial structures).

The magnitude of this effect depends on the area affected and the frequency, intensity, and duration of oxygen depletion. Benthic mass mortality has been observed, for example, after long-lasting hypoxic periods (i.e. "dead" zones; Diaz and Rosenberg, 2008; Seitz *et al.*, 2009). Additionally, bottom-water oxygen deficiency also alters biogeochemical processes that control nutrient exchanges at the sediment–water interface (i.e. benthic–pelagic coupling), for example, by the release of phosphorus from bottom sediment (e.g. Jensen, H., *et al.*, 1995; Conley *et al.*, 2009). Another well-documented example of the effect of depleted oxygen conditions on biogeochemistry is the reduction in denitrification (e.g. Childs *et al.*, 2002) caused by low concentrations of bottom-water nitrate and a less-efficient reoxidation of reduced elements. However, until now, the extent to which climate change, by increasing hypoxic events, will affect the mortality of benthic species and nutrient fluxes remains unclear. Extensive oxygen-depletion zones were found (e.g. in the North Sea) during the 1980s, but less so after this period, although bottom-water temperatures were above average. The oxygen depletions during the 1980s were considered to be at least partly related to eutrophication (von Westernhagen *et al.*, 1986; Rachor, 1990), and possible temperature effects in recent years might have been masked by a reduction in riverine nutrient input to the North Sea.

As mentioned above, changes in thermal stratification of the water column have an important impact on heat flux, which can lead to oxygen depletion. Conversely, if the climate becomes stormier, stratification will decrease because of increased mixing depth, and the risk of oxygen depletion will be reduced. For example, Rabalais *et al.*

(2007) demonstrated that the 2005 hurricanes in the Gulf of Mexico disrupted stratification and aerated bottom waters. But in turn, physical disturbance by wave stress during storm events can itself increase mortality of benthic species, at least in shallow waters (<50 m), although studies of such effects are limited (Rees *et al.*, 1977; Nehls and Thiel, 1993; Turner *et al.*, 1995; Posey *et al.*, 1996). It is still unclear whether the frequency, intensity, and pathways of storms or extra-tropical cyclones have changed or will do so in future (see Section 2). The findings are equivocal, demonstrating evidence for an increasing trend in storm activity (Alexandersson *et al.*, 2000; Ulbrich *et al.*, 2009), as well as for stable conditions (Bärring and von Storch, 2004; Raible *et al.*, 2008), during the past century in the Northeast Atlantic. Nevertheless, modelling studies based on global warming scenarios indicate a weak increase in storm activity in future (WASA Group, 1998; Donat *et al.*, 2010). However, storms are not an unusual disturbance event in marine benthic systems and can be attributed to natural variability within the system. Nevertheless, local changes in the granulometry or lithology of the bottom sediment caused by changes in storminess could have a long-term effect on the benthos, although this is unclear at present.

Future changes in stratification of the water column may not only have the impacts mentioned above, but can also indirectly affect the benthos via changes in food supply. In temperate stratified waters (e.g. the North Sea), primary and secondary production is elevated along thermohaline frontal regions where summer-stratified waters are separated from permanently mixed waters. The quality and quantity of sedimenting organic matter is an important factor influencing benthic communities (Rosenberg, 1995; Dauwe *et al.*, 1998). The relatively high primary production and the prolonged sedimentation of fresh organic matter along fronts affect abundance, biomass, growth, and functional composition of benthic communities (Dauwe *et al.*, 1998; Amaro *et al.*, 2003, 2007). Climate-change projections of the spatial extent of stratified waters in the North Sea indicate a northward expansion of the stratified areas (J. Van der Molen, pers. comm.) and, thus, would lead to changes in the position of seasonally developed frontal regions and their associated benthic communities.

The hydrodynamic regime plays an important role in structuring benthic communities, as demonstrated by many correlative studies (Butman, 1987; Snelgrove and Butman, 1994; Wieking and Kröncke, 2001; Kröncke, 2006; see also Section 8.4). Marine benthic systems, which are often dominated by organisms with planktonic life stages, are especially sensitive to alteration in oceanographic patterns affecting dispersal and recruitment (Òlafsson *et al.*, 1994; Gaylord and Gaines, 2000). It is conceivable that altered patterns of mass transport could tip the balance of larval recruitment to adult mortality and lead to local population reduction or even extinction (Svensson *et al.*, 2005). Given the uncertainty of the response of hydrodynamics to climate projections, potential associated changes in the benthos are currently unpredictable.

8.3.3 Ocean acidification

Global industrialization has led to increasing levels of CO_2 in the atmosphere, reaching a rate which is 100-fold faster than any change during the past 650 000 years (Fabry *et al.*, 2008). Approximately one-third of the anthropogenic CO_2 in the atmosphere has been taken up by the oceans over the past 200 years (Sabine *et al.*, 2004). The solution of CO_2 in seawater leads to an increased partial CO_2 pressure (hypercapnia), and a reduction in pH and calcium carbonate saturation, with diverse effects on marine organisms. If the rate of growth of CO_2 production continues, the expected pH of seawater could fall during the 21st century by up to 0.5 units below its pre-industrial level of pH 8.2 (Caldeira and Wickett, 2003; Blackford and Gilbert, 2007). A reduced calcium carbonate saturation results in lower calcification rates in marine organisms, and a diminished pH affects various physiological processes. Combined, these effects may result in changes in biodiversity, trophic interactions, and other ecosystem processes (Fabry *et al.*, 2008). At present, benthic organisms are mostly neglected when calculating global carbon-flux models. However, several benthic groups contribute substantially to the global carbon budget and their physiology is also affected by acidification. The omission of benthic processes from global carbon models leads to false estimates of fluxes at large scales and future predictions of climate-change scenarios (Lebrato *et al.*, 2010).

Until now, calcification processes of tropical reefs and planktonic coccolithophores have been the main focus of research on ocean acidification, and information on other taxa and/or processes is scarce. Reviews by Langdon and Atkinson (2005) and Kleypas and Langdon (2006) have outlined the effects of acidification on coral reefs. For deep-sea fauna, especially cold-water corals, which are normally adapted to very little variation in pH (Fabry *et al.*, 2008), calcification may be severely affected, and changes in distribution can be expected (Guinotte *et al.*, 2006; Turley *et al.*, 2007). Cold-water corals are probably one of the most vulnerable habitat-forming calcifiers in the North Atlantic, providing habitat for a variety of associated benthic species (Jensen, A., and Frederiksen, 1992; Mortensen *et al.*, 1995; Husebø *et al.*, 2002). They are found throughout the North Atlantic, usually between depths of 200 and 1000 m (Figure 8.5), but shallower records also exist from Norwegian fjords (Fosså *et al.*, 2002). In UK waters, the distribution of the cold-water coral *Lophelia pertusa* has been recorded mainly off the continental shelf. Most records are from the Sea of the Hebrides, west of Scotland. These reefs were first mapped in 2003 and are known as the Mingulay Reef Complex (Roberts *et al.*, 2005, 2009b). Roberts *et al.* (2009b) confirmed the distribution of live coral-reef areas at 120–190 m depth. Distinctive mounded bathymetry was formed by reefs of *L. pertusa*, with surficial coral debris dating to almost 4000 years BP (Figure 8.5). Guinotte *et al.* (2006) estimated that the calcification of ca. 70% of the cold-water corals worldwide will be affected by predicted ocean acidification within the next 100 years. Unfortunately, no experimental results on the effect of acidification on cold-water corals have yet been published (Turley *et al.*, 2007). However, palaeo-ecological studies have already revealed that acidification events 50 million years ago, at ranges similar to those predicted for future changes, resulted in the extinction of a substantial proportion of benthic calcifiers (Zachos *et al.*, 2005).

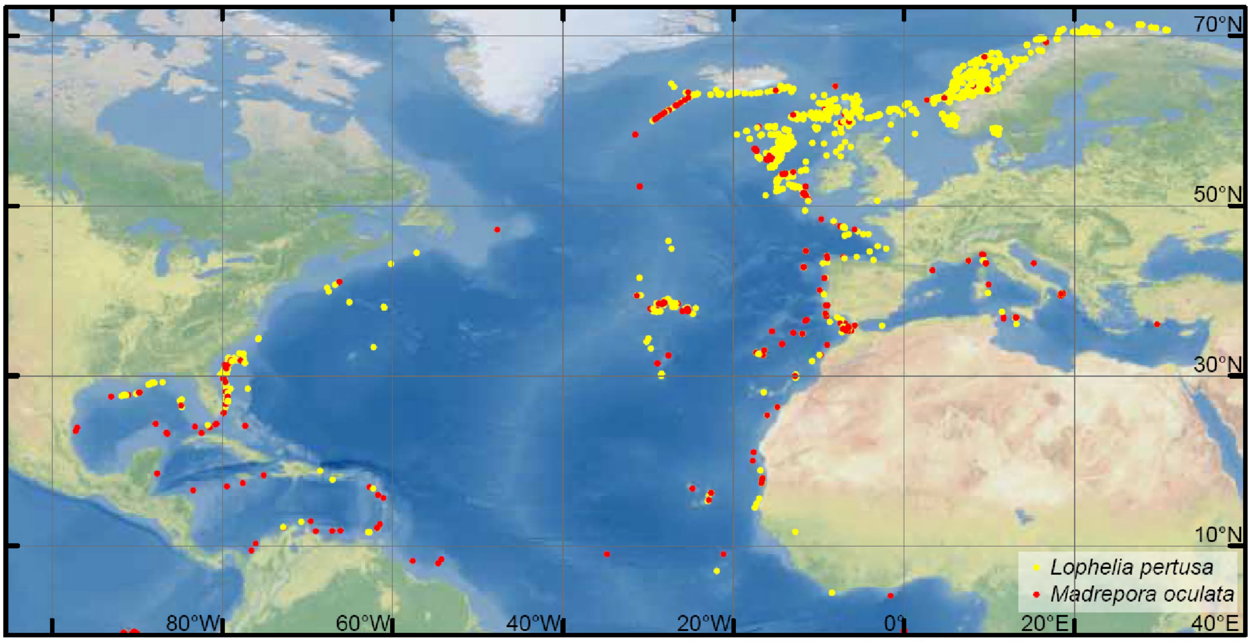

Figure 8.5. Upper panel: Distribution of *Lophelia* and *Madrepora* reefs throughout the North Atlantic (map plotted by J. Titschack; cold-water corals extracted from version 2.0 of the global points dataset compiled by UNEP World Conservation Monitoring Centre (UNEP-WCMC) from various scientific institutions, 2006). Lower panel: Polyps of the cold-water coral *Lophelia pertusa* collected at Mingulay Reef Complex. (Courtesy of Murray Roberts.)

Some studies on other calcareous organisms, such as echinoderms, bivalves, barnacles, foraminifera, and gastropods, suggest that they will also experience difficulties in the formation (calcification) of their shells and skeletons (see references in Table 8.1). Shell construction in echinoderms in particular is severely affected. This may, even on a global scale, have unforeseen effects because echinoderms contribute a substantial part of the global production of carbonate (Lebrato *et al.*, 2010). Laboratory experiments conducted under normal and reduced pH, demonstrated the effects of acidification on the brittlestar *Amphiura filiformis*. These echinoderms managed to rebuild missing arms, although their skeleton suffered from this activity. The need for more energy provoked brittlestars in more acidic water to break down their muscles. At the end of 40 days, their intact arms had 20% less muscle mass than those from normal seawater (Wood *et al.*, 2008). Other physiological processes, such as fertilization success, developmental rates, and larval size, may reduce with increasing CO_2 concentrations (Kurihara and Shirayama, 2004), eventually leading to increased mortality of the affected organisms.

Most existing studies have focused on organisms that live on or above the seabed, which were assumed to be most susceptible; little is known about the sensitivity of the benthic infauna (Widdicombe and Spicer, 2008). Recent experiments have identified significant variability in the pH sensitivity of a number of different benthic groups. Even among organisms that depend on $CaCO_3$ structures, variability in tolerance has been observed, with echinoderms displaying less tolerance of pH change than molluscs (Shirayama and Thornton, 2005). Some infaunal species, however, inhabit naturally hypoxic and hypercapnic environments (e.g. Atkinson and Taylor, 1988), and they are able to tolerate a lower pH (e.g. the polychaete *Nereis virens* tolerates a pH as low as 6.5; Batten and Bamber, 1996; Widdicombe and Needham, 2007), whereas others may temporarily compensate against a lower pH, but are susceptible to long-term exposure (Table 8.1). Benthic species have different acid–base regulation abilities, leading to the prediction that some species with high metabolic rates may be more severely affected by ocean acidification because oxygen binding in their blood is more pH sensitive (Pörtner and Reipschläger, 1996).

Differential effects between species may lead to major changes in the composition of the benthic community, as some species are severely affected and other less so. A number of ongoing large research projects are currently addressing the effects of ocean acidification on the physiology of benthic organisms, such as molluscs and echinoderms (e.g. the European Project on Ocean Acidification (EPOCA), Biological Impacts of Ocean Acidification (BioACID), UK Ocean Acidification Research Programme (UKOARP), and Mediterranean Sea Acidification (MedSeA)). Although effects on biodiversity are predicted by many authors, published evidence to support this contention is scarce. Hall-Spencer *et al.* (2008) demonstrated a large biodiversity loss of 30% in the benthic community associated with a gradient of pH from 8.2 to 7.8 away from hydrothermal vents in the Mediterranean that provided a natural CO_2 source. Prediction of the long-term implications for the diversity of marine organisms and for ecosystem functioning at larger scales is challenging (Widdicombe and Spicer, 2008).

Table 8.1. Published reactions of benthic species to increased CO_2 levels and low pH. Extended from Table 1 in Fabry *et al.* (2008) and other sources listed in the table.

Taxa	**Species**	**Description**	**CO_2 system parameters**	**Sensitivity**	**Reference**
Mollusca	*Haliotis laevigata*	Greenlip abalone	pH 7.78; pH 7.39	5 and 50% growth reductions	Harris *et al.* (1999)
	Haliotis rubra	Blacklip abalone	pH 7.93; pH 7.37	5 and 50% growth reductions	Harris *et al.* (1999)
	Mytilus edulis	Blue mussel	pH 7.1 10 000 ppmv	Shell dissolution	Lindinger *et al.* (1984)
			pCO_2 740 ppmv	25% decrease in calcification rate	Gazeau *et al.* (2007)
			pH 6.6	100% mortality within 30 days	Bamber (1990)
	Mytilus galloprovincialis	Mediterranean	pH 7.3 ~ 5000 ppmv	Reduced metabolism, growth rate	Michaelidis *et al.* (2005)
	Crassostrea gigas	Pacific Oyster	pCO_2 740 ppmv	10% decrease in calcification rate	Gazeau *et al.* (2007)
			pH 6.0	100% mortality within 30 days	Bamber (1990)
	Placopecten magellanicus	Giant scallop	pH <8.0	Decrease in fertilization and embryo development	Desrosiers *et al.* (1996)
	Tivela stultorum	Pismo clam	pH <8.5	Decrease in fertilization rates	Alvarado-Alvarez *et al.* (1996)
	Pinctada fucada martensii	Japanese pearl oyster	pH 7.7	Shell dissolution, reduced growth	Reviewed in Knutzen (1981)
			pH 7.4	Increasing mortality	
	Mercenaria mercenaria	Clam	Ωarag =0.3	Juvenile shell dissolution, leading to increased mortality	Green *et al.* (2004)
	Strombus lohuanus	Gastropod	pH 7.9	Survival rate significantly lower	Shirayama and Thornton (2005)
Arthropoda	*Cancer pagurus*	Edible crab	1% CO_2 ~10 000 ppmv	Reduced thermal tolerance, aerobic scope	Metzger *et al.* (2007)
	Porcelana platycheles	Porcelain crab	pH 7.4	After 40 days no effect detected	Calosi *et al.* (2009)
	Callianassa sp.	Mud shrimp	pH 6.3	Tolerant	Torres *et al.* (1977)
	Necora puber	Swimming crab	pH 6.16	100% mortality after 5 days	
	Amphibalanus amphitrite	barnacle	pH 7.4–8.2	Weakening of shell	McDonald *et al.* (2009)
Echinodermata	*Strongylocentrotus pupuratus*	Sea urchin	pH ~6.2–7.3	High sensitivity inferred from lacking of pH regulation and	cf. Burnett *et al.* (2002)
	Psammechinus miliaris	Sea urchin		Passive buffering via test dissolution during emersion	Spicer (1995); Miles *et al.* (2007)
	Hemicentrotus pulcherrimus	Sea urchin	~500–10 000 ppmv	Decreased fertilization rates, impacts larval developments	Kurihara and Shirayama (2004)
	Echinometra mathaei	Sea urchin			
	Cystechinus sp.	Deep-sea urchin	pH 7.8	80% mortality under simulated CO_2 sequestration	Barry *et al.* (2002)
Sipuncula	*Sipunculus nudus*	Peanut worm	1% CO_2 10 000 ppmv	Metabolic suppression	Pörtner and Reipschläger (1996)
				Pronounced mortality in 7-week exposure	Langenbuch and Pörtner (2004)
Polychaeta	*Nereis virens*		pH 6.5	Tolerant	Batten and Bamber (1996)
Nematoda	*Procephalotrix simulus*		pH <5.0	Tolerant	Yanfang and Shichum (2005)
Foraminifera	*Marginoptera kudakajimensis*		pH 7.7–8.3	Decline in calcification rate, possibly precluding survival	Kuroyanagi *et al.* (2009)

8.3.4 Sea-level rise: coastal squeeze

In many European estuaries, extensive areas of intertidal habitat could disappear in future as a result of rising sea levels that squeeze tidal flats against established sea defences (Fujii and Raffaelli, 2008). Increasingly, beaches are also becoming trapped between human development on land and rising sea levels (Schlacher *et al.*, 2007). Over the past century, for example, there has been a landward encroachment of the low-water mark along 67% of the eastern coastline of the UK (Taylor *et al.*, 2004). This phenomenon is better known as "coastal squeeze" (Doody, 2004). The impact of coastal squeeze on marine benthic organisms is more complex than merely the loss of habitat. Various associated environmental changes, such as steepening of the intertidal slope, sediment coarsening, and upstream saline water intrusion in estuarine environments, might also be expected (Fujii and Raffaelli, 2008).

Hosting a rich benthic fauna, fulfilling various ecological functions (McLachlan and Brown, 2006), and providing various goods and services to mankind (Beaumont *et al.*, 2007; Rönnbäck *et al.*, 2007), intertidal systems may be impoverished by coastal squeeze. In the Humber Estuary, UK (Fujii and Raffaelli, 2008), for example, model simulations demonstrated that a sea-level rise of 0.3 m could result in a 23% loss of macrobenthic biomass. Some nuances are, however, needed here: in the Wadden Sea, sea-level rise is expected to result in increased amounts of intertidal zoobenthos in areas with predominantly high tidal flats, whereas declines are expected in lower-lying areas (Beukema, 2002). However, such changes will occur only if sea-level rise proceeds too rapidly to be compensated by extra sedimentation. Sea-level rise is further expected to not only cause a shift in the position of the intertidal zones but also to narrow or broaden them and, in this way, to affect total biomass and productivity of the benthos. In some cases (e.g. on the Basque coast), human pressures during the 20th century overwhelmed the effects of sea-level rise on benthic habitats because they were much more dominant in intensity and extension (Chust *et al.*, 2009).

Human interventions (e.g. shoreline armouring, beach nourishment) to combat changes in beach environments, such as erosion and shoreline retreat, may add to the ecological impact of sea-level rise (Schlacher *et al.*, 2007). As demonstrated by various monitoring programmes, the *in situ* ecological consequences of such engineering activities on beaches can be substantial at local scales and include loss of biodiversity, productivity, and critical habitats, as well as modifications of the subtidal zone, which is an important recruitment zone for many sandy-beach animals (e.g. Speybroeck *et al.*, 2006). In addition, *ex situ* effects on the benthos can be observed. In the case of beach nourishment, fill-sands are usually collected offshore, causing various impacts on the offshore benthos, such as shifts towards lower size classes of nematodes (Vanaverbeke *et al.*, 2003), with a consequent recovery of 4.5 to more than 10 years (Foden *et al.*, 2009). In cases of shoreline armouring, the high demand for clay as soil material for dikes has been shown to cause local destruction of saltmarsh ecosystems at clay excavation sites, with the first signs of terrestrial recovery evident from 8 years onward (Vöge *et al.*, 2008).

8.4 Climate-variability proxies (North Atlantic Oscillation)

Climate-change effects on benthos can rarely be studied at the long time-scales of climate. In this context, cores from marine sediments act as a natural archive, reflecting pelagic and benthic processes from past millennia (Hald, 2001). Changes in calcareous nanoplankton communities in the eastern North Atlantic during the past

130 000 years, preserved in sediment cores, record the major climate-change events of the past (Stolz and Baumann, 2010). Comparisons between planktonic and benthic foraminiferan communities in the cores show that changes in plankton were also evident in the benthic environment, indicating a strong bentho–pelagic coupling (Bauch *et al.*, 2001). Thus, palaeoecological studies demonstrate that past climate-change events have substantially affected pelagic and benthic species and communities.

In order to reveal links between present-day benthic species or communities and climate on shorter time-scales, comparisons are made with proxies for climate variability. One of these proxies, important for the North Atlantic region, is the NAO. The NAO is a pattern of atmospheric variability in the North Atlantic region, and the derived NAO index is a measure of the strength of the sea-level air-pressure gradient between Iceland and the Azores (see Sections 2 and 10). The NAO index represents an integration of several climatic variables (e.g. water temperature, prevailing wind direction and speed, precipitation). Changes in biomass, abundance, community structure, and function of benthic systems, directly or indirectly related to variability in the winter NAO index (Figure 8.6), have been described from a number of different areas in recent decades (Frid *et al.*, 1996; Kröncke *et al.*, 1998, 2001; Frid *et al.*, 1999, 2009b; Wieking and Kröncke, 2001; Dippner and Kröncke, 2003; Franke and Gutow, 2004; Schröder, 2005; Rees *et al.*, 2006; Van Hoey *et al.*, 2007; Neumann *et al.*, 2008).

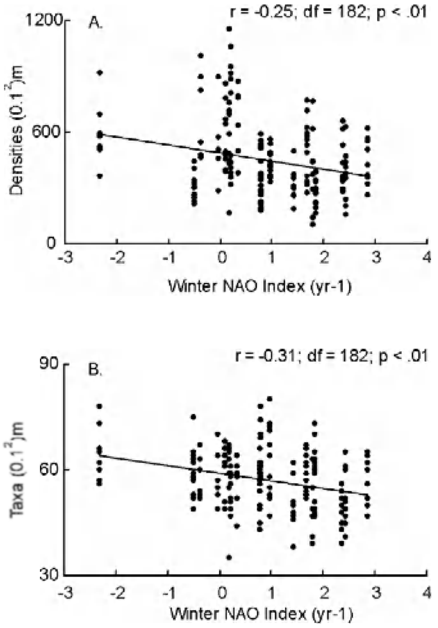

Figure 8.6. Example of the relationship between (A) average density and (B) numbers of taxa across the annually sampled stations off the Tyne (UK) and the North Atlantic Oscillation (NAO) index for the preceding year. (Source: Rees *et al.*, 2006.) Note that opposite relationships with the NAO index were also found (see text).

In the North Sea, severe winters, which are associated with a low NAO index, as occurred in 1962/1963, 1978/1979, and 1995/1996, led to a marked reduction in the number of benthic species and a shift in community structure, not only in the intertidal and shallow subtidal but also in deeper offshore areas (Ziegelmeier, 1964; Beukema, 1979; Kröncke *et al.*, 1998; Armonies *et al.*, 2001; Reiss *et al.*, 2006; Neumann *et al.*, 2009). The link to cold winters is probably related to increased mortality of sensitive benthic species. Changes in the frequency of occurrence of extremely cold winters may alter the structure of benthic communities in the long term, depending on the resilience of the community. In the German Bight, the benthos changed on a decadal scale between the 1970s, 1980s, and 1990s, again with a substantial decline in diversity and abundance after severe winters (Schröder, 2005; Rehm and Rachor, 2007). On the other hand, mild meteorological conditions connected with a positive NAO index resulted in an increase in the abundance, species number, and biomass of the macrofauna (Beukema, 1990; Kröncke *et al.*, 2001).

Kröncke *et al.* (1998, 2001) described changes in a nearshore macrofauna community in the southern North Sea and found that total abundance, species numbers, and total biomass in spring correlated significantly with the NAO index, with SST being the mediator between climate and fauna. Furthermore, Dippner and Kröncke (2003) demonstrated in a modelling study that atmospheric winter circulation over the North Atlantic area is an optimal predictor in forecasting the structure of macrofaunal communities the following spring (Figure 8.7), although since 2000, this correlation and hence the predictability of the structure of the macrofauna community disappeared (Dippner *et al.*, 2011). Significant correlations with the NAO index were found for species diversity in the western Baltic and an Arctic fjord in Svalbard (Beuchel *et al.*, 2006; Gröger and Rumohr, 2006) and for abundance and biomass in the Skagerrak and Kattegat (Tunberg and Nelson, 1998).

All of these examples from correlative research approaches demonstrated that climate variability may have an important influence on benthic community structure, abundance, and species diversity, but the factors causing these changes are not well understood. For example, mortality can be affected by winter temperatures and disturbance of the entire community by storms (see above); both climatic parameters are correlated with the NAO index. Also, major changes in dominant wind direction are related to changes in the NAO. Thus, changes in benthic communities may occur through a variety of single mechanisms or combinations of mechanisms, which may also act synergistically or antagonistically. For example, Wieking and Kröncke (2001) described the effects of the NAO index on North Sea ecosystem processes via a temperature increase or decrease and via changes in hydrodynamics affecting primary production, larval supply, sediment composition, and food availability. Indirect effects of climate change may also occur through changes in food supply to the benthic system.

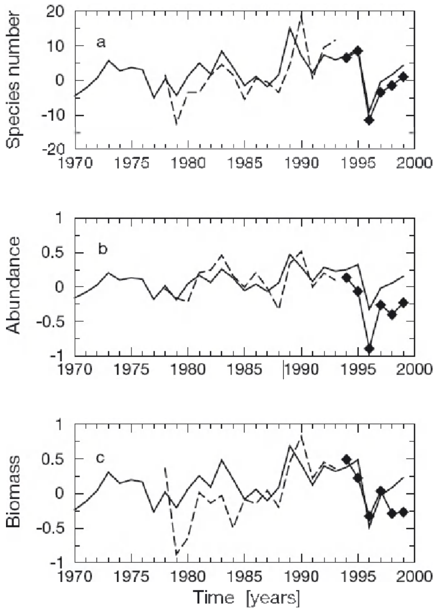

Figure 8.7. Time-series anomalies of macrofauna in the southern North Sea. Anomalies of (a) species number m^{-2}, (b) log abundance m^{-2}, and (c) log biomass m^{-2} predicted from the NAO winter index (solid line). Dashed line = observations in the fitting period 1978–1993; solid line with ♦ = observations in the forecast period 1994–1999. (Source: Dippner and Kröncke, 2003.)

The relationship between the NAO and benthic communities also seems to depend on local environmental conditions and species composition. Species diversity, for example, was found to be positively as well as negatively correlated with the NAO index (Dippner and Kröncke, 2003; Beuchel *et al.*, 2006; Rees *et al.*, 2006). Furthermore, some benthic communities respond more slowly to climate variability than others (e.g. Hinz *et al.*, 2011). This indicates that the autecology and biogeography of the local species pool plays a significant role in the response of benthic communities to climate variability, which is logical because climate stressors act on individual organisms and not on entire communities.

A number of patterns and changes seen in benthic communities are comparable with those found in plankton (e.g. Beaugrand, 2004; Bonnet and Frid, 2004; Wiltshire and Manly, 2004; Kirby *et al.*, 2007; McQuatters-Gollop *et al.*, 2007) and in fish stocks (Ehrich and Stransky, 2001; Reid *et al.*, 2001b; Kirby *et al.*, 2006; Ehrich *et al.*, 2007). Reid and Edwards (2001) and Beaugrand (2004) concluded that a regime shift occurred at the end of the 1980s, which was directly related to a significant increase in the NAO index (see Section 10).

8.5 The effects of human disturbances and climate change

Climate influences in marine systems can be distinguished as change and variability (Perry *et al.*, 2010) that together alter species and ecosystems. Climate change is considered to affect large-scale processes over the long term, whereas climate variability refers to temporal scales ranging from years to decades. The level of variability depends on the inherent characteristics of marine ecosystems (Perry *et al.*, 2010). This variability is largely the result of climate forcing, a combination of internal dynamics (e.g. interactions between species) and human activities, such as fishing, sand extraction, dredging, and construction (Perry *et al.*, 2010). The magnitude and effect of human activities on benthic systems has been studied in detail (Rachor, 1990; Frid *et al.*, 1999; Boyd *et al.*, 2005; Birchenough *et al.*, 2006; Rees *et al.*, 2006;

Birchenough *et al.*, 2010), but there is still limited understanding of interactions between these disturbances and climate variability and change.

The benthic communities of the North Sea have been studied for many decades. These studies have concentrated on describing the structure of communities and changes caused by human disturbance. There are clear gaps in understanding the multiple effects from human disturbance (e.g. fishing, aggregate extraction) in combination with those caused by climate change. Some of the examples outlined below have begun to explore these relationships and highlight the need for integrated approaches in order to determine relative responses to climate and human disturbance.

The benthic community structure in the western North Sea (northeast coast of England) and the eastern North Sea (Skagerrak) exhibited a transition during the late 1970s. This transition coincided with observed changes between the 1970s and 1980s in the zooplankton community in the western and eastern North Sea (Austen *et al.*, 1991; Evans and Edwards, 1993). It has been shown that changes in pelagic and benthic ecosystems are linked when climate change is the common cause (Kirby *et al.*, 2007, 2008, 2009). Long-term analysis of the North Sea pelagic system has identified yearly variations in larval abundance of the benthic phyla Echinodermata, Arthropoda, and Mollusca in relation to SST. Furthermore, larvae of benthic echinoderms and decapod crustaceans increased after the mid-1980s, coincident with a rise in North Sea SST, whereas bivalve larvae underwent a reduction (Kirby *et al.*, 2008). If climate change is affecting planktonic communities, inevitably there will be repercussions for benthic systems.

Off the northeast coast of England, Buchanan (1963) initiated the "Dove Time-series" (Buchanan *et al.*, 1986) during the 1960s at two stations (M1 and P). These long-term series have been used to assess natural fluctuations in benthic communities alongside fishing impacts (Figure 8.8; Frid *et al.*, 2009a). Research has also highlighted additional influences on the benthos resulting from a combination of phytoplankton supply and climatic effects (Frid *et al.*, 2009b).

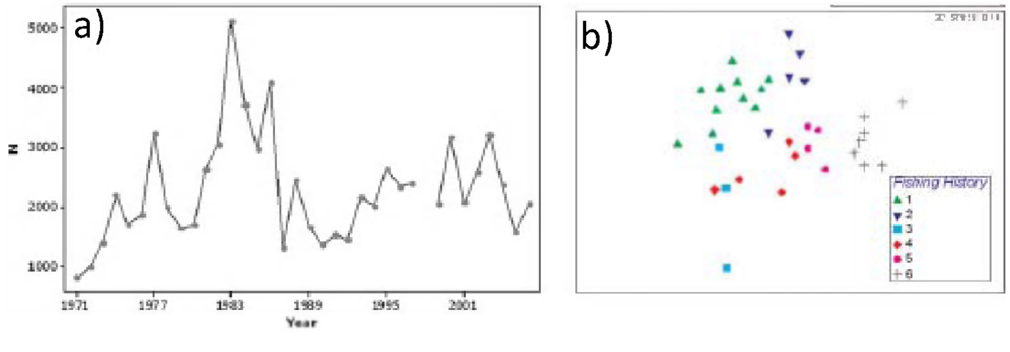

Figure 8.8. (a) Time-series plot for macrofaunal abundance (individuals m^{-2}) at the Dove Time-series Station P (west-central North Sea), based on at least five replicates, and (b) non-metric multidimensional scaling ordination of Bray–Curtis similarities in genera comparison of the macrobenthos at Station P for 1971–2006, showing variation by fishing history (fishing intensity increased in periods 1 and 2, peaked in period 3, and has subsequently declined through periods 4, 5, and 6.; Source: Frid *et al.*, 2009a.)

Callaway *et al.* (2007) compared the North Sea epibenthos between periods at the start and end of the 20th century (1902–1912, 1982–1985, and 2000) and described a biogeographic shift in many epibenthic species. Most of these changes were observed in the epibenthos before the 1980s; since then, the communities have become more resilient to long-term impacts (trawling gear removes large-bodied epifauna, such as *Modiolus modiolus* and *Aequipecten opercularis*, Figure 8.9). The reasons for the changes in the distribution of the epibenthos were considered to be a combination of high trawling effort, climate change, and eutrophication.

Recent evidence indicates that climate change is adding complexity to climate variability, and that overfishing is a global problem for marine systems. It has been suggested that marine species have developed the capacity to cope with climatic variability over long periods of time (Planque *et al.*, 2010). New approaches, based on the structure and properties of fish communities, have been proposed by Jennings and Brander (2010). These approaches have concentrated on understating underlying processes that determine size-structure of fish communities (e.g. metabolic scaling, predator–prey interactions, and energy transfer via foodwebs). This information is used to determine the size structure and productivity of the community for different climate scenarios. These tools potentially allow predictions of the effect of climate change on fish communities and thus on fisheries. This level of information is important to understand the dependence of fish communities on benthic systems. In the event that climate change could alter benthic systems, these effects could have repercussions for higher trophic levels (e.g. fish consumption).

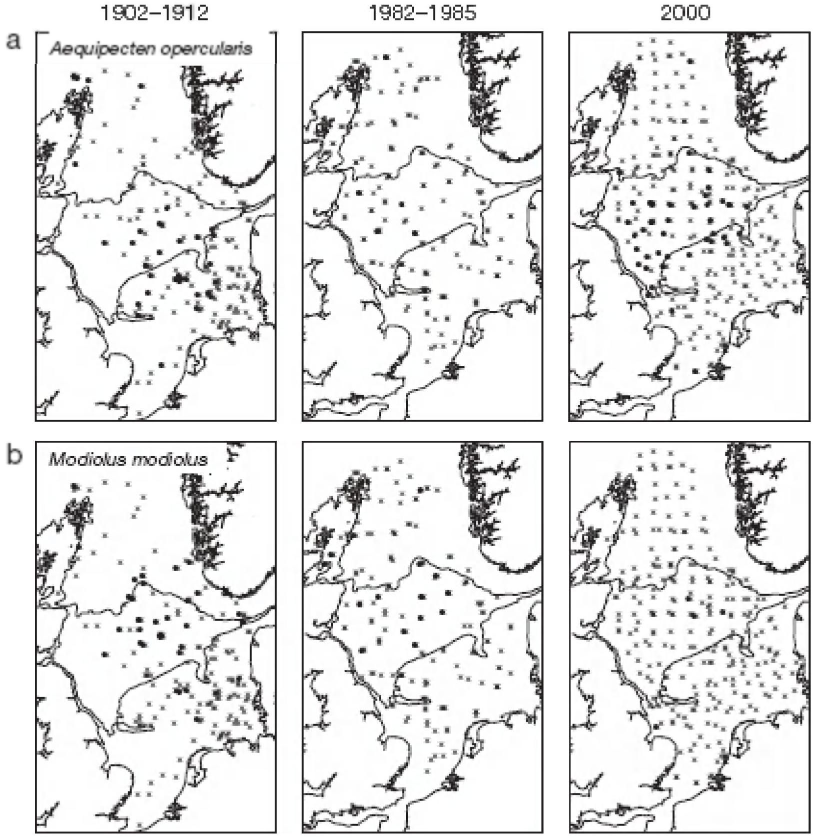

Figure 8.9. Trends in the spatial occurrence of (a) ***Aequipecten opercularis*****, and (b)** ***Modiolus modiolus*****. Species with a reduced presence in 1982–1985 and 2000 compared with 1902–1912; • = species present, x = sampled station. (Source: Callaway** ***et al.*****, 2007.)**

In the west-central North Sea, Rees *et al.* (2006) monitored benthic communities at a former sewage-sludge disposal site off the northeast coast of England (stations located in the proximity of the Dove Time-series station P). Sewage-sludge disposal at sea was phased out in 1998 in UK waters. Long-term datasets at the former sites are useful because they provide information on benthic distributions in the recovery phase after the disposal of sewage ceased (Figure 8.10). Analysis of these datasets demonstrated a temporal correlation between faunal measures and winter values of the NAO for the preceding year (Figure 8.6). The densities and varieties of species tended to be lower in warmer winters characterized by westerly airflows, as occurred in the 1990s. This represents a pattern of response where taxa with a more northerly (cold-water) distribution are not compensated by an increase in species with a southerly association. Overall, macrobenthic responses following the cessation of sewage-sludge disposal in this area were predictable in relation to mild organic enrichment. A decline in species number to references levels was observed after three years.

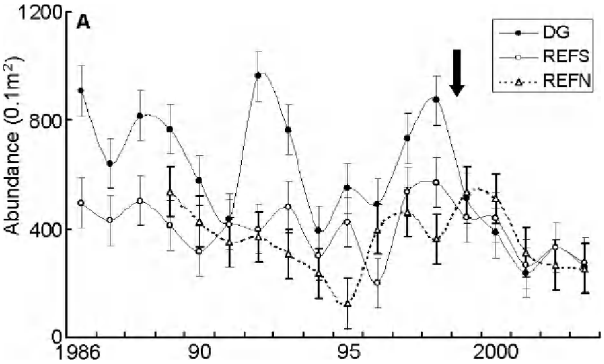

Figure 8.10. Annual trends in the abundance of the macrobenthos at the former Tyne sewage-sludge disposal site. The arrows indicate the date when the disposal at sea stopped. DG = disposal ground; REFS = south reference; REFN = north reference. (Source: Rees *et al.*, 2006.)

Additional examples of research conducted on climate and human activities in both coastal (Garmendia *et al.*, 2008) and estuarine areas (Pérez, L., *et al.*, 2009) in the Basque Country (northern Spain) has demonstrated that benthic variability is mainly explained by climate factors in coastal areas, whereas for estuarine assemblages inhabiting the same region, the observed changes were driven primarily by anthropogenic activities (e.g. wastewater discharges, habitat alteration). This indicates that human activities can mask the effects of climate change on benthic systems in estuaries, but have less effect offshore.

8.6 Conclusions

A series of mechanisms have been identified in this review by which benthic communities may be influenced by climate change, although a direct link between these effects can only be demonstrated for a limited number of cases. However, strong evidence for direct links between environmental factors and benthic organisms are evident for more cases. As climate change will affect many of these factors, it will also alter the benthos.

A number of examples of latitudinal shifts in the distribution of benthic species, largely resulting from increases in sea temperature, have been described for the Northeast Atlantic, with most examples from fauna on intertidal hard substrata. In intertidal and subtidal soft sediment, the rate of shift in distribution may be up to 50 km decade^{-1}. Under climatic influences, some key organisms, such as habitat-forming or parasitic species, will shift north of their normal distribution, and substantial impacts are to be expected. It has been suggested that, in some cases, marine benthic species have developed the capacity to cope with "stressors" (e.g. climatic variability or other pressures) over long periods of time.

A variety of biotic and abiotic factors interact with life-history features of benthic species, which may be directly or indirectly influenced by climate change. As a consequence, benthic ecosystems show complex interactions and species-specific responses in relation to climate change. A temporal mismatch between primary producers and consumers, for example, can have cascading effects on the entire foodweb, with potential effects on both larval and juvenile benthic organisms. Altered hydrodynamics on the other hand may (i) affect the distribution of benthic species, owing to changes in the dispersion of (post-) larval and/or juvenile benthic organisms (altered ocean currents), (ii) contribute to a spatial and temporal extension of anoxic and hypoxic zones (stratification), and/or (iii) affect benthic communities, especially in intertidal and shallow areas (coastal squeeze, increased storminess).

The effects of ocean acidification on coral reefs are well known, but as this process intensifies, it might also affect all benthic and other calcareous organisms. Next to calcification problems, other physiological processes (e.g. fertilization success) may be hampered, and mortality may increase as a result of ocean acidification.

Most of the impacts mentioned above are, however, deductive and, therefore, do not demonstrate a proven link between climate change and benthic ecosystems. In this perspective, lessons can be drawn from the study of the ecosystem impacts of the NAO, a descriptor of present-day climate variability. Statistically significant correlations have been found between the NAO and benthic community structure, species abundance, biomass, and species diversity, but many broke down when using the latest data, indicating that the processes behind these correlations are still unknown. Improved information on the synchronicity of benthic change in relation to other ecosystem components and their responses to human activities is needed in order to understand and confidently describe patterns of benthic responses to climate change. Finally, it is important to highlight that changes in benthic structure will have repercussions on the whole marine ecosystem, with consequences for ecosystem functioning and services, including climate regulation.

8.6.1 Knowledge gaps

Most of the impacts on the benthos from climate change are deductive and/or speculative. In order to improve this situation, the following gaps in knowledge have been identified.

- A causal relationship between a temporal mismatch between benthic species, their food resource, and climate change is difficult to prove, given the relatively poor knowledge of the life cycle of many benthic species.
- The mechanisms behind the cause–effect relationship between benthic ecosystems and the NAO remain largely unknown and need clarification. Other teleconnection patterns (i.e. Eastern Atlantic) could be influential to benthic communities in mid-latitudes (e.g. Bay of Biscay), in which the signature of the NAO is much lower.
- Although causal links between the benthos and hydrodynamics have been described, knowledge of the relationship between climate change, hydrodynamics, and benthos is still based on circumstantial evidence.
- The effects of climate change are largely the outcomes of processes acting on individuals, but are generally observed at population, community, and ecosystem levels. Therefore, it is necessary to concentrate efforts on the description of changes to species and complement these observed responses to other levels of the ecosystem.

- Almost all studies on the effect of ocean acidification and the benthos focus on specific taxa over very limited areas and time. At present, integrated, large-scale studies focusing on climate change, ocean acidification, and human activities are lacking.

8.6.2 Research needs

Evidence provided in this review has highlighted scientific gaps in this rapidly developing climate-change research. There is a need for a "three-track" approach to future studies of how climate change impacts benthic ecosystems. These key stages are (i) integrated monitoring, (ii) experiments, and (iii) modelling.

Our conceptual framework (Figure 8.2) highlights the importance of a well-designed assessment procedure that will reliably detect changes in the benthic ecosystem in order to meet the high-level objectives associated with international policies (e.g. MSFD). There is, therefore, a need for long-term, large-scale, integrated inventories and monitoring in order to provide the background information necessary to test and modify current hypotheses that are based on short-term and localized data. Standardized national monitoring strategies need to be coordinated in order to permit a regional assessment of the effects of climate change on the benthos (see also Birchenough and Bremner, 2010; Dauvin, 2010). These studies should not only focus on the classic structural descriptors of benthic communities, such as abundance and species richness, but should also address population genetics. In this way, the connectivity between populations, or species–species and species–environment interactions, may be explored in order to increase general knowledge of life cycles and the functioning of benthic ecosystems. Empirical programmes should be complemented with experimental studies (e.g. mesocosm experiments), which will lead from general observation to a wider understanding of specific responses. Furthermore, this will contribute to our understanding of the life history of benthic organisms, which is needed to explain population dynamics and to predict benthic ecosystem responses. This approach will improve our understanding of change and will allow the formulation of predictions against future scenarios.

The ability to make predictions about the responses of subtidal communities to future climate change is poor. Current capabilities to generate such information through predictive modelling techniques are mainly targeted at fish populations. These methods need to be expanded to benthic systems.

8.7 Acknowledgements

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9 Effects of climate variability and change on fish

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9.1 Introduction

Warming seas and changes in ocean currents are the most prominent features of ongoing and projected impacts of climate change on marine fish and marine ecosystems in general. Although this section covers these main aspects, we note that ocean acidification (see Sections 5, 8.3.3, and 11.6), as well as a number of other processes linked to climate change, such as changes in chemical properties, wind, upwelling, salinity, precipitation, and sea-ice cover, may affect marine fish species.

Fish are a key component of the ecosystem and the focus for much of the work of ICES, which has long been involved in examining climate change and its effects on fish. For example, the ICES/GLOBEC Working Group on Cod and Climate Change (WGCCC), established in 1992, addressed many aspects of cod growth, including the role of ambient temperature in both inter- and intrastock variability. The WGCCC found that mean bottom temperature accounts for 90% of the observed (tenfold) difference in growth rates between different stocks of cod (*Gadus morhua*) around the North Atlantic. This exemplifies the importance of environmental conditions for the growth of fish in the wild. More recently, the ICES Working Group on Fish Ecology (WGFE) examined changes in the distribution of species in relation to climate change, summarizing and extending the recent work in this area. These are just two examples of how ICES has been extensively involved in issues related to climate change and the effects on fish.

This section provides information on features of climate change (water temperature and ocean currents) that may affect fish populations by influencing recruitment (productivity), maturation, growth, and distribution. These processes are complex and highly interactive, so the distinction between forcing by climate change vs. other drivers (e.g. fishing, hypoxia, or eutrophication) is often unclear. The section concludes with recommendations for future research that are necessary to advance our understanding of climate-driven impacts on marine fish.

9.1.1 Climate-driven physiological impacts

Individual growth in fish is the integrated result of a series of physiological processes, namely feeding, assimilation, metabolism, transformation, and excretion (Brett, 1979; Michalsen *et al.*, 1998). These internal processes are affected by climate-driven changes in physical and biological characteristics of ecosystems. Change in water temperature has the greatest effect because most fish are poikilotherms, i.e. their internal temperature matches that of the ambient environment. As a consequence, changes in water temperature directly affect physiological processes, which in turn influence growth, survival, and behaviour.

Laboratory experiments have characterized optimum growth curves for different life stages (eggs, larvae, juveniles, and adults) under conditions where food supply is not limiting, whereby increasing temperatures result in increased growth (and development) up to a certain optimum temperature, above which growth decreases (Fonds and Saksena, 1977; Fonds *et al.*, 1992; Peck *et al.*, 2003). In the wild, species do not live at their optimum temperature for the whole year, nor are feeding conditions ideal everywhere, resulting in spatial and temporal differences in growth (e.g. Buckley and Durbin, 2006). The key to determining possible climate impacts is to examine when and where changes transcend normal (long-term) fluctuations within a population.

There is considerable variability of the physiological tolerance and response to environmental conditions among individuals within the same population. For example, differences in growth rate are commonly observed among fish in the same population/cohort, particularly during the larval (e.g. Folkvord *et al.*, 1994) and early juvenile periods (Peck *et al.*, 2004; Sogard, 1997). Individuals may undergo either an acute negative response to temperature or acclimation, depending on the degree and rapidity of temperature change, the condition of the individual, and/or other factors, such as availability of food and presence of other stressors. Inability to adjust physiologically to change may result in a spectrum of responses, including reduced growth, reproduction failure, or even death.

Acclimation may occur as a chronic response (e.g. to seasonal changes), whereas adaptation is measured in time-scales of generations and denotes an evolutionary response. Population-level differences have been observed by Svåsand *et al.* (1996), who found significantly higher growth rates and lower condition factors for Norwegian coastal cod compared with Arcto-Norwegian cod when fish from both populations were reared in the same conditions. *In situ* acclimation to rising temperatures is one possible response. If adaptation is not physiologically possible, then avoidance through movement constitutes another adaptive strategy.

Species may generally adapt to short-term variation in the environment (fluctuations) but longer-term, climate-driven changes in the bioenergetics of growth may have consequences for the success of a species in terms of its population abundance (Rijnsdorp *et al.*, 2009). Favourable environmental conditions, such as warmer temperatures prior to or during spawning, can lead to greater egg production and phenological changes in the onset and duration of spawning (Genner *et al.*, 2010). For example, earlier spawning periods have been demonstrated to occur for both plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in relation to increasing sea temperature in the North Sea (Teal *et al.*, 2008). Higher temperature extends the growing season for juveniles of both species, ultimately resulting in an increase in length of 0-group fish by the end of the year. However, at some point, increasing temperature becomes detrimental to the reproductive process. This threshold varies among species and populations. An understanding of the effects of such changes on species/populations is needed in order to develop a predictive approach to climate effects.

9.1.2 Climate-induced changes in recruitment, abundance, growth, and maturation

Marine fish recruitment is determined by the quantity of eggs spawned and, more importantly, by the cumulative mortality experienced by prerecruits, which, in most marine fish, results from the outcome of processes occurring during the first year of life (Houde, 2008). Mortality in early life stages is high and variable, generating large fluctuations in annual recruitment. As early life-history stages are likely to be more sensitive to environmental change than later stages, climate change is expected to greatly affect the abundance and distribution of fish through its influence on recruitment.

Recruitment is influenced by a variety of mechanisms, including the match–mismatch between the timing of reproduction relative to the production of food and/or predators (Cushing, 1990; Temming *et al.*, 2007) and connectivity (retention or transport) between spawning and nursery areas (Sinclair, 1988; Wilderbuer *et al.*, 2002; Han and Kulka, 2007). Environmental changes induced by climate change may affect the dynamics/availability of prey resources in different ways, resulting in mortality from starvation in the early life stages of fish. Changes in current patterns are a key feature of climate change, and timing of the strength and direction of currents may have a profound effect on the survival of eggs and larvae because of transport to unsuitable locations. Also, it has been suggested that the frequency of extreme events (e.g. temperature, storms, and rainfall) will increase as a response to global warming. The development of a storm during larval dispersal may transport larvae to locations where the chance of survival is low, or an acute warming event might be enough to seriously reduce the abundance of a species. Such an occurrence was observed for eelpout (*Zoarces viviparus*) in the Wadden Sea, where thermally limited oxygen delivery was observed to match temperatures beyond which growth and abundance decreased (Pörtner and Knust, 2007).

Multiple forcing and complex, sometimes offsetting, reactions to climate change make it difficult to establish unequivocal links between changes in the physical environment and the response of fish stocks. For example, a rise in temperature may increase growth rate while reducing the survival of eggs or larvae, resulting in lower recruitment. However, some climate effects seem clear for changes in recruitment or growth (Sissenwine, 1984; Cushing and Dickson, 1976; Drinkwater *et al.*, 2003). Interstock comparisons have indicated a dome-shaped pattern in recruitment strength. Key environmental factors, such as water temperature experienced during spawning, may significantly affect this pattern in both demersal and pelagic fish (e.g. Brander, 2000; MacKenzie and Köster, 2004). However, predicting future changes caused by climate change is challenging without a thorough knowledge of underlying recruitment processes or space- and time-specific climate change.

Pronounced long-term cycles in small pelagic species have been linked to climate variation (Schwartzlose *et al.*, 1999; Checkley, D., *et al.*, 2009). For example, the spring-spawning stock of herring (*Clupea harengus*) in the Norwegian and Barents seas has undergone remarkable fluctuations during the 20th and early 21st centuries. Spawning-stock biomass increased from a low of ca. 2 million tonnes early in the 20th century to more than 15 million tonnes in 1945. From about 1950, it decreased until collapse in the late 1960s (Toresen and Østvedt, 2000). The stock has undergone a large increase in biomass since the late 1980s and is now close to record levels. These long-term fluctuations, believed to be caused by variations in recruitment and survival of recruits, are strongly correlated with long-term variations in the mean annual temperature of the Atlantic water masses flowing into the Barents Sea from the south (Toresen and Østvedt, 2000; Klyashtorin *et al.*, 2009). Among marine fish, it appears that small pelagic species are particularly sensitive to environmental change.

The ICES/GLOBEC WGCCC found that higher temperatures lead to faster growth rates. The fastest growing cod are found in the Irish Sea, where a 4-group fish is, on average, fivefold larger than a 4-group fish off Labrador. Temperature not only accounts for differences in growth rates between stocks, but also for year-to-year changes in growth rate within a stock. In the Northwest Atlantic, declines in sea temperature were responsible for ca. 50% of the observed reduction in size-at-age of Atlantic cod on the northeastern Scotian Shelf and off Newfoundland from the mid-1980s to the mid-1990s. This is particularly important, given that 50–75% of the reduction in the spawning-stock biomass of the Newfoundland, Gulf of St Lawrence, and northeastern Scotian Shelf cod stocks during this period was the result of reduced weight-at-age (Anderson *et al.*, 2002; Ottersen *et al.*, 2004). Although the changes described above relate to cooling, substantial effects are also expected as a result of warming. Therefore, changes in the environment induced by climate change will probably have a profound effect on gadoids, and many other species, in the North Atlantic (Ottersen *et al.*, 2010).

9.1.3 Responses to climate in distribution and migration patterns

Change in the distribution of fish in response to climate-driven environmental factors, particularly temperature, may be limited by their ability to find tolerable/preferred temperatures. This potentially limits the species at different life stages if preferred temperature ranges are not accessible.

Based on an affinity for specific temperature ranges and biogeographical characteristics, species can be generally grouped as Mediterranean, Lusitanian, Boreal, and Arctic (Yang, 1982; Engelhard *et al.*, 2011). This classification allows the correlation of climate-change effects on the distribution of single species and can be extrapolated to species groups that have similar temperature and biogeographical preferences. In particular, fish species classified as "temperature keepers" (*sensu* Perry and Smith, 1994), such as wolffish (Anarhichidae; Figure 9.1), remain within a given temperature range by changing their range or depth distribution (Kulka *et al.*, 2004). Under warming conditions resulting from climate change, it is likely that such species and groups will move out of areas where temperatures rise above their preferred limits and enter new areas where the temperature regime is more suitable. A possible result of warming is either a shift or a breakdown in the traditional biogeographical zones and community dynamics as species that are more sensitive to temperature are likely to change location more than others (Beaugrand *et al.*, 2008). However, this scenario may be further confounded because different life stages of the same species often have different temperature requirements (Rijnsdorp *et al.*, 2009). For example, it would be detrimental to a population if adults moved to locations that were suitable for them but unsuitable for other stages.

Ocean currents are also decisive in determining the distribution of species and may be altered by climate change (Corten, 1990; Corten and Van de Kamp, 1996). For example, the eggs, larvae, and juveniles of many species require currents to transport them to specific nursery areas that provide suitable physical characteristics, sufficient food resources, or refuge from predation.

Figure 9.1. Striped wolffish (*Anarhichas lupus*). (Photo by D. W. Kulka.)

Thus, adults may move into new areas because of a rise in ambient temperature, but if currents there do not retain the early life stages or transport them to locations suitable for their survival, the species cannot establish successfully. This can lead to a chronic reduction in recruitment and a general decline in the population (Han and Kulka, 2007; Peck *et al.*, 2009).

Some species are specialized and confined to specific substrata (e.g. the lesser weever (*Echiichthys vipera*) on sandbank crests in the North Sea (Ellis *et al.*, 2010) or structures (e.g. cold-water reef fish in the Northeast Atlantic (Costello *et al.*, 2005). Any climate-driven changes (e.g. temperature, prey resource) that make these habitats less suitable are expected to have important consequences for their survival. However, predicting future effects for such specialized species will be difficult. Only a thorough knowledge of the habitat associations and impending change to specific locations will provide the information required to predict the effects of climate change.

As global temperatures increase, the water cycle is expected to alter, with consequent changes in patterns of precipitation, river discharge, and salinity, particularly in coastal areas. In response to warming and increased salinity (Furevik *et al.*, 2002), modelling indicates that sea-ice cover in the Barents Sea will disappear within a few decades. The maximum extent of the edge of the sea ice in winter is predicted to retreat at an average speed of 10 km year^{-1}, leaving the entire shelf area ice-free by the year 2070. Sea-ice cover plays an important role in the productivity of more northerly species. For example, its extent has been linked to the feeding success of fish larvae (Fortier *et al.*, 1996) and to the survival of some species, such as polar cod (*Boreogadus saida*; Fortier *et al.*, 2006). Winter sea-ice cover also imposes a limit on the expansion of some fish species into higher latitudes, despite the availability of summer (ice-free) conditions that may be suitable for survival. Sea ice imposes a short period of extreme conditions that limits the capability of species to survive or permanently inhabit the area. Although the scale of the impacts from a rapid reduction in sea ice is not known, many species could be affected.

The interactive aspects of climate change may cause multiple bottlenecks to form in the distribution and survival patterns of fish (Figure 9.2). Defining the mechanistic factors that cause bottlenecks in population growth and geographic distribution of species is essential to the production of model populations and projection scenarios. Some projections have been made using "bioclimatic envelope (niche) modelling", which takes into account various environmental conditions correlated with the survival or current distribution of a species (Pearson and Dawson, 2003). Projected physical changes in water temperature and circulation, among other factors within ecosystems, can thus be translated into predicted changes in distribution and productivity that are based upon the ecological niche of a species.

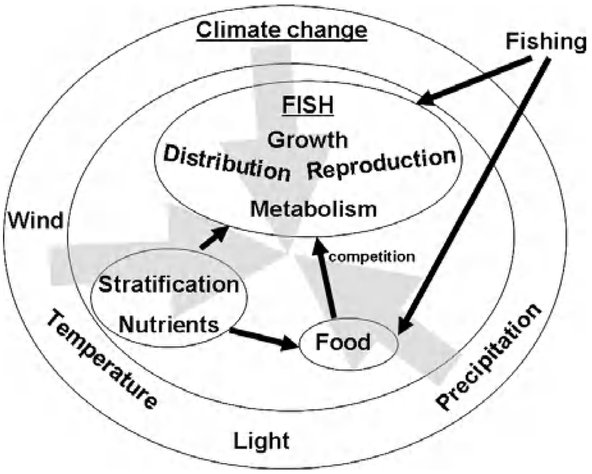


Figure 9.2. Schematic representation of climatic drivers that affect fish populations directly or indirectly. The outer circle represents the climatic drivers, which affect (grey arrows) most aspects of the ecosystem (the inner circle). The three innermost circles represent biotic factors (fish and food) and abiotic factors (stratification and nutrients). The black arrows represent the impact from fishing (or other anthropogenic effects), abiotic factors, and food for fish.

Much of what we understand about the effects of climate change on fish populations comes from correlative studies between time-series data for single species or stock complexes and climate variables. Such analyses have revealed changes in the abundance and distribution of fish that correlate with environmental variables, including changes that are identified as regime shifts. Shifts in distribution are generally most evident near the northern or southern boundaries of the geographic range of a species, where warming or cooling theoretically drives species to higher or lower latitudes, respectively (Rose, 2005). The warming trend in the Northeast Atlantic, for example, has instigated a northward shift in the distribution of fish species from southerly latitudes (Quero *et al.*, 1998; Beaugrand *et al.*, 2002; Beare *et al.*, 2004; Perry *et al.*, 2005; ICES, 2008a). Similar findings have been reported for a variety of regions, including the Arctic and the Nordic and Barents seas (Quero *et al.*, 1998; Toresen and Østvedt, 2000; Björnsson and Pálsson, 2004; Astthorsson and Palsson, 2006; Astthorsson *et al.*, 2007; Loeng and Drinkwater, 2007; Drinkwater, 2009), the North Sea/English Channel (Reid *et al.*, 2001b; Brander *et al.*, 2003; Beare *et al.*, 2004; Genner *et al.*, 2004; Alheit *et al.*, 2005; Perry *et al.*, 2005; Rindorf and Lewy, 2006; Dulvy *et al.*, 2008), the Celtic Sea (Stebbing *et al.*, 2002; Sims *et al.*, 2003; Cotton *et al.*, 2005; Houghton *et al.*, 2006; ICES, 2007d), the Bay of Biscay and Iberian coast (Quero *et al.*, 1998; Sánchez and Serrano, 2003; Blanchard and Vandermeirsch, 2005; Bañón and Sande, 2008), and the Baltic Sea (Nielsen *et al.*, 1998; Aro and Plikshs, 2004). (See Figure 9.3 for schematic examples of climate-induced changes in the ICES Area.)

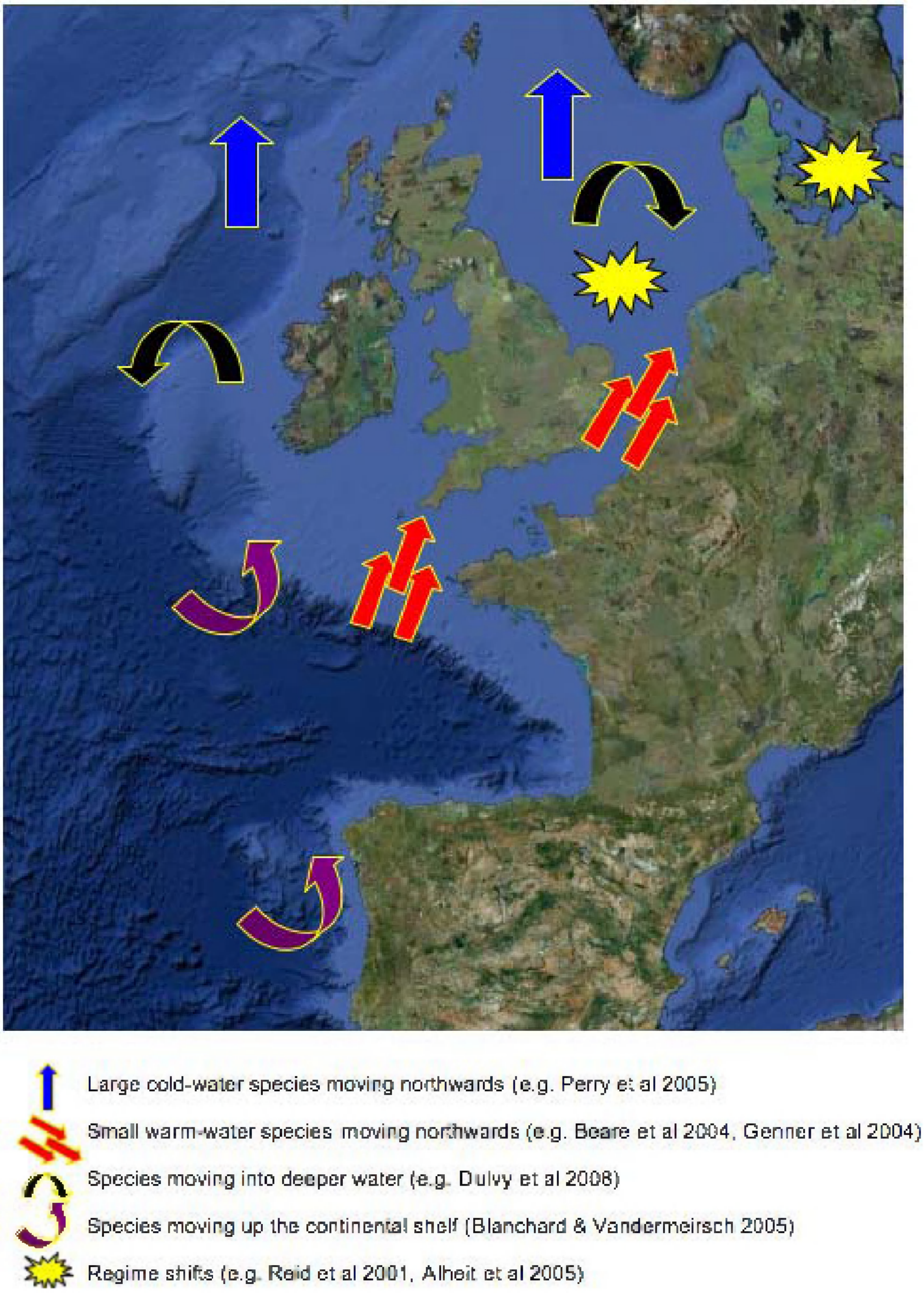


Figure 9.3. Reported climate-induced changes in the distribution of species and composition of assemblages.

Altered distributions of fish species can also be attributed to changes in the range of a species that coincide with a change in overall abundance. For example, the summer–autumn distribution of the northern blue whiting (*Micromesistius poutassou*) stock expanded during the early 2000s throughout the Norwegian Sea and farther east into the Barents Sea as a result of increased recruitment and abundance, trends attributed to a warming of the region (Hátún *et al.*, 2009b). Numbers of Norwegian spring-spawning herring increased with an increase in temperature during the 1990s (Toresen and Østvedt, 2000). The population now migrates out into the Norwegian and Greenland Seas towards Iceland to feed and spawn (ACIA, 2005), whereas capelin (*Mallotus villosus*), whiting (*Merlangius merlangus*), haddock (*Melanogrammus* *aeglefinus*), and anglerfish (*Lophius piscatorius*) have exhibited large increases in abundance simultaneously with distribution extensions corresponding to the recent warming (Astthorsson *et al.*, 2007). Fluctuations in the relative abundance of basking sharks (*Cetorhinus maximus*) within the Celtic Sea area have been positively correlated with sea surface temperature and the North Atlantic Oscillation (NAO; Cotton *et al.*, 2005). Although prey density is a key factor in determining short-term distribution patterns (Sims and Quayle, 1998), long-term behavioural choices by basking sharks may relate more closely to occupation of an optimal thermal habitat that acts to reduce metabolic costs and enhances net energy gain (Crawshaw and O'Connor, 1997; Sims *et al.*, 2003).

Warming in the North Sea has been pronounced. The latitudinal response to warming in demersal fish assemblages in this region is varied; however, two composite patterns have emerged: (i) a northward shift in the average latitude of abundant and widely distributed thermal specialists (e.g. pilchard (*Sardina pilchardus*), saithe (*Pollachius virens*), John dory (*Zeus faber*), grey gurnard (*Eutrigla gurnardus*), poor cod (*Trisopterus minutus)*, striped red mullet (*Mullus surmuletus*)); and (ii) a southward shift of relatively small, southerly species with limited and sporadic occupancy and a northern range boundary in the North Sea (e.g. scaldfish (*Arnoglossus laterna*), solenette (*Buglossidium luteum*), bib (*Trisopterus luscus*), sole, and lesser-spotted dogfish (*Scyliorhinus canicula;* Dulvy *et al.*, 2008; ICES, 2008a). The availability of shallow habitats can be temporary, because a single cold winter may cause species to vacate the area (e.g. solenette and scaldfish; van Hal *et al.*, 2010), recolonizing when conditions improve.

The shift of warm-tolerant Lusitanian species is consistent with climate change acting through the warming of suitable shallow habitats in the southern North Sea and through NAO-linked inflows of warm water into the North Sea proper. For example, increase in abundance of striped red mullet, pilchard, John Dory, and snake pipefish (*Entelurus aequoreus*; Beare *et al.*, 2005; ICES, 2008a) has been related to an increase in the flow of Atlantic water through the Strait of Dover coupled with favourable winter conditions (Corten and Van de Kamp, 1996; ICES, 2008a). This effect can be illustrated in the changes in spatial distribution for anchovy (*Engraulis encrasicolus*) and Atlantic cod in the North Sea. In the case of anchovy, a more southerly species, the increase in abundance occurred evenly over almost the entire area except the northernmost extent (Figure 9.4). For cod, a more northerly species, the decrease in density occurred throughout the North Sea but was much greater near the coast of the Netherlands and Germany in the south where waters are warmest (Figure 9.5).

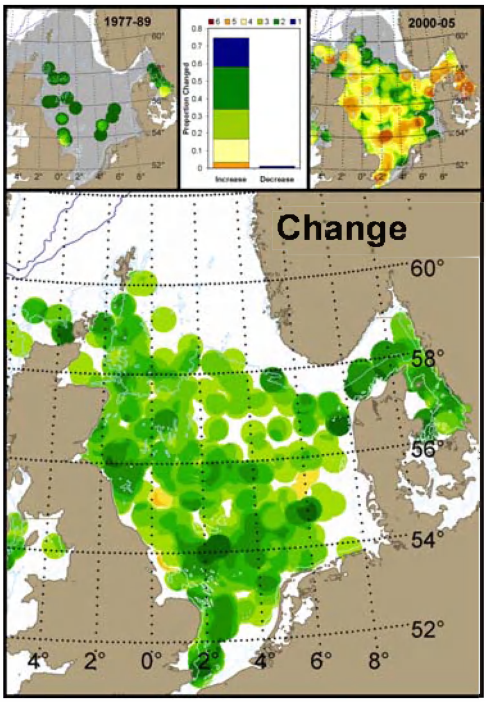


Figure 9.4. Change in the distribution of anchovy (*Engraulis encrasicolus*) between 1977–1989 and 2000–2005 in the North Sea, quarter 1 (ICES, 2008a). Upper left panel: distribution in the initial period (1977–1989); upper right panel: distribution in 2000–2005 (grey = sample areas with no catch; green to orange = low to high catch rate. Lower panel: change in distribution between 1977–1989 and 2000–2005 (blue to green colours = increasing density, with darker colours indicating the largest change; yellow to red = decreasing density, with red indicating the largest changes. Upper centre graph: proportion of the total survey area where there was an increase and decrease in the area occupied, broken down by amount of increase or decrease; 1–6 = low to high density. (Source: Tasker, 2008.)

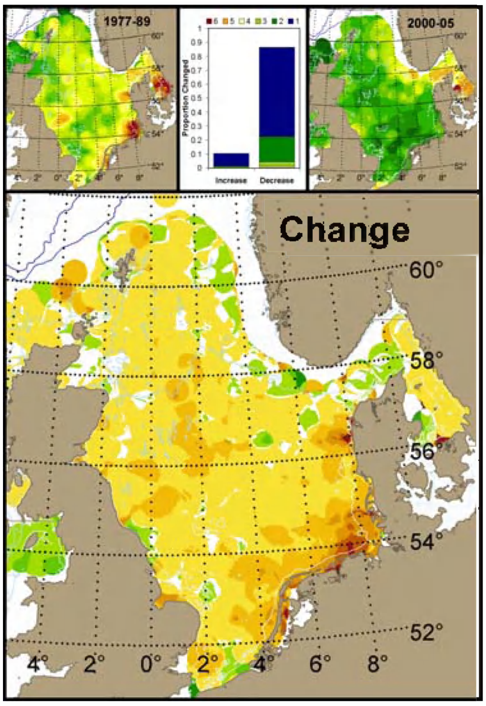


Figure 9.5. Change in the distribution of Atlantic cod (*Gadus morhua*) between 1977–1989 and 2000–2005 in the North Sea, quarter 1 (ICES, 2008a). Upper left panel: distribution in the initial period (1977–1989); upper right panel distribution for 2000–2005. See Figure 9.4 for characterization of the colour categories. (Source: Tasker, 2008.)

Along with latitudinal shifts in distribution, many species have followed temperature gradients that have resulted in change in depth distribution. This can be seen in a number of the North Sea demersal fish assemblages that increased their depth distribution by ~3.6 m decade^{-1} in response to climate change (Van Keeken *et al.*, 2007; Dulvy *et al.*, 2008). Thus, although mean latitude reveals no change for some species, a response to climate may be found instead as a shift to deeper, cooler waters, for example, plaice (Perry *et al.*, 2005; Van Keeken *et al.*, 2007), and cuckoo ray (*Leucoraja naevus*; Perry *et al.*, 2005). Hedger *et al.* (2004) demonstrated that cod were found in deeper water during 1990–1999 compared with 1980–1989, but their distribution with respect to temperature was unchanged. A similar large-scale shift of many demersal species to deeper waters was observed in Newfoundland/Labrador waters in the Northwest Atlantic in response to a period of cooling when species moved to deeper, warmer waters (Atkinson, 1994).

Warming can result in the appearance and increase in abundance of rarer migrant species to a particular area. An example is the influx of snake pipefish to the North and Norwegian seas (Lindley *et al.*, 2006; Harris, M. P. *et al.*, 2007; Kloppmann and Ulleweit, 2007; van Damme and Couperus, 2008), which is hypothesized either (i) to coincide with a rise in winter, spring, and summer sea temperatures (January–September), when eggs are developing and larvae are growing (Kirby *et al.*, 2006); or (ii) to result from changes in zooplankton (prey) availability, which in turn has been caused by changes in the hydroclimatic environment (van Damme and Couperus, 2008). In the Celtic Sea, an increase in sightings of rare migrant species, such as bluefin tuna (*Thunnus thynnus*), triggerfish (*Balistes capriscus*), thresher shark (*Alopias vulpinus*), blue shark (*Prionace glauca*), sting-rays (Dasyatidae, Stebbing *et al.*, 2002), ocean sunfish (*Mola mola*; Houghton *et al.*, 2006), and sailfin dory (*Zenopsis conchifer*; Swaby and Potts, 1999) have been reported. Similarly, new records of species with a tropical affinity have increased in the Bay of Biscay and along the Iberian coast (Punzón and Serrano, 1998; Bañón, 2000, 2004; Bañón *et al.*, 2002, 2006, 2008; Arronte *et al.*, 2004; Bañón and Sande, 2008).

Two species related to this phenomenon were the grey triggerfish (*Balistes carolinensis*) and the Senagalese sole (*Solea senegalensis*), previously unknown but now providing a measurable biomass in demersal surveys (Bañón *et al.*, 2002). In most of the cited papers, climate change is described as the driving agent of this increase, with ocean warming and/or changes in current patterns in the North Atlantic bringing more southerly water into the northeast. However, an increase in the exploration of deep-sea fish resources in recent years may also have enhanced the discovery of new deep-water species north of their known distribution (Bañón *et al.*, 2002). Thus, change (expansion) in survey area must be differentiated from expansion in species distributions.

Although species habitat occupancy and latitudinal and depth distributions appear to be changing in response to warming and/or hydrography, there is no factor that consistently responds to a single measure of temperature or hydrography across a range of species. Instead, considerable heterogeneity is found in the response of individual species to various measures of climate variability. There is still scope to determine the underlying ecological factors, such as niche (pelagic/demersal), trophic level, and particularly body size, that contribute to the heterogeneity of response.

Comparative studies reveal that a substantial number of species do not appear to change distribution in response to climate change, at least when considered over the range of variability observed over the past 50 years. Species that are not temperatureseekers are affected less by thermal conditions and more by other factors. The analyses presented by e.g. ICES WGFE (ICES, 2007d, 2008a) seem typical of multispecies climate–biological response analyses, where species demonstrate heterogeneous responses and, as a consequence, it can be difficult to recognize general patterns. As individual species demonstrate specific responses to climate change, classifying groups of species into sets of "ecotypes", based on similarities in certain relevant biological characteristics (biogeographical affinity, reproductive mode, body size, trophic niche, and habitat), may facilitate extrapolation and allow projections of the potential effects of climate change on fish assemblages. Perry *et al.* (2005) found it difficult to define a single relationship between life histories and distributional response, and based their conclusion on a categorical test (large vs. small), rather than treating body size as a continuous variable. It may be that the variance in the trends of individual species confounds efforts to uncover a general pattern. The focus of climate–fish studies is thus developing toward an ecosystem-scale indicator of the biotic response of aggregate demersal fish assemblages to climate variability and longer-term climate change (Genner *et al.*, 2004; Dulvy *et al.*, 2008).

9.2 Joint effects of climate and fisheries

Although climate variability and change evidently affect marine fish populations as described above, fish communities have also been under intensive harvesting pressure for many years. Distributional changes of fish in relation to climate are often exacerbated or confounded by the effects of fishing pressure and related mortality. Apparent temperature-related shifts in species distribution may, at least in part, be a consequence of local patterns of fishing pressure (Hutchinson *et al.*, 2001; Daan *et al.*, 2005; Wright *et al.*, 2006) leading to different rates of depletion in spatially segregated substocks (Hutchinson *et al.*, 2001; Wright *et al.*, 2006) overlain by warming effects.

Effects of fishing on fish populations are well studied and are known to lead to broad-scale changes in the abundance, distribution, and size structure of fish stocks (Bianchi *et al.*, 2000; Rochet and Trenkel, 2003; Dulvy *et al.*, 2004; Shin and Cury, 2004; Daan *et al.*, 2005). In addition, changes in life-history parameters (Grift *et al.*, 2003; Jorgensen *et al.*, 2007; Hidalgo *et al.*, 2009) and a reduction in genetic diversity and effective population sizes (Hutchinson *et al.*, 2003; Hoarau *et al.*, 2005) have been observed. Furthermore, the intensive pressure of fisheries is known to cause changes in fish community assemblages, including reduction in diversity (Smith *et al.*, 1991; Bianchi *et al.*, 2000; Jackson and Mandrak, 2002; Worm *et al.*, 2006). This can lead to further implications for the ecosystem, such as trophic cascades or regime shifts (Myers and Worm, 2003; Frank *et al.*, 2005; Daskalov *et al.*, 2007; Möllmann *et al.*, 2008). Although these effects are well known, the question remains as to how, and by how much, fishing-induced changes may affect the ability of fish populations to respond to climate variability and change.

Evidence already exists that exploitation may change the demographic structure of populations and structural components of ecosystems, altering their ability to respond to climate change. The demographic effects of fishing (removal of large/old individuals) are likely to have substantial consequences in terms of the capacity of populations to withstand the deleterious impacts of climate variability via a variety of pathways (e.g. direct demographic effects, effects on migration, parental effects). Similarly, selection of population subunits within metapopulations may lead to a reduction in the capacity of populations to withstand climate variability and change. At the ecosystem level, fishery-induced reduction in biocomplexity may be destabilizing and ultimately lead to reduced resilience to climate perturbations. Differential exploitation of marine resources might also promote increased turnover rates in marine ecosystems, which could exacerbate the effects of environmental change (Möllmann *et al.*, 2008; Planque *et al.*, 2010).

9.3 Future research directions

Synergistic effects of multiple drivers on fish populations, as well as counteracting processes, need to be investigated further. Also, the response of fish stocks to climate needs to be considered in conjunction with fishing. Projecting the future impacts of fishing and climate change, and the interactions between the two drivers on fish populations, is a key challenge for future research (Lehodey *et al.*, 2006; Greene and Pershing, 2007). Part of this challenge will be to develop ecosystem models capable of representing the effects of multiple drivers on the fish community. These models will allow the exploration and development of management approaches that maintain the resilience of individuals, populations, communities, and ecosystems to the combined and interacting effects of climate and fishing. Perry *et al.* (2010) demonstrated that marine systems that are fished at lower levels and managed with respect to functional groups and communities, as opposed to heavily fished systems under single-species management, are likely to provide more stable catches with climate variability and change.

Building on the largely descriptive body of research carried out on climate-change effects to date, greater emphasis needs to be placed on understanding the underlying mechanisms and processes of response to, and species resilience and adaptations to, climate change. Future research needs to address the following.

- The effects of climate variability on annual to multidecadal scales and climate change on marine systems.
- The nature of the physiological processes underlying climate–fish response.
- The differences in response and vulnerability of all life stages of fish, identifying potential bottlenecks and the factors and processes limiting growth, survival, and population persistence.
- The similarity in the response of species to climate change and the development of potential groupings of species by their climate response.
- The interactions between climate change and fisheries effects on fish populations and the resilience and ability of communities to adapt to climate change.
- The effects of climate change on fisheries through modifications of fish growth, maturation, recruitment, survival, etc.
- The development of numerical modelling techniques to study the synergistic top–down (fisheries) and bottom–up (climate) effects on populations and communities.

The application of different types of models to study different aspects of species response, including distributional and bioenergetic change.

10 Sensitivity of marine ecosystems to climate and regime shifts

Jürgen Alheit (corresponding author) and Hans-Otto Pörtner

10.1 Marine ecosystems and climate

The effects of climate variability on marine ecosystems are the result of changes in abundance and distribution of populations and assemblages that are determined by growth, survival, and behavioural dynamics. All of these processes are affected by the sum of the immediate effects of the proximate environment on physiological processes within each individual of the assemblage (for a recent review see Rijnsdorp *et al.*, 2009). Whereas climate variability and change are sufficient to induce substantial bottom–up impacts on marine ecosystems, there are often other external drivers operating concurrently. These include the effects of fishing, aquaculture, ocean acidification, coastal development, eutrophication, pollution, dredging for aggregate extraction and for navigational purposes, marine noise, and introduced alien species. Consequently, the assessment of the responses of ecosystems to climate variability and change must be considered together with other drivers. Multiple drivers on marine ecosystems can result in coactive effects and simultaneous changes to different components of the ecosystem. For example, climate change can induce bottom–up effects that influence temperature and nutrient supply, and thus plankton productivity, while concurrent top–down impacts are occurring, for example, through predator and biomass removal by fishing (Möllmann *et al.*, 2008, 2009).

All of these multiple stressors are likely to increase the sensitivity of ecosystems to climate variability and change, particularly when acting synergistically. Sensitivity is defined here, after Perry *et al.* (2010), as:

> a measure of the strength of the relation between the biotic variable(s) (within an ecosystem) and the climate variable(s) so that, for example, increasing sensitivity implies an increasing correlation between fluctuations in population abundance (or another characteristic) and some climate signal.

Ocean warming and intensive fishing are especially detrimental in this context (Harley and Rogers-Bennett, 2004; Kirby *et al.* 2009; Planque *et al.*, 2010).

10.1.1 Ecosystem sensitivity to ocean warming

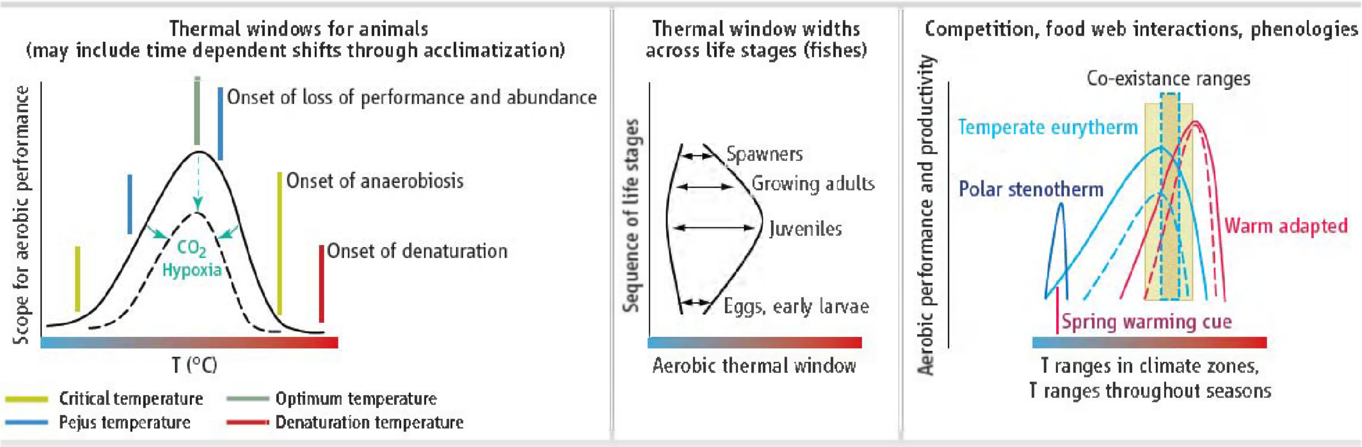
Climate variability affects all levels of ecological organization and pertinent changes have been observed in individuals, populations (life history and shifts in geographic range), and communities (species composition), and in the structure and function of ecosystems (McCarty, 2001). As most organisms are ectotherms and specialized to live within a limited range of temperature, they are, in consequence, sensitive to temperature fluctuation. Temperature shapes the large-scale biogeography of marine species. It influences physiological processes from the molecular level to the cellular and whole organism level, and at an ecosystem scale (Schmidt-Nielsen, 1990; Beaugrand *et al.*, 2009). It is well known that temperature, through its effect on physiology, can modulate species distributions, interactions, and trophodynamics. Past evidence and future predictions suggest a warming trend over the next century (e.g. Sheppard, 2004).

In terms of the impact of temperature on marine ecosystems, it is not necessarily the annual mean that has the highest influence but rather the temperature extremes operating at the edges of the thermal envelope of a species (Pörtner and Peck, 2010). For example, winter minimum temperatures may determine northern limits of

Lusitanian species, whereas summer maximum temperatures may determine the southern limits of Boreal species. Furthermore, the development of winter or summer temperature means and extremes may determine reproductive timing and success, and larval survival, and, in combination, contribute to the strength of recruitment pulses. In most cases, the mechanisms that come into play between the climate signal and the reaction of populations, communities, and ecosystems are obscure, and most studies to date have been based largely on correlation analysis. Physiological studies are needed that predict climate effects on ecosystems at species and community levels if we are to fully understand the mechanisms that contribute to the sensitivity of organisms and their life stages to climate signals (Pörtner and Knust, 2007; Pörtner and Farrell, 2008). With regard to temperature, which is the climate variable that has received most attention in terms of its effects, and which is likely to be the most important climate variable influencing marine ecosystems, a mechanistic understanding of cause-and-effect chains is emerging (e.g. Pörtner, 2002; Pörtner and Knust, 2007; Pörtner and Farrell, 2008). Pörtner and Knust (2007) and Pörtner *et al.* 2010 argued that the "concept of oxygen and capacity-limited thermal tolerance (OCLTT) in aquatic ectotherms", as explained below, could provide an integrative framework for developing a cause-and-effect understanding of the influence of climate change and variability on marine ecosystems, including foodweb structure, recruitment success, and fish landings.

Temperature acts on individuals through growth, reproduction, and mortality, and on populations through recruitment, distribution, and phenology. All organisms are living in thermal windows, the limits of which are set by minimum and maximum temperatures (see review by Pörtner and Farrell, 2008). These windows are as narrow as possible in order to minimize maintenance costs, and they are species-, life-stage- and even population-specific. When the environment of aquatic animals surpasses the "pejus" (meaning "turning worse") temperature thresholds at either end of the thermal envelope (Figure 10.1a), the aerobic scope of the organism is reduced, leading to hypoxaemia, caused by the limited capacity of circulatory and ventilatory systems to match oxygen demand (Pörtner and Knust, 2007). In this way, the thermally limited functional capacity of tissues, including those involved in oxygen supply to tissues, could lead to biogeographic shifts. Below and above the critical temperatures, only anaerobic performance is possible. These principles shape the performance capacity of the organism and the rate of all higher functions, such as muscular activity, behaviour, growth, and reproduction. The width of thermal windows changes with developing life stages, increasing from eggs to juveniles, and narrowing again towards spawning adults (Figure 10.1b). It has been suggested that reduced aerobic performance, instigated by environmental temperature surpassing the pejus limit, makes the organism more sensitive to mortality from predation or starvation (Pörtner and Knust, 2007).

The direct effects (expressed as biogeographic shifts) and indirect effects of warming on two key species in the North Sea demonstrate the sensitivity of an ecosystem to climate impacts. As a result of a direct response to increasing temperature in association with a positive NAO index, the North Sea cod (*Gadus morhua*) moved polewards (Perry *et al.*, 2005) and is considered to have reduced its reproductive performance (Pörtner *et al.*, 2008; see Figure 10.1b for the tightening thermal window of spawners). One of the major prey items of cod larvae, the copepod *Calanus finmarchicus*, has also adopted a more northerly distribution and declined markedly in abundance in the North Sea in response to, *inter alia*, rising temperature, thereby probably contributing to an observed reduction in cod recruitment (Beaugrand *et al.*, 2003). The North Sea copepod community has shifted from a system dominated by *C. finmarchicus* to one where the congeneric species *C. helgolandicus*, which has a higher thermal optimum (Helaouët and Beaugrand, 2007), is most abundant. The latter species, however, is not an adequate replacement in the diet of larval cod, because of its smaller size, poorer nutritional value, and its occurrence later in the year (Beaugrand *et al.*, 2003), leading to a classical match–mismatch problem (Cushing 1990). According to Pörtner and Farrell (2008), this difference in thermal windows might contribute to changes in species interactions and lead to shifts in spatial or temporal overlap (Figure 10.1c). Such a link between physiology, ecological niches (thermal windows), and biogeographic shifts opens promising leads for a better understanding of the response of species, populations, communities, and ecosystems to predicted global change (Helaouët and Beaugrand, 2009). Furthermore, the OCLTT conceptual framework is able to integrate the effect of additional stressors through their effects on temperature-dependent performance and limitation. Synergistic or antagonistic effects of temperature as a master variable, and of other abiotic and biotic stressors, describe the dynamics of the ecological niche of a species and reflect the multiple influences associated with effects of climate change (Pörtner, 2010; Pörtner *et al.*, 2010).



(a) (b) (c)

Figure 10.1. Temperature effects on aquatic animals. The thermal windows of aerobic performance. (a) Display optima and limitations by "pejus" ("turning worse"), critical, and denaturation temperatures, when tolerance becomes increasingly passive and time-limited. Seasonal acclimatization involves a limited shift or reshaping of the window by mechanisms that adjust functional capacity, endurance, or protection. Positions and widths of windows on the temperature scale shift with life stage. (b) Acclimatized windows are narrow in stenothermal species, or wide in eurotherms, reflecting adaptation to climate zones. (c) Windows still differ for species whose biogeographies overlap in the same ecosystem (arbitrary examples). Warming cues start seasonal processes earlier (shifting phenology), causing potential mismatch with processes timed according to routine cues (light). Synergistic stressors, such as ocean acidification and hypoxia, narrow thermal windows according to species-specific sensitivities (broken lines), further modulating biogeography, ranges of coexistence, and other interactions (Source: Pörtner and Farrell, 2008.)

The impact of warming on an ecosystem is not necessarily gradual. Beaugrand *et al.* (2008) suggest that there may be critical thermal thresholds leading to abrupt ecosystem shifts. Thus, they claim that the sensitivity of North Atlantic ecosystems is determined by a critical thermal boundary of 9–10°C. This threshold might reflect an abrupt change in the capacity to perform aerobically, as suggested by Pörtner and Farrell (2008). According to Beaugrand *et al.* (2008), abrupt ecosystem regime shifts (e.g. in the North and Baltic seas (Alheit *et al.*, 2005) and the Northwest Atlantic

(Greene and Pershing, 2007)) are associated with the movement of a biogeographical boundary characterized by the 9–10 °C isotherm. This boundary, which also marks the transitional region between the Atlantic Polar and the Atlantic Westerly Winds biomes, and is linked to the southern edge of the distribution of cod, has exhibited a marked northerly movement in the North Sea over the past 40 years, apparently generated by a rise of ca. 1 °C in annual mean SST (sea surface temperature) over the same period (Beaugrand *et al.* 2008).

10.1.2 Ecosystem sensitivity to climate and fishing

Traditionally, the effects of climate variability and fishing on ecosystems have been studied separately, with the aim of being able to predict climate and manage fishing (Perry *et al.*, 2010). At present, however, it is clear that the results and skill of prediction and attempts at management have been poor, largely because of the difficulty in disentangling the impacts of these two forcing mechanisms, which act in combination. It is the interaction of the effects of both climate and fishing that has driven the pronounced changes in ecosystems observed recently (Beaugrand *et al.*, 2008; Perry *et al.*, 2010; Planque *et al.*, 2010). It is still far from clear how the synergistic alliance of climate change and fishing pressure will affect the trophodynamics, biocomplexity, and productivity of marine ecosystems in future (Kirby *et al.*, 2009).

The effects of fishing pressure on fish communities include a decline in mean trophic level; a reduction in the mean size of fish; and, because smaller fish have higher metabolic rates, a reduced mean turnover time (Perry *et al.*, 2010). These changes affect the sensitivity of fish communities to climate because fish populations consisting of smaller individuals are more susceptible to climate variability (e.g. because the duration of the spawning period is reduced). This, and the impact of climate on individual fish and their populations, influences the sensitivity of whole ecosystems to climate forcing in the context of top–down and bottom–up control. The removal of large top predators leads to a considerable increase in small pelagic fish populations as their predation control is released (Pauly *et al.*, 1998). In the central Baltic, after the collapse of the cod stock, sprat (*Sprattus sprattus*) increased substantially in abundance at a time when the North Atlantic Oscillation (NAO) index entered a strongly positive phase in the late 1980s, becoming the most important fish species in the Baltic in terms of biomass (Alheit *et al.*, 2005). The removal of top predators can cascade down the foodweb over several trophic levels (Kirby *et al.*, 2009; Perry *et al.*, 2010). Such a cascade over the entire range, from cod down to primary producers, was suggested by Frank *et al.* (2005) for the eastern Scotian Shelf ecosystem, and by Möllmann *et al.* (2008) and Casini *et al.* (2008) for the Baltic Sea. In a similar vein, for the North Sea, Kirby *et al.* (2009) suggest that there have been two main periods over the past 50 years or so during which the community ecology was influenced by cod abundance and climate. They postulate that the interactions of reduced top–down control by cod and warmer SSTs since the mid-1980s (*nota bene*: not the late 1980s, when the NAO index increased) led to an increase in the abundance of decapods in the plankton and benthos (Figure 10.2).

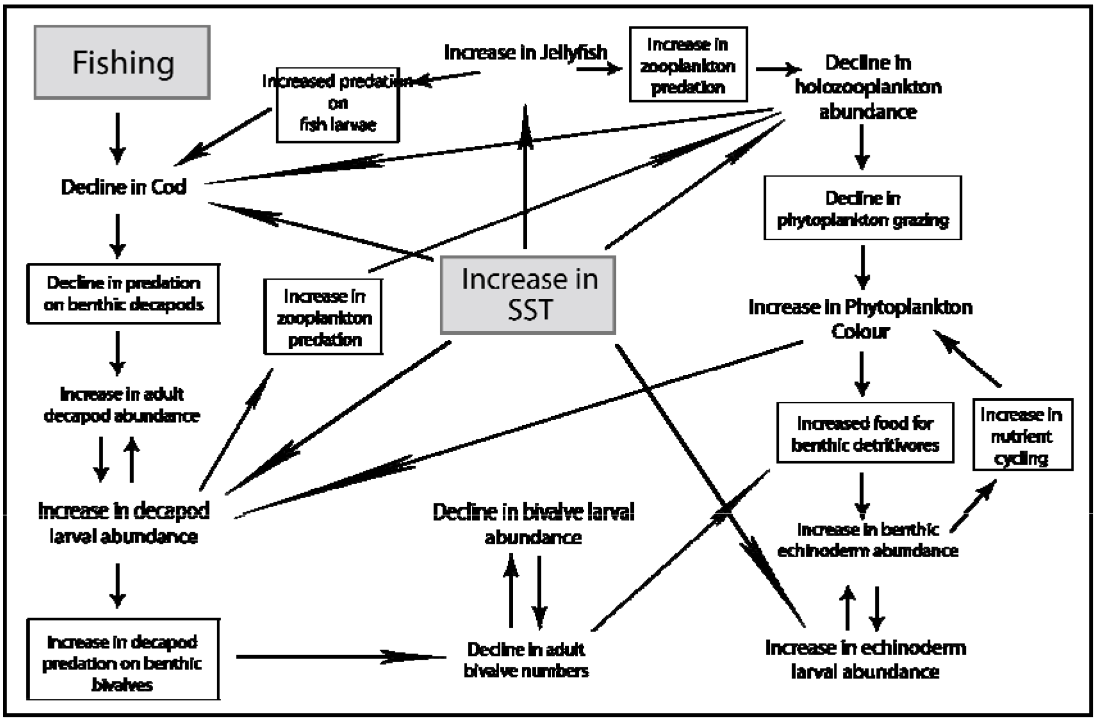


Figure 10.2. Schematic summary of the potential mechanisms affecting ecological interactions between cod, plankton, and benthic organisms in the North Sea. A decline in cod, driven by fishing, climate change, and consequent changes in the holozooplankton, releases benthic decapods from top–down control. The SST influences the larval abundance of benthic decapods, echinoderms, and bivalves positively. Reduced top–down predation and increased SST, therefore, benefits decapod abundance. Decapod predation on holozooplankton may affect cod recruitment, favouring decapods further. In the benthos, decapod predation on bivalves reduces bivalve abundance, despite warmer temperatures. Reduced grazing by holozooplankton contributes to the increased Phytoplankton Colour Index, which benefits decapod larvae and benthic detritivores. Macroinvertebrate bioturbation enhances nutrient cycling to support increased primary production in the plankton. A proliferation of jellyfish in the North Sea, which may exert top–down and bottom–up control on fish recruitment, may signal the climax of these changes. (Source: Kirby *et al.*, 2009.)

Hunt *et al.* (2002) and Litzow and Ciannelli (2007) give examples from the North Pacific of how ecosystems, driven by temperature, oscillate between top–down and bottom–up control. Brander *et al.* (2010) state that, with the exception of the major upwelling systems, warm low-latitude species-rich ecosystems are bottom–up controlled, so that, with decreasing poleward distance and decreasing temperature, species richness and fungibility (the degree to which species are interchangeable with others of the same functional type within the ecosystem) decreases and the tendency for top–down control of the low trophic levels increases. High species richness and fungibility seem to reduce the sensitivity of marine ecosystems to climate impact. Similarly, Planque *et al.* (2010) argue that overall reduction in marine diversity at individual, population, and ecosystem levels (e.g. by elimination through fishing) will probably lead to a decrease in the resilience and an increase in the response of populations and ecosystems to future climate variability and change. In their summary on ecosystem sensitivity to climate forcing, Perry *et al.* (2010) argue that ecosystems under heavy fishing pressure might face a stronger bottom–up control. According to their hypothesis, the selective removal of top predators could lead to (i) a reversal from top–down to bottom–up control, and (ii) an increase in the extent of bottom–up control in systems where this forcing dominates. Both alternatives would increase ecosystem sensitivity to climate forcing (Figure 10.3). According to Planque *et al.* (2010), the greater sensitivity of overexploited communities to bottom–up processes suggests that climate variability will have a greater impact on the structure of these communities, leading to greater variation in biomass and production, and to more rapid changes in species composition.

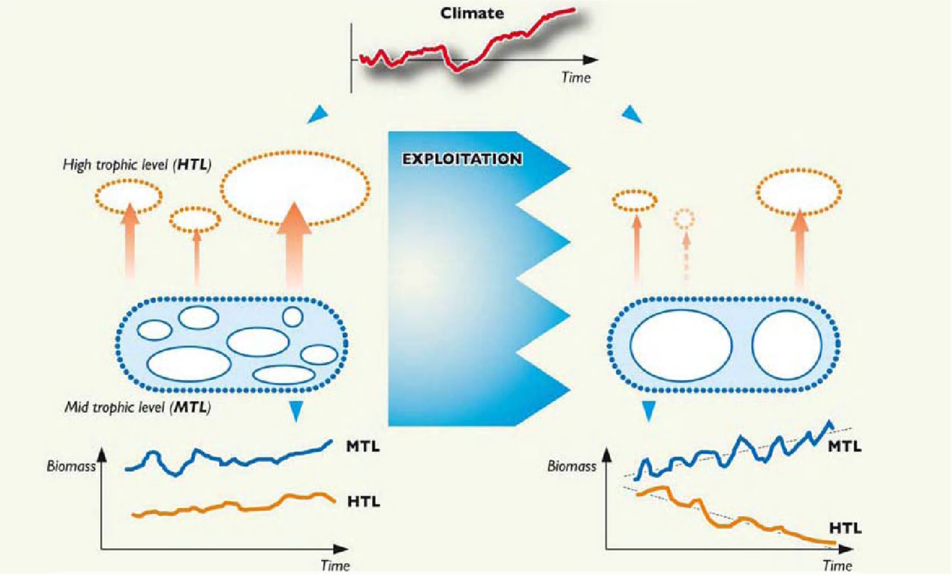


Figure 10.3. Schematic illustrating expected responses of unexploited and exploited simplified marine ecosystems to climate forcing. Left: an unexploited ecosystem with multiple high-trophic-level species that have high levels of abundance (top), supported by several mid-trophic-level species with large and low levels of abundance (middle), and how their aggregate biomasses vary through time (bottom). Right: how that same climate forcing is experienced by an ecosystem that has been exploited. The number and abundance of the high-trophic-level species have decreased (top), and the mid-trophic level has been simplified to a smaller number of species, but with higher levels of abundance (middle). The aggregate biomass of these mid-trophic levels now tracks the climate forcing more closely, whereas the high-trophic levels decline in abundance owing to exploitation (bottom). (Source: Perry *et al.*, 2010.)

10.2 Ecosystem regime shifts with a strong climatic background

10.2.1 Introduction

In the marine realm, the term "regime" was first used by Isaacs (1976) to describe distinct climatic and/or ecosystem states and, as early as 1989, Lluch-Belda *et al.* (1989) stated that regime shifts are transitions between different regimes. There is no universally accepted definition. Lees *et al.* (2006) listed several, but none of them is quantitative. Criteria for definition include sudden, high-amplitude, infrequent events, the number of trophic levels affected by the shift, and biophysical impacts (Lees *et al.*, 2006). A practical definition has been suggested by deYoung *et al.* (2004): regime shifts are changes in marine system function that are relatively abrupt, persistent, occurring at large spatial scales, and observed at different trophic levels. It is important to note that the duration of the shift itself is much shorter than that of the regime following the shift.

Regime shifts have taken place in all oceans, and their occurrence has been widely accepted; however, the concept of regime shifts remains controversial (Hsieh *et al.*, 2005; Lees *et al.*, 2006; Beaugrand, 2009). The mechanisms underlying these observed changes are largely unknown (deYoung *et al.*, 2008). Integrated physiological and ecological studies should be promising approaches to elaborate cause and effect (see Section 10.1.1). A better understanding of the nature of regime shifts is required so that they can be considered in the movement towards ecosystem-based management of living resources and their environments. Regime shifts may be caused by natural forcing (climate, internal community dynamics) and by anthropogenic forcing (fishing, pollution, habitat destruction). Both groups of drivers might act synergistically, and it is often difficult to disentangle them (Planque *et al.*, 2010). Here, we focus on climatic drivers, with the aim of clarifying the contribution of climate forcing.

During the past decade, many papers on regime shifts in marine ecosystems have been published, particularly in relation to climate variability in the North Atlantic and in the North and South Pacific (Benson and Trites, 2002; Alheit and Niquen, 2004; Beaugrand, 2004). This is partly the result of several long-term sampling programmes reaching a duration of 40 years or more and, in the wake of climate change, to an increasing interest in their results. The successful international GLOBEC programme (1992–2009) contributed in an important way to our understanding of regime shifts. Theoretical concepts of regime shifts stem largely from freshwater (lake) studies (Scheffer *et al.*, 2001). However, they are not easily transferable to marine systems, because regime shifts in lakes, which occur in closed systems and are usually much smaller in extent, are much easier to understand.

Detection of regime shifts is difficult. Until now, they have only been defined by retrospective analyses of long time-series that included a number of abiotic and biotic variables. For example, in several large marine ecosystems in the northern hemisphere, substantial changes were observed around the late 1980s, but it was approximately 10 years before scientists working on the North Sea became aware of the shift (Reid *et al.*, 2001a) and, for the Baltic Sea, it was approximately 15 years (Alheit *et al.*, 2005). However, as the subject of regime shifts became fashionable only in the second half of the 1990s, the scientific community has only recently taken notice of such observations. Nowadays, the pendulum has swung to the other extreme, and there seems to be a tendency to proclaim the occurrence of a regime shift after a very short period of observations, which might later prove to be unjustified if the new "regime" is not persistent (Peterson and Schwing, 2003). Several statistical analyses can be used to identify, characterize, and quantify a regime shift, such as time-series analysis, ordination, and cluster analysis (Beaugrand, 2009). Also, a sequential version of the partial Cumulative Summation (CUSUM) method combined with a *t*-test, and known as STARS, has been widely used (Rodionov, 2004).

It was suggested by deYoung *et al.* (2008) that a shift like that in the late 1980s in the North Sea, because it was caused by a change in mean climate, might be predictable, given an improvement in knowledge and the application of new prognostic atmosphere–ocean climate models. Although it is important to search for a better understanding of drivers and the causative mechanisms for changes in marine communities, because this is key to the prediction of how ecosystems might react to regime shifts associated with climate (Lees *et al.*, 2006), the prospects for realistic predictions in the near future appear poor. The main stumbling block is that sudden shifts in the climate system, knowledge of which is essential to forecasting the reaction of marine communities, apparently cannot be predicted at present.

What are the management implications of regime shifts? An ability to predict regime shifts would greatly improve the management of fisheries. As long as this remains unachievable, fishery management needs to develop and adopt precautionary measures that take account of and adapt to regime shifts. This might be easier in systems with a low diversity of species, such as the Baltic Sea, or systems which are largely dominated by a single-species stock, such as the Peruvian anchovy–sardine (*Engraulis ringens–Sardinops sagax*) complex. In regard to those Pacific ecosystems that support large anchovy or sardine populations, it seems best, once a system has entered a new regime, to assume that this situation will persist for several years and to increase fishing pressure on the species that is building up its population, thereby relaxing the pressure on the declining species (Alheit and Niquen, 2004).

10.2.2 Recent regime shifts in the North Atlantic with a strong climatic background

North Sea

After the increase in the NAO index in the late 1980s, SSTs in the North Sea were elevated (throughout the entire annual cycle) in most years (Alheit *et al.*, 2005), the average monthly windspeed increased from October to March, and the wind direction tended to be west–southwest (Siegismund and Schrum, 2001). This increased strength of westerly winds accelerated the inflow of oceanic water into the northern North Sea (Drinkwater *et al.*, 2003; Reid *et al.*, 2003b). Around the time of the increase in the NAO index, the North Sea experienced rapid changes in many biological and ecosystem processes, including the linkages between different components of the ecosystem, such as phytoplankton, zooplankton, benthos, fish, and seabirds. The North Sea plankton community directly responded to the environmental changes in the late 1980s, and Figure 10.4 depicts parallel changes in temperature and three trophic levels, including mero- and holozooplankton (Beaugrand, 2009). These changes were associated with a shift in the proportion of cold- and warm-water species of *Calanus* (Reid *et al.*, 2003b), an influx of oceanic species (Lindley *et al.*, 1990), an increase in warm-water zooplankton species (Beaugrand *et al.*, 2002), and a shift in dominance from holoplankton to meroplankton (Kirby *et al.*, 2007). The increasing abundance of meroplankton, particularly of echinoderm larvae, was related to warmer conditions occurring earlier in the year and increased phytoplankton abundance since the late 1980s. A significant decrease in zooplankton biomass was also observed (Beaugrand, 2004), caused by the decline of some of the key taxa typical of cold waters. Warmer water temperatures have induced changes in the phenology of many plankton species, whose seasonal peak occurrences shifted to earlier or later dates within the annual cycle (Greve *et al.*, 2001; Edwards and Richardson, 2004; Edwards *et al.*, 2006a). Phenological relationships have been decoupled, leading to trophic mismatch situations between phyto-, zooplankton, and fish (Beaugrand *et al.*, 2003; Edwards and Richardson, 2004). A large number of studies have reported a regime shift in the North Sea in the late 1980s (e.g. Edwards *et al.*, 2001b, 2004; Kröncke *et al.*, 2001; Reid and Edwards, 2001; Reid *et al.*, 2001a, 2001b; Beaugrand *et al.*, 2002; Beaugrand and Reid, 2003; Beaugrand, 2004; Alheit *et al.*, 2005; Weijerman *et al.*, 2005; Alheit and Bakun, 2010). Weijerman *et al.* (2005) applied principal component analysis and regime-shift analysis to a set of ca. 100 biological and physical variables and demonstrated that 1988/1989 was a major breakpoint in the data. This coincided with the change in the winter NAO index, indicating a possible relationship between climate, temperature, and the regime shift. Beaugrand *et al.* (2009) suggest that the regime shift in the late 1980s was caused by the North Sea having passed a critical thermal boundary of 9–10 °C. This regime shift of the late 1980s appears to be superimposed on a long-lasting biogeographic boundary shift to the north encompassing phytoplankton (Edwards *et al.*, 2006a), zooplankton (Beaugrand *et al.*, 2002; Beaugrand, 2004), and fish (Perry *et al.*, 2005). In addition, abrupt changes in the dynamics of zooplankton and fish populations were observed in the mid-1980s, the mid-1990s, and around 2000, which, however, do not fulfil all of the regime shift criteria listed above. A great challenge is to disentangle the effects of the positive periods of both the NAO and AMO.

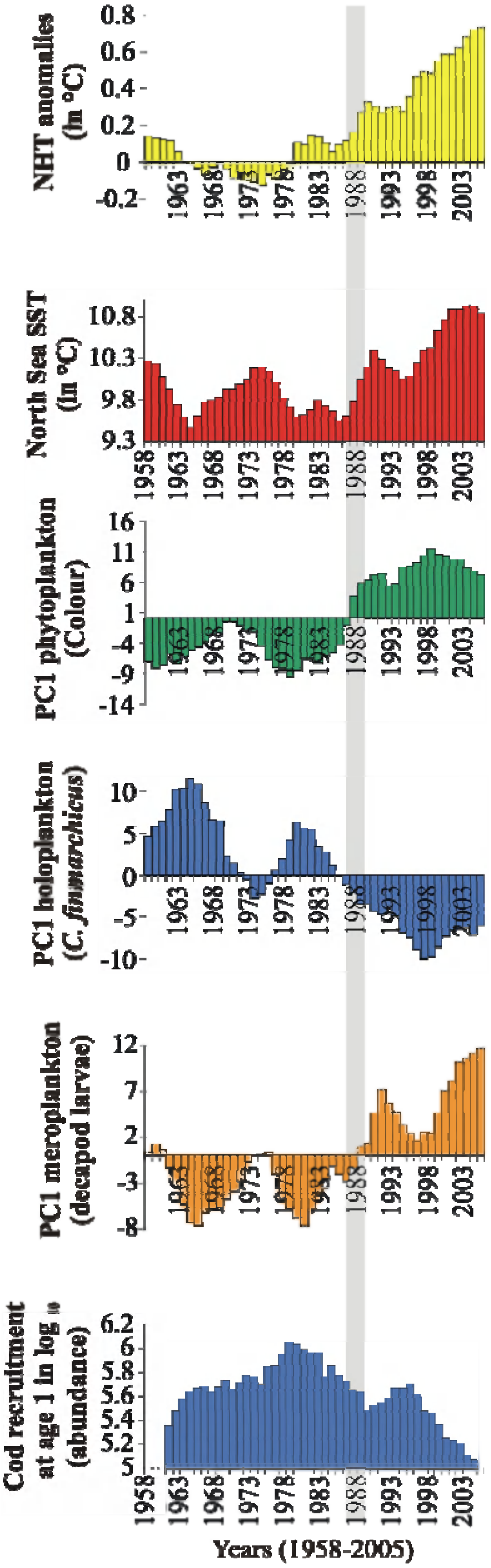


Figure 10.4. Long-term changes in northern hemisphere temperature anomalies, sea surface temperature in the North Sea, the Continuous Plankton Recorder Phytoplankton Colour (first principal component, PC1), *Calanus finmarchicus* (PC1), decapod larvae (PC1), and cod (*Gadus morhua*) recruitment at age 1 (PC1). (Source: Beaugrand, 2009.)

Baltic Sea

When the NAO index changed to a strongly positive phase in the late 1980s, the central Baltic Sea exhibited three temperature-mediated reactions: (i) a general temperature increase above the halocline; (ii) a reduction/lack of deep convective mixing in spring, resulting in an earlier stabilization and stratification of the water column; and (iii) an increased frequency in the intrusion of warm water from the North Sea in summer and autumn, heating up the halocline area (Alheit *et al.*, 2005). These temperature-mediated processes had important consequences for the pelagic communities above the halocline. Spring diatom biomass dropped markedly from 1988 to 1989 and stayed at a low level, whereas dinoflagellate biomass exhibited a steady increase from 1989 until the mid-1990s and stabilized thereafter (N. Wasmund, pers. comm.). Spring biomass anomalies of the dominant copepods *Temora longicornis* and *Acartia* spp., the different stages of which constitute the main food items of the larvae of the three dominant fish species (cod, herring (*Clupea harengus membras*), and sprat (*Sprattus sprattus*)), were negative from 1960 to the late 1980s but have remained positive since. The increase in copepod biomass was the result of improved reproduction, survival, and growth, favoured by higher temperatures and by increased hatching of resting eggs from the deeper sediments in spring; this, in turn, was a consequence of higher temperature in the halocline area between 50 and 80 m (Alheit *et al.*, 2005). After very low abundance in the early 1980s, sprat abundance and biomass began to rise in the late 1980s, just when the cod stock reached a minimum size. If there had been a strong cod stock, it is unlikely that sprat would have reached this high biomass in the 1990s. However, the decline of the cod is probably not the only reason for the rise in sprat because the period (ca. 8 years) between the beginning of the cod decline and the recovery of sprat is too long. Based on an analysis of 52 biotic and abiotic variables using multivariate statistics, Möllmann *et al.* (2009) suggested that the central Baltic exhibited two different regimes between 1974 and 2005, which were separated by a transition period from 1988 to 1993 (Figure 10.5).

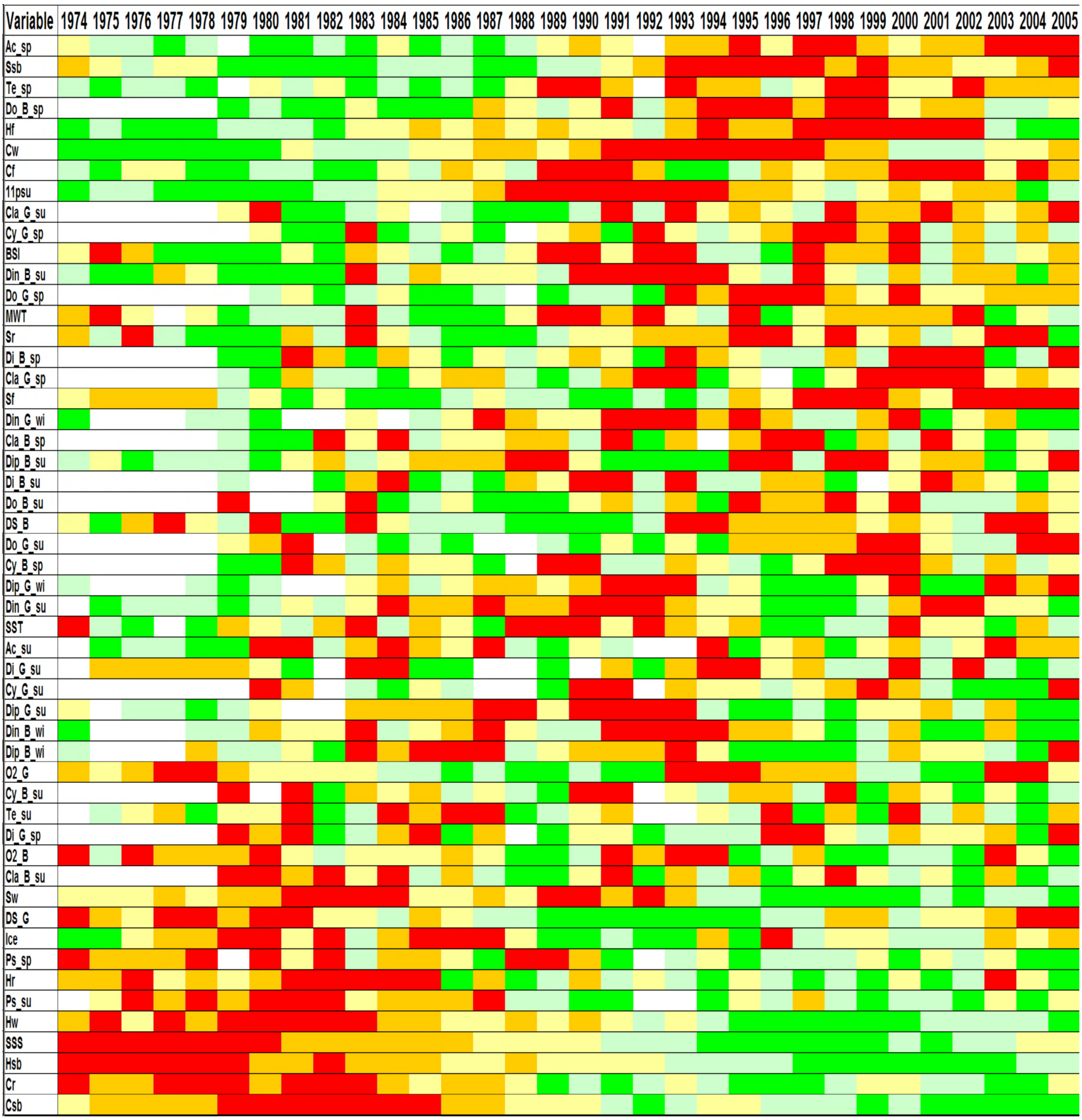


Figure 10.5. Traffic-light plot representing the development of the central Baltic Sea ecosystem; time-series transformed into quintiles and sorted according to the first component (PC1) of a principal component analysis; red = high values and green = low values of the respective variable. (Source: Möllmann *et al.*, 2009.)

Northwest Atlantic

The strengthening of the Arctic Oscillation in the late 1980s was followed by widespread changes in Arctic seas (Morison *et al.*, 2006). The pattern of water circulation and ice drift shifted, resulting in an enhanced outflow of low-salinity water that caused a reduction in the salinity of shelf waters from the Labrador Sea to the Mid-Atlantic Bight (Greene and Pershing, 2007), with associated changes in circulation and stratification. In addition, melting of permafrost, snow, and ice on land, together with higher precipitation, has contributed to an increase in river discharge into the Arctic Ocean. At the same time, the extent and thickness of Arctic sea ice have decreased. Lindsay and Zhang (2005) forward the hypothesis that 1989 represents a tipping point for the Arctic ice–ocean system, which has entered a new state, with very large extents of summer open water and winter first-year ice. At approximately this time, relatively low-salinity water started to appear from the Canadian Arctic Archipelago and influenced shelf sea ecosystems downstream from the Labrador Sea to the Mid-Atlantic Bight (Greene and Pershing, 2007). In the following year, a regime shift in the Northwest Atlantic was observed, with changes in the abundance and phenology of phytoplankton, zooplankton, and fish populations (Frank *et al.*, 2005; Greene and Pershing, 2007). The freshening led to increased stratification, which resulted in higher phytoplankton production and abundance (Figure 10.6) during autumn, in contrast to previous years when production tended to decrease because of eroding stratification, deeper mixing, and associated light limitation. Increased stratification and phytoplankton production were associated with a reassembly of the copepod community (Greene *et al.*, 2008). Smaller, shelf-associated copepods (e.g. *Centropages typicus*, *Metridia lucens*, *Oithona* spp., and *Pseudocalanus* spp.) increased, as did early copepodid stages of *Calanus finmarchicus*. However, abundance of later stages of *Calanus* did not increase, probably owing to increased size-selective predation by herring (*Clupea harengus*; Pershing *et al.*, 2005). This reorganization of the plankton community was accompanied by large changes in commercially exploited fish and crustacean populations, the most pronounced being the collapse of cod during the early 1990s (Greene *et al.*, 2008). The main reason for the collapse was overfishing, but the cold, low-salinity Arctic waters entering from the Canadian Archipelago must also have played a role (Greene *et al.*, 2008). Other species of fish and crustaceans have increased in abundance during this time, perhaps as a consequence of released predation from cod (Frank *et al.*, 2005; Pershing *et al.*, 2005). In a series of papers, Frank and colleagues have suggested an alternative hypothesis for explaining the regime shift in the Scotian Shelf ecosystem (Frank *et al.*, 2005, 2007; also Choi *et al.*, 2005). They attributed all of these changes to a trophic cascade, released by the overfishing of cod, which exerted top–down control in these areas as long as it was not much affected by fishing. However, Greene *et al.* (2008) claim that, despite the heavy predation pressure by cod and other demersal fish, and of cod overfishing, bottom–up processes linked to climate played the most important role in the observed regime shift. As described in Section 10.1.1, a synergistic interaction between the effects of climate and fishing has probably contributed to the changes in the shelf systems of the Northwest Atlantic.

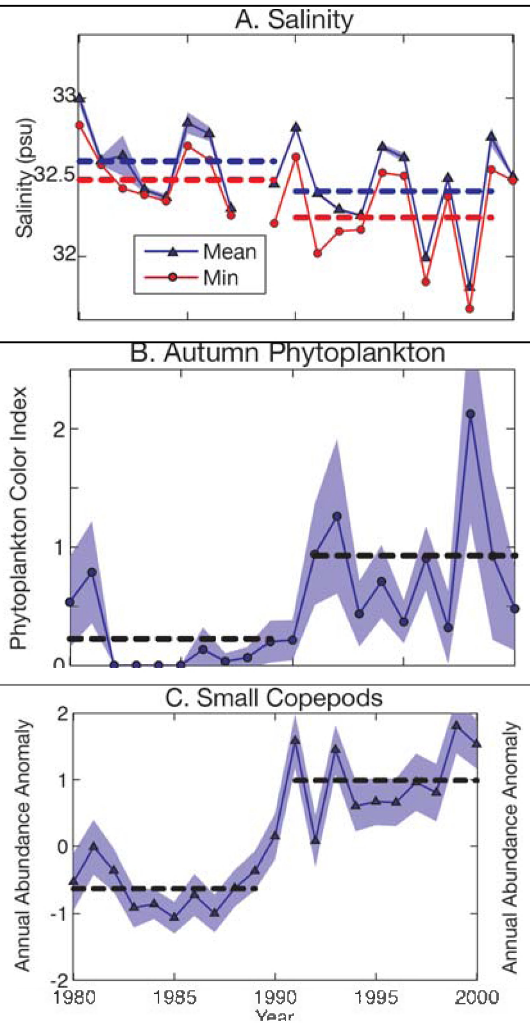


Figure 10.6. Ecosystem changes associated with a regime shift in the Northwest Atlantic from the Gulf of Maine and Georges Bank: (top) annual mean (blue) and annual minimum (red) salinity – decrease after the regime shift; (middle) autumn phytoplankton abundance as annual means of the Phytoplankton Colour Index – increase after the regime shift; (bottom) mean copepod abundance as annual mean anomalies of small copepods – increase after the regime shift. Dashed lines = mean values during 1980–1989 and 1990–1999; shaded areas = 95% confidence intervals. (Source: Greene and Pershing, 2007.)

10.2.3 Historical regime shifts

One way of investigating future scenarios under climate change is to use past events as a proxy. Changes in marine populations in response to the dynamics of the NAO and, more recently, the AMO (Atlantic Multidecadal Oscillation) have been observed in the past. "The largest and most significant climate-induced regime shift of the last century in the North Atlantic" occurred in the 1920s and 1930s and was much greater in geographical extent than those described above (Drinkwater, 2006). The event occurred in association with an elevated period of the AMO index during the first half of the 20th (Drinkwater, 2009) as a response to a pronounced warming of air and ocean temperatures in the northern North Atlantic and the high Arctic (Johannessen *et al.*, 2004). ICES reacted by organizing the first scientific meeting on climate change in 1948 in Copenhagen (Drinkwater, 2006) under the title "Climate Changes in the Arctic in Relation to Plants and Animals". A large number of fish stocks increased in abundance and northward shifts in biogeographic distribution were reported for many Boreal and Subtropical species, including benthic species, fish, marine mammals, and seabirds, whereas Arctic species retracted (Drinkwater, 2006). One good example is the Norwegian spring-spawning herring, whose biomass increased in the mid-1920s and decreased again around 1960. It then remained at a very low level before increasing again in the late 1980s (Figure 10.7). Large-scale changes in the extent of the population's distribution were observed between warm and cold periods. During warm periods, the herring migrate to feeding grounds off northeast Iceland, whereas, during cold periods, it stays near the Norwegian coast to feed (Drinkwater, 2006). However, fishing also played an important role in the decline of the herring. Although it is difficult to hindcast the relative contributions of climate and fishing, a rough estimate suggests that the curve of the spawning-stock biomass shown in Figure 10.7 (red) would have been similar to that of temperature (blue; S. Sundby, pers. comm.). Cod in high-latitude regions in the North Atlantic responded similarly to the first warming event (Drinkwater, 2009). The cod stocks of West Greenland, Iceland, and the Barents Sea increased in abundance and migrated northwards, probably driven by bottom–up processes. During the second warming period, the West Greenland and Barents Sea cod stocks also exhibited increased abundance and recruitment, whereas the Icelandic cod did not react. The study of cod reactions to the two warming periods demonstrates that we cannot necessarily expect similar responses under comparable external forcing in future (Drinkwater, 2009). Strong fishing pressure and other anthropogenic influences have often substantially changed the structure of populations (e.g. age composition, age of first maturity) and ecosystems so that the outcome of the forcing might be different. This must be taken into account when developing scenarios of the future, based on past experience (Drinkwater, 2009).

Long-term investigations in the western English Channel, which started around 1888 and are continuing, revealed that southern species of fish, plankton, and intertidal fauna increased in abundance between 1926 and 1936 and declined again in the early 1960s (Hawkins *et al.*, 2003), at about the time of the rise and fall of the AMO index. This phenomenon is known as the "Russell Cycle". Also, fish species of a more southern character, such as anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), migrated through the Channel into the North Sea (ICES, 2010b) and spawned in the German Bight, as has occurred again since the mid-1990s (Alheit *et al.*, 2007).

The cyclic, multidecadal-scale appearance and disappearance of fish populations in response to climate variability can be traced back for European sardine and herring populations, including the Bohuslän herring, for several centuries (Alheit and Hagen, 1997). Palaeoecological studies of marine and freshwater sediments reveal variability of the populations of sardine, anchovy, salmon (*Salmo salar*), and other species on centennial and millennial time-scales in response to climatic periods, such as the little ice age (Finney *et al.*, 2010). However, because of a lack of additional information for other trophic levels, it is questionable whether or not these changes can be termed regime shifts.

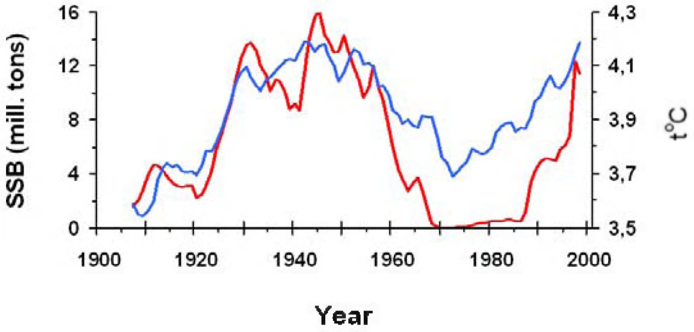


Figure 10.7. Estimates of Norwegian spring-spawning herring stock biomass (SSB, red line) and the 19-year running mean of temperature from the Kola Section (blue line). (Source: Drinkwater, 2006.)

10.3 Gaps in knowledge and research needs

- At present, we do not know if the characteristics of regime shifts will be affected by climate change. The initial assumption is that they are unlikely to be affected (in terms of their frequency, features, etc.) and, therefore, that marine ecosystems can be expected to experience regime shifts in future (e.g. variability as the climate changes). As a consequence, regime shifts and other threshold-like responses will make the observation and understanding of marine systems, and forecasting changes, more difficult.
- In order to understand the processes leading to climate-induced ecosystem regime shifts, a much better knowledge of the impact of the coupled ocean–atmosphere system on physical variables (e.g. advection, temperature) directly affecting abundance, distribution, and trophodynamics of plankton, benthos, and fish populations is essential. Cooperation with physical oceanographers and climatologists has been only rudimentary so far and needs to be substantially improved.
- At present, it is not possible to forecast climate-induced ecosystem regime shifts because the climatic forcing cannot be predicted. Research and modelling to develop an improved understanding of the mechanisms involved is needed.
- Regime shifts have usually been detected approximately 10 or more years after they happened. Attempts should be made to identify physical and biological indicators that allow earlier detection. Consequently, there is a need for an appropriate observation and monitoring system that will provide the relevant variables for the identification and prediction of regime shifts and climate change.
- More research needs to be dedicated to synergisms between climatic and anthropogenic forcing of ecosystem regime shifts.

Acknowledgements

We thank Ian Perry for critically reading the manuscript and for his useful suggestions.

11 Climate change and non-native species in the North Atlantic

Judith Pederson (corresponding author), Nova Mieszkowska, James T. Carlton, Stephan Gollasch, Anders Jelmert, Dan Minchin, Anna Occhipinti-Ambrogi, and Inger Wallentinus

11.1 Introduction

Species introduced to regions outside their native ranges as the result of human activities are known as "non-native species" (Shine *et al.*, 2000; Carlton, 2001). Non-native species that are known to affect native biodiversity in the ecosystem within which they become established, and/or have a negative economic effect on human society, are referred to as "invasive species" (Eno *et al.*, 1997; Shine *et al.*, 2000; Olenin *et al.*, 2010). However, Carlton (2002) has noted that, in marine systems, no quantitative boundaries have been placed on the criteria by which species are designated as invasive.

Many novel anthropogenic pathways for the introduction of marine species to new areas have arisen during the past century, and the speed and frequency of global shipping activities has also increased. As a result, non-native species introductions have become increasingly common along the Atlantic coasts of Europe and North America (Carlton and Geller, 1993; ICES, 2007b), and are now being reported on a regular basis (Pederson *et al.*, 2005; Arenas *et al.*, 2006; Mathieson *et al.*, 2008). Although we focus here on species that have been transported by human activities (e.g. the movements of ships and shellfish) to the North Atlantic, we note that human-mediated alterations to the environment (e.g. climate change) have led, or will lead, to invasions of species previously absent from the North Atlantic, either from the north, through newly created Arctic corridors, or from the south. For example, Therriault *et al.* (2002) and Reid *et al.* (2007) document the arrival of the North Pacific diatom *Neodenticula seminae* in the North Atlantic, whereas Sorte *et al.* (2010) summarize global examples of marine range shifts in general.

This section deals with the impacts of climate change that have already been observed for non-native species, and predicts the likely consequences of continued large-scale pervasive warming and ocean acidification for future invasions. The implications of regional-scale processes that include extreme weather events, storm frequencies, wave exposure, and the introduction and spread of species outside their natural distributional ranges in the North Atlantic are also discussed.

Although it has been suggested that a rise in records of non-native species may, in part, also be attributed to increased awareness and reporting by both scientists and amateur naturalists, it is often possible to distinguish new sightings from new invasions by a careful examination of the historical record in order to determine the probability of a species having been previously overlooked (Carlton and Geller, 1993). Moreover, the well-known decline in available expert systematists in many regions of the world means that a very large number of invasions among smaller and taxonomically difficult marine taxa are not reported, leading to a considerable under-reporting of the scale of invasions (Carlton, 2009).

The geographic scope of this section covers the Northwest and Northeast Atlantic and the North and Baltic seas, but excludes the Mediterranean. The focus on near-coastal marine and brackish-water benthic species reflects the lack of information currently available for non-native species in offshore benthic or pelagic communities. Exceptions include a compound sea squirt (*Didemnum vexillum*), which has been found to 80 m depth, forming extensive mats on the pebble gravel substrata of Georges Bank, smothering infauna, and potentially affecting fishing and aquaculture (Valentine *et al.*, 2007; Bullard *et al.*, 2007). Another is the American comb jelly (*Mnemiopsis leidyi*), a planktonic species that, during the past decade, has been recorded both in the North Sea, the Skagerrak, the Kattegat, and the southern Baltic, and can cause a substantial reduction in zooplankton populations. There is, however, no apparent connection between its appearance in northern Europe and climate change, and Eurasian populations appear to have originated from two geographically different areas in North America (Reusch *et al.*, 2010). Information is also available for the red king crab (*Paralithodes camtschaticus*), which was intentionally introduced into the Barents Sea for commercial purposes but has spread beyond the country of introduction to new areas. Its subsequent expansion on the shelf north of Norway is not linked to climate change (ICES, 2005b).

The pelagic realm is briefly discussed, addressing non-native plankton. Occasional rare records (vagrants), for which there is no evidence of a reproducing population (Lusitanian species in the Northeast Atlantic, or cryptogenic species and micro-organisms that may be complexes and whose histories remain debated), are not included. For harmful algal bloom (HAB) species, there is no good evidence of species being introduced by human vectors into Northeast Atlantic waters. Any link in their occurrence to climate change is weak at best (Don Anderson, pers. comm.; Scholin *et al.*, 1995). For example, all of the *Alexandrium* problems off the northeast coast of North America, and the *Karenia brevis* blooms in the Gulf of Mexico, which occasionally extend along the Atlantic coast, are natural occurrences that may be attributable to storms or widespread coastal blooms; it is clear that, in most cases, there are records of the presence of the species that pre-date more recent outbreaks, in the latter case for centuries. However, in a recent review, Hallegraeff (2010) suggested that a number of responses to climate change can be expected from HAB taxa in future, which may reduce existing blooms in some areas and cause the development of new blooms in other areas where they are not currently a problem. Any response may be even more complicated; Masseret *et al.* (2009), using molecular analysis, have demonstrated that the toxic dinoflagellate *Alexandrium catenella* exhibits great intraspecific diversity. It is evident that it is not possible to clearly define speciation and migration patterns with the techniques currently available, and that this situation may apply broadly to the taxonomic status of native and non-native HAB species and other micro-organisms.

11.2 Colonization and impacts of non-native species

The history and vectors of many non-native introductions in the North Atlantic are detailed in previous ICES reports. (e.g. ICES, 1999, 2004b, 2007b; see also Rilov and Crooks, 2009). Major anthropogenic pathways and transportation vectors of non-native marine species include shipping (via water, sediment in ballast tanks and ballasted cargo holds, hull fouling, sea chests, seawater pipe systems, anchor systems, and other hard surfaces), aquaculture, mariculture, recreational fishing, marine recreation, aquaria, the live seafood trade, education and research activities, the construction of canals, and the movement of structures such as drilling platforms, dry docks, pontoons, and log booms (ICES, 2005b). The initial sites of introduction and colonization of non-natives within the marine environment are often within man-made features, such as ports, marinas, and aquaculture or mariculture facilities (Pederson *et al.*, 2005; Minchin, 2006), making near-coastal and brackish waters particularly susceptible to invasions. Marine and estuarine invasions are the subject of research and recording programmes throughout the North Atlantic (e.g. the Global

Invasive Species Database (GISD) of the International Union for the Conservation of Nature (IUCN); the North European and Baltic Network on Invasive Alien Species (NOBANIS; http://www.nobanis.org/about.asp); the Marine Invader Tracking Information System (MITIS); the Non-Indigenous Species Database Network (NISbase; http://invasions.si.edu/nemesis/merge/spsearch.jsp); the Non-indigenous Aquatic Species Database (NAS) of the US Geological Survey; and the Delivering Alien Invasive Species Inventories for Europe (DAISIE; http://www.europe-aliens.org/; ended in 2008)).

The impact of non-native species on existing marine communities is both species-specific and regionally variable. Non-natives may act as dominant ecological engineers, competitors, and/or predators, leading to the alteration of the structure, functioning, and composition of some marine communities/habitats (Olenin *et al.*, 2007). They may, on occasion, also enhance population sizes of previously present species (Kochmann *et al.*, 2008; Rilov and Crooks, 2009) and provide substrate for additional non-native colonization. Such introductions can, therefore, result in both negative and positive changes within marine ecosystems (Olenin and Leppäkoski, 1999; Wallentinus and Nyberg, 2007).

To date, there has been no direct evidence to indicate that non-native species cause extinctions in recipient coastal communities. Few studies are sufficiently long term to facilitate the tracking of post-invasion demographic trajectories over extended periods, and there is limited study of potential extinctions among smaller marine taxa (J. T. Carlton, pers. comm.). Numerous studies since the 1950s demonstrate that species such as the Australasian barnacle *Austrominius modestus* (= *Elminius modestus*) became established in Europe during World War II and thereafter. Initial studies predicted that it would outcompete native cirripedes (Crisp, 1958), but at many natural shores throughout northern Europe where it became established, abundance subsequently declined to levels comparable with native co-occurring barnacles in most open-coast habitats (Southward, 1991; Harms, 1999; Mieszkowska *et al.*, 2005). Most recently, experimental studies indicate that it is outcompeting *Semibalanus balanoides* and *Balanus crenatus* in northern Europe in areas of lower salinity and embayments (Witte *et al.*, 2010).

11.3 Climate change in the North Atlantic

The marine climate of the North Atlantic has oscillated between warmer and cooler phases during the 20th century, with an incremental trend of increasing temperatures associated with global warming since the mid-1980s (see Section 3; Figure 3.4). In addition, changes to seawater chemistry (e.g. acidification; see Section 5), oceanic and coastal currents, and land–sea interactions, as well as biological aspects (including benthic–pelagic coupling, productivity, and eutrophication), may all have implications for established non-natives and their potential future colonizations. Recent climate-driven changes in geographic distributions and the relative abundance of native species of both warm- and cold-water origins have focused on regions of biogeographic transition between temperate and boreal waters (see Section 8). If climate change is a major driver of shifts in non-native species, it is likely that some of the first effects will also be seen at these boundaries.

Both global and regional climate models predict a continuation of the current warming trend throughout the 21st century, with the extent of warming depending on the emission scenario used in the models of the Intergovernmental Panel on Climate Change (IPCC, 2007a; see also Murphy *et al.*, 2009, and the US National

Oceanic and Atmospheric Administration (NOAA) National Weather Service Climate Prediction Center, http://www.cpc.noaa.gov/products/precip/cwlink/climatology/.)

11.4 Impacts of climate change on non-native species

Successful climate-driven invasions will depend upon a change in local or regional environmental conditions driving the system to a different environmental state (Walther, G. R., *et al.*, 2009). As a result of this alteration in climate, some native species will fail to adapt to their surrounding environment, whereas others will be able to take advantage of these altered climatic regimes. Climate change has not been a major driver of recent colonizations, but it exerts, and is likely to continue to exert, direct and indirect impacts on both native (see Section 8) and non-native marine species once successfully introduced. Recent patterns of response by non-native species are difficult to attribute to climate warming alone because of a paucity of both ecological and physiological data (Occhipinti-Ambrogi, 2007).

This section provides some examples of climatic impacts observed to date, with a relative assessment of confidence ascribed to each. The species have been selected on the grounds that:

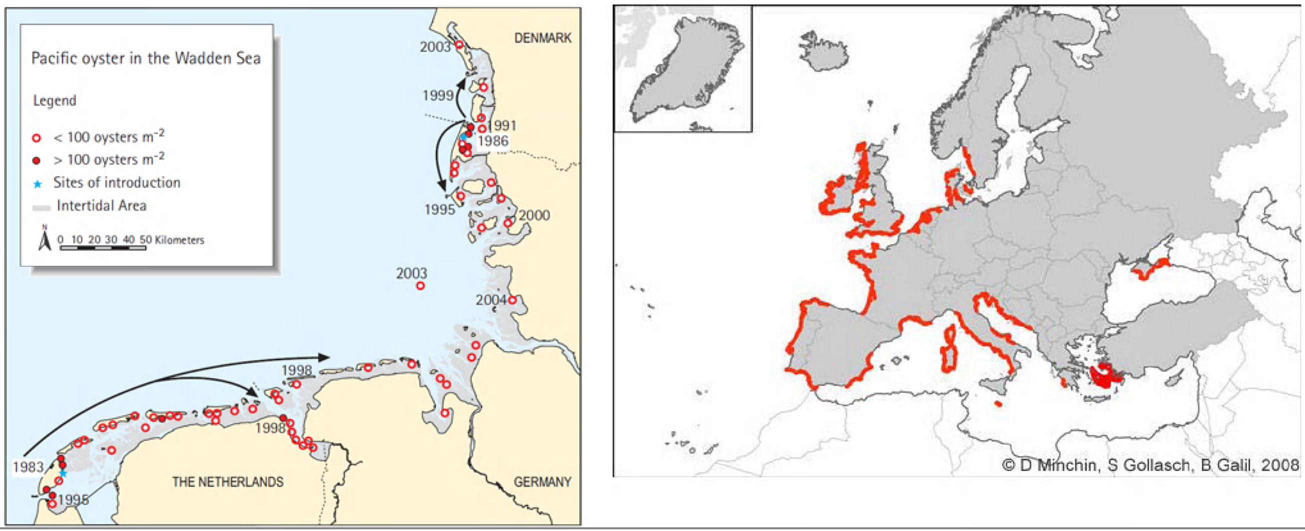
1) the current ranges of established, reproducing populations are well known and the species are not thought to be cryptogenic;
2) the species are taxonomically well described and defined, i.e. there is little or no debate on whether two or more species are being mistakenly discussed under another synonym;
3) the biology and ecology is well understood, with sufficient peer-reviewed literature on key life-history attributes to assess impacts of potential future environmental shifts on distribution, reproductive output, or phenologies;
4) the species have already exhibited an impact (environmental, economic, societal, or otherwise) where they have become established.

11.4.1 High confidence

Pacific oyster (*Crassostrea edulis*)

The Pacific oyster (*Crassostrea gigas*) has become established on natural shores in western Europe since its deliberate introduction in the 1970s from farmed stocks in British Columbia and Japan (Figure 11.1). *Crassostrea gigas* (as *C. angulata*) was introduced from Portugal to the UK in 1926, but populations declined rapidly when importation ceased (Utting and Spencer, 1992). In 1965, the then Ministry of Agriculture, Fisheries and Food granted licences for the importation of *C. gigas* to the UK after physiological tests revealed that this species required higher temperatures than those experienced at that time in UK waters (18–23°C over a prolonged period) in order to successfully recruit (Mann, 1979; Utting and Spencer, 1992). Wild spatfall and successful localized recruitment first occurred in the vicinity of oyster farms in southwestern England and North Wales after the unusually warm summers of 1989 and 1990 (Spencer *et al.*, 1994).

In the Wadden Sea, mean monthly sea temperatures exhibited increased deviations of 1–3°C from long-term means during the summers of 1994, 1997, 2001, 2002, and 2003 (Diederich *et al.*, 2005), consistent with observed higher European shelf sea temperatures (see Section 3, Figure 3.4). Enhanced spatfall was observed in Schleswig-Holstein during these periods and may have contributed to an increased spread of feral populations of *C. gigas* in the Danish Wadden Sea (Nehls and Büttger, 2007). Similar invasions of natural habitats have taken place along the Atlantic coastline of Europe up to Scandinavia as temperatures warmed sufficiently to allow successful recruitment (ICES, 2009b; Wrange *et al.*, 2010). Additional factors, including changes in the composition/availability of food, may affect juveniles and adult reproductive outputs, thereby accounting for some of the variability observed at different locations (Gosselin and Qian, 1997). Laboratory experiments indicate that declining rates of calcification, resulting from increasing concentrations of pCO_2, are less pronounced for oysters than for other bivalves, but these results have yet to be confirmed for wild populations (Gazeau *et al.*, 2007).



(a) (b)

Figure 11.1. (a) ***Crassostrea gigas*** **in the Wadden Sea. Blue stars indicate introduction sites (Texel, in the Netherlands, and Sylt, in Germany). Years indicate first records of settlement. Circles refer to mean Pacific oyster abundance in 2003 (from (Reise** ***et al.*****, 2005); (b) European distribution from DAISIE (http://www.europe-aliens.org/pdf/Crassostrea_gigas.pdf) and Sharma (2010).**

In the northeastern US, attempts to grow *C. gigas* have been unsuccessful. Environmental conditions at the proposed locations were not suitable, and the benefits were insufficient to justify replacing the cultivation of the native species *C. virginica*. The public strongly opposed its introduction (Calvo *et al.*, 1999).

Impacts. *Crassostrea gigas* now forms extensive reefs in Europe (Figure 11.2) and may outcompete native species, including mussels and other sessile rocky fauna (Nehls and Büttger, 2007; ICES, 2009b). However, it may also facilitate localized increases in biodiversity on soft substrata, where it stabilizes the sediment and creates a three-dimensional biogenic habitat (Mieszkowska, unpublished data), thereby having a positive impact within some systems. In contrast, there has been a negative socio-economic impact where reefs of sharp oyster shells have formed on public sandy beaches (ICES, 2009b). Spat from natural populations are used by growers as a seed source in southeastern England (Syvret, 2008), and fisheries are also sustained by natural spatfalls in France and the Netherlands (Maggs *et al.*, 2010).

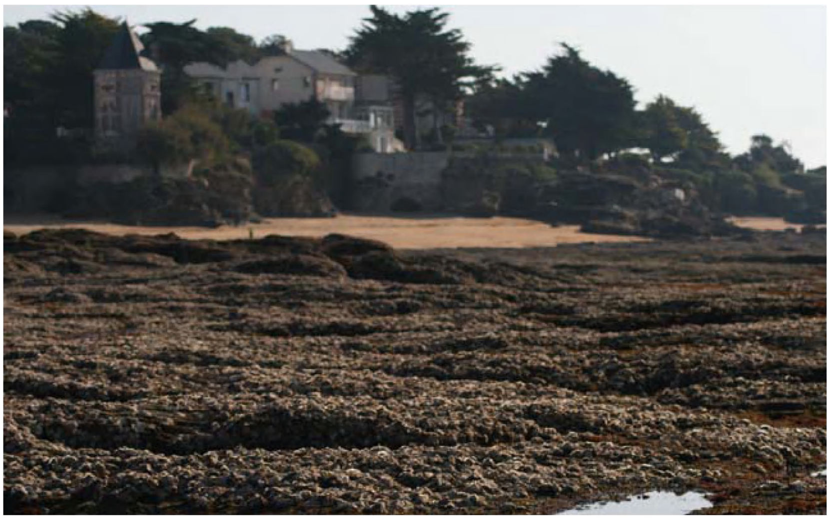


Figure 11.2. *Crassostrea gigas* forming a dense natural reef across the entire intertidal zone, Pornic, northern France. (Source: Graham Ledwith.)

11.4.2 Medium confidence

Codium fragile* subsp. *fragile

The task of attributing spread and proliferation of non-native species is further complicated by the potential for geographic differences in genotypes, expressed as adaptation to local thermal conditions. One such example is the non-native macroalga *Codium fragile* subsp. *fragile* (formerly subsp. *tomentosoides*), a green alga that is native to the western Pacific (Chapman, 1999). This species is now found on both sides of the Atlantic. It is considered to be a nuisance species in the Northwest Atlantic, but despite being found from northern Norway (by the 1970s) to Portugal, it has not aggressively colonized coastal habitats in the Northeast Atlantic, where it is usually in low abundance and cannot be readily distinguished from native species of *C. fragile* (Chapman, 1999). In the Northwest Atlantic, in contrast, *C. fragile* subsp. *fragile* is the only alga of this genus present, and has a marked impact on ecosystems because it is not a preferred food for herbivores and is in competition with other seaweeds so it can alter habitat extensively.

Codium fragile subsp. *fragile* was first reported in Europe in the 1800s, in the US in 1957, and, more recently, in Canada in 1991, with introduction attributed to shipping and aquaculture. Within Europe, the species has the potential to colonize more locations within its present range because its distribution is currently patchy. Although it can survive below-freezing temperatures, its temperature and salinity requirements necessitate prolonged periods for growth and gametogenesis. Its success in establishing in shallow estuaries and embayments in northern areas (e.g. Scandinavia and Prince Edward Island), but not in surrounding open seas, suggests it may be temperature-limited. However, the potential evolution of cold-adapted genotypes of *C. fragile* subsp. *fragile* may expand the colonization repertoire of this species. For example, as early as the 1970s, evidence revealed a divergence in the temperature tolerances of *C. fragile* subsp. *fragile* populations in Maine and populations farther south (Malinowski, 1974; Carlton and Scanlon, 1985). The predictive models of Burrows *et al.* (2009) forecast increased site occupancy and related impacts for *Codium* spp. (both native and non-native species) in the UK with rising sea temperatures of 0.4–3.3 °C by 2080.

Impacts. The alga can attach to commercial shellfish (e.g. oysters and scallops) to the extent that harvesting is seriously impaired (Coulautti *et al.*, 2006; ICES, 2007b). In the US, *C. fragile* subsp. *fragile* has a negative socio-economic impact because it washes ashore in such abundance that bathing beaches are closed during peak summer periods until the alga is removed from the affected areas (J. Pederson, pers. obs.). It has also successfully occupied areas where eelgrass (*Zostera marina*) has died back and may prevent its re-establishment. As a species that is present all year in New England, *C. fragile* subsp. *fragile* serves as a stepping stone for several non-native species, such as the bryozoan *Membranipora membranacea*. In the UK, the invading *C. fragile* replaces native *Codium* species (Reid *et al.*, 2009a), although it is likely to enhance local biodiversity because of the number of epiphytes it supports (C. Maggs, pers. comm.).

Manila clam (*Ruditapes philippinarum*)

The Manila clam (*Ruditapes philippinarum*) is another bivalve that was introduced into the North Atlantic for aquaculture. At the time, thermal thresholds for reproduction were considered to be greater than the regional summer seawater temperatures (Laing and Utting, 1994). The culture of *R. philippinarum* began in Europe during the cooler 1970s and 1980s. Only recently has this species formed self-sustaining populations in the wild, which are now of sufficient size to sustain small commercial fisheries in Poole Harbour, southern England (Jensen, A. C., *et al.*, 2004). These introductions have been linked to rising summer temperatures (Laruelle *et al.*, 1994; Caldow *et al.*, 2007). Latitudinal variation in the timing and reproductive activity of *R. philippinarum* is positively related to temperature gradients, and there is growing evidence that the colonization ability of the species is enhanced in warmer locations.

Impacts. In the Brittany region of France, *R. philippinarum* has a greater capacity to colonize than the native conspecific *R. decussatus* owing to its prolonged reproductive period (Laruelle *et al.*, 1994). With warming seawater temperatures, *R. philippinarum* also outcompetes other functionally similar native venerid clams where it becomes established.

Slipper limpet (*Crepidula fornicata*)

The slipper limpet (*Crepidula fornicata*) is native to Atlantic North America. Established introductions occurred in southeastern England in the late 1800s as *C. fornicata* spat escaped from imported *Crassostrea virginica* stocks, and individuals were transported via ship hulls. Spreading throughout inlets in southeastern England during the 1900s, its distribution until recently was confined mainly to the south and southeast coasts (Crouch, 1894; Fretter and Graham, 1981; Maggs *et al.*, 2010). Minimum winter temperatures may be important in limiting the ability to develop extensive populations in northern Europe (Minchin *et al.*, 1995; Thieltges *et al.*, 2004). *Crepidula fornicata* now occurs from southwestern Norway to Spain. It was reported at a few sites on the Atlantic seaboard of Scandinavian countries between the 1930s and 1960s, but the populations were not sustained, possibly because of cold winters. Self-sustaining populations now exist, coinciding with recent warming in the Northeast Atlantic and supporting the view that climate change has been responsible for this relatively recent northern range extension that has occurred more than a century after its initial introduction (Nehls *et al.*, 2006).

Impacts. *Crepidula fornicata* is a filter-feeder that occurs intertidally and subtidally on rocky shores, on soft bottoms attached to shells, and in association with oyster and mussel culture operations. It competes with other filter-feeding organisms and modifies habitat by creating extensive three-dimensional hard substrate for the attachment of epizoics.

Hundreds of thousands of tonnes of *Crepidula* occur in some areas, such as Mont-St Michel Bay in northern France (Goulletquer *et al.*, 2002). The occurrence of *C. fornicata* in large numbers results in competition for food and a consequent reduction in native biodiversity. In addition, the high biomass leads to the accumulation of faeces and pseudofaeces, thus increasing the deposition of mud, which smothers native habitats and species, and can prevent the settlement of oyster spat, resulting in a severe reduction in their productivity (Barnes *et al.*, 1973). The excreta contain enhanced levels of biogenic silicate that may stimulate diatom growth and thus reduce the potential for the production of harmful algal blooms (Ragueneau *et al.*, 2002).

Styela clava

Styela clava is an Asian solitary tunicate (sea squirt; Figure 11.3). Detection in southwestern England in 1952 (Carlisle, 1954) was followed by observations of a subsequent spread along the south coast of England and Wales, and across into France by 1968 and to Ireland by 1972 (Minchin and Duggan, 1988). It is continuing to spread northward in both Europe and North America and is now found on both sides of the North Atlantic from Norway (A. Jelmert and F. Moy, pers. comm.), Denmark, Ireland, and the UK to Portugal (DAISIE), and from New Jersey, USA, to Prince Edward Island, Canada. Spawning is thought to take place once water temperatures reach 15°C (http://www.jncc.gov.uk/page-1722). Transmission is via shipping, the hulls of vessels, and movement of molluscan stock, but successful establishment requires suitable temperatures. This information supports the theory that its introduced range is temperature-limited, but other studies suggest that high temperatures experienced in the wild can also constrain growth (Davis and Davis, 2009). There are insufficient experimental and field data to confirm the driving role of climate change in range expansions to date.

Figure 11.3. *Styela clava* from Queen Anne's Battery Marina, Plymouth, UK. (Source: John Bishop, Marine Biological Association of the UK.)

Impacts. *Styela clava* is a fouling organism, which grows on oysters and mussels, and can colonize artificial substrate and natural rock. Around Prince Edward Island, Canada, it is one of several tunicates that have a negative impact on mussel aquaculture by competing for food. In addition, as the ascidians grow, their additional weight may cause the mussel culture ropes to sink into anoxic sediment below the cultivation sites (Thompson and MacNair, 2004). High densities of *S. clava* may be found in marinas on pontoons, buoys, boat hulls, and other structures (Figure 11.4). Within man-made areas, such as marinas and harbours, it may increase local biodiversity by providing a biogenic habitat that facilitates subsequent settlement by other species (Figure 11.5), which, in the Northwest Atlantic, are frequently introduced species (J. Bishop, pers. comm.; http://www.jncc.gov.uk/page-1722).

Figure 11.4. ***Styela clava*** **with epibionts from Queen Elizabeth II Marina, St Peter Port, Guernsey, UK. (Source: sealordphotography.net.)**

Figure 11.5. Photograph of ***Styela clava*** **covering mussel "socks", a buoy, and portions of the rope. (Source: Arsenault** ***et al.*****, 2009; open access image.)**

11.4.3 Low confidence

Climate change has been suggested as the primary driver of range expansions into higher latitude areas of the North Atlantic for several species, including the Chinese mitten crab (*Eriocheir sinensis*; Ojaveer *et al.*, 2007), harpoon weed (the alga *Asparagopsis armata*), Japanese wireweed (*Sargassum muticum*), and wakame (*Undaria pinnatifida*; Figure 11.6); for reviews see ICES (2007a, 2007b); Reid *et al.* (2009a). The common saltmarsh cord-grass (*Spartina anglica*) is a nuisance and is ranked among the world's worst 100 non-native species by the IUCN; flowering and seed formation is enhanced by mild winters and warm summers in Scandinavia (Nehring and Adsersen, 2006) and the Wadden Sea (Loebl *et al.*, 2006). All of these species were introduced via human vectors, but the delay in expansion after their initial invasion, coupled with recent rapid extensions of their introduced region, suggest that warmer temperatures may be promoting their spread.

Figure 11.6. The basal fertile parts of the brown alga *Undaria pinnatifida* attached to floating pontoons in Plymouth, UK. (Source: Dan Minchin.)

11.5 Community- and regional-level impacts

The effects of climate change and non-native species have been implicated in the decline and even collapse of several marine systems (Harris and Tyrrell, 2001; Stachowicz *et al.*, 2002b; Frank *et al.*, 2005). In the Gulf of Maine, USA, an epifaunal marine community, dominated by mussels, sponges, hydroids, and native ascidians, has shifted to a non-native-dominated community within a 30-year period. The shifts in species diversity and dominance resulted from a greatly diminished population of mussels, which provided secondary substrate to the seasonally abundant non-native ascidians that are the dominant species (Dijkstra and Harris, 2009).

Both rising winter temperatures and biotic interactions appear to play a role in the observed changes in community structure. Many ascidians recruit early, settle, and grow quickly, preventing other species from settling until they senesce, usually with the onset of cold weather; this makes the community vulnerable to invasions the next season (Dijkstra and Harris, 2009). Chemical compounds that may deter predation and prevent secondary settlement may also be involved (Pisut and Pawlik, 2002). It has been suggested that warm winter temperatures favour some non-native ascidian species, probably because they originate in areas where environmental regimes are typified by mild winter seasons that facilitate their continued dominance of primary habitat space (Stachowicz *et al.*, 2002a, 2002b; Stachowicz and Byrnes, 2006). These results must be approached with caution, however, because one of the species classed as non-native cannot be demonstrated to originate outside the region, and because the small number of study species and limited size of the study area make inferences problematic at the wider scale. For example, the sea squirt *Didemnum vexillum* survives at low temperatures throughout the Northwest Atlantic and may persist subtidally as large colonies on the bottom of Georges Bank for several years before regressing with the onset of colder conditions, with a resumption of growth again as temperatures rise (S. Gallager, P. Valentine, and J. Pederson, pers. obs., 2008).

In a recent study, Sorte *et al.* (2010) compared the range shifts of native species and non-native introductions using field and laboratory studies and field observations to assess impacts. Of the 109 species identified as meeting their criteria, 75% of species shifts were polewards and 70% were probably the result of climate change. Other researchers have also reported higher rates for native marine species compared with native terrestrial species, suggesting that they are responding more quickly to climate warming (Parmesan and Yohe, 2003; Mieszkowska *et al.*, 2005; Beaugrand *et al.*, 2009). A slightly higher average rate of spread was derived for non-native species (Sorte *et al.*, 2010), but there was no demonstrable link between this expansion rate and climate change. In addition to rising temperature, species interactions and other environmental variables modulate the expansion of both native and non-native species.

Invasion of brackish waters in the Baltic Sea by the predatory cladoceran *Cercopagis pengoi*, most probably in the ballast water of shipping, may affect the ecosystem by lengthening food chains; this species is now an important food source for some fish species (Gorokhova, 2004; Vanderploeg *et al.*, 2002). There is no indication that the spread of this species is linked to climate change. Another cladoceran, *Penilia avirostris*, invaded the southern North Sea in the early 1990s and rapidly increased in numbers in autumn as a consequence of exceptionally high sea temperature (Johns *et al.*, 2005). The dormant resting eggs facilitate the distribution of these two species, which are likely to extend their ranges farther with rising temperature.

11.6 Predicted impacts

Climate change is likely to affect the introduction and spread of non-native species, the persistence of established non-native species, and the sensitivity of non-native species to direct and indirect impacts. Direct effects may include the removal of physiological constraints; new colonizations by species of warm-water affiliation, and persistence of founder populations, all of which will be facilitated by warmer climatic regimes in the North Atlantic, particularly in boreal/temperate regions (Carlton, 2000; Hulme, 2005). Some native and established non-native species from tropical/subtropical latitudes are also predicted to be driven polewards as temperatures become too warm for their survival and climatic regimes become suitable for the extension of their northern range boundaries. The thermal range of the region to which a species is native will determine thermal tolerances upon translocation, although local adaptation is to be expected in successful establishments. The impacts are likely to be manifested as increases in abundance, density, and distribution, and may be mediated by factors such as an extended breeding season, increased reproductive output, and increased survival.

In contrast, introduced species originating in cooler waters may be less likely to successfully colonize new regions if the thermal regime continues to rise above their upper pejus limits (*pejus* meaning "becoming worse"), beyond which the ability of animals to increase aerobic metabolism is reduced, or if low temperature thresholds for reproduction are not reached. Cold-water non-native and native species are likely to suffer in the warmer, lower-latitude parts of their introduced range as population abundance declines and local extirpation results in a northward retreat to cooler waters at higher latitudes.

Second-order results of changing abundance or new invasions will probably result in either further reductions or increases in the establishment of non-natives (J. T. Carlton, in prep.). Any increase in the abundance of native or established non-native species within a community can lead to fewer opportunities for new invasions through increased competition or predation. Similarly, increased competition and predation from increased numbers of resident non-native species, thermophilic native species, or new invasions, could result in a reduction in the abundance and distribution of already established non-native species (particularly susceptible may be cold-tolerant invaders, weakly competitive thermophilic non-natives, and susceptible non-native prey). Indirect climatic effects, such as shifts in the timing and extent of primary production, may also affect the success of non-natives through changes in food provision (known as the match–mismatch hypothesis; Cushing, 1972, 1990) and the lack of, or reduction in, predators within the native community (known as the prey-release hypothesis; Edwards and Richardson, 2004). Native species have co-evolved with predators and competitors and may be less successful in new environments (Sorte *et al.*, 2010). Conversely, non-native species often arrive with few parasites or are less susceptible to native predators (Coulautti *et al.*, 2004; Torchin and Mitchell, 2004) and have life-history characteristics that favour their establishment, spread, and survival (Nyberg and Wallentinus, 2005).

Encompassed within the North Atlantic are warm and cold temperate marine biogeographic provinces, which are also subjected to environmental influences from subtropical areas, such as the Mediterranean and the Gulf Stream in the south, and boreal conditions deriving from the Arctic. Climate-driven change within the marine systems of the North Atlantic have often been recorded in the region of these major biogeographic breakpoints, where species of warm- and cold-water origins overlap and reach their respective limits of distribution (Mieszkowska *et al.*, 2006; Beaugrand *et al.*, 2009). Information on the ecological and biological mechanisms underpinning these changes in native species provides a basis for the prediction of the responses of non-natives from different thermal provinces within the major biogeographic regions.

If temperatures in Arctic waters, as predicted by models, continue to increase, environmental conditions may favour the introduction, survival, and establishment of non-native species from adjacent regions and between ocean basins. Seasonal transportation by ships in the Arctic is expected to increase significantly in the 21st century, owing to reduced sea ice, but Arctic voyages are expected to be overwhelmingly regional and not trans-Arctic by 2020 (Arctic Council, 2009; Bambulyak and Frantzen, 2009). Viability of the Arctic sea route will depend on the available navigable window and the extent and distribution of sea ice during summer/autumn in the 21st century (Somanathan *et al.*, 2009), as well as on a considerable reduction in the currently imposed fees for ice-breaking (Liu and Kronbak, 2010). Ballast-water treatment will be required by 2016 (but implementation may be slow for many ships), so impacts from non-native biota may be tempered, although hull fouling will continue to be an important route of transmission (Minchin and Gollasch, 2003).

Temperature is not the only environmental variable influenced by climate that will affect organisms. Ocean acidification may also affect the success of non-native species. A shift in the carbonate chemistry of seawater as a result of increased atmospheric concentrations of carbon dioxide is already occurring in the oceans (Doney *et al.*, 2009). This emergent field of research has demonstrated the deleterious effects of a reduction in the pH of seawater on general health, physiological processes, and the ability of calcareous species to form calcium carbonate structures such as shells or liths (see Section 5). Currently, there is no field evidence that indicates any impacts from ocean acidification on natural populations or non-natives in the North Atlantic, but it is likely that the scenarios of a pronounced reduction in pH within the 21st century (Caldeira and Wickett, 2003; Blackford and Gilbert, 2007), in combination with elevated temperatures, may result in severe reductions in the fitness of marine species (Findlay *et al.*, 2009), including non-natives.

All of the above phenomena may result in important alterations to the structure and functioning of native marine communities, potentially disrupting key ecological processes and affecting the supply of goods and services to society. Additional climatic factors, such as storm intensity and wave height, in addition to acidification, will also affect the role that non-native species play in ecosystem structure and functioning. Climate change may result in enhanced opportunities for non-native species (Figure 11.7) at each stage (introduction, colonization, establishment, and impact) of the invasion process (Maggs *et al.*, 2010), as well as for range-expanding native species.

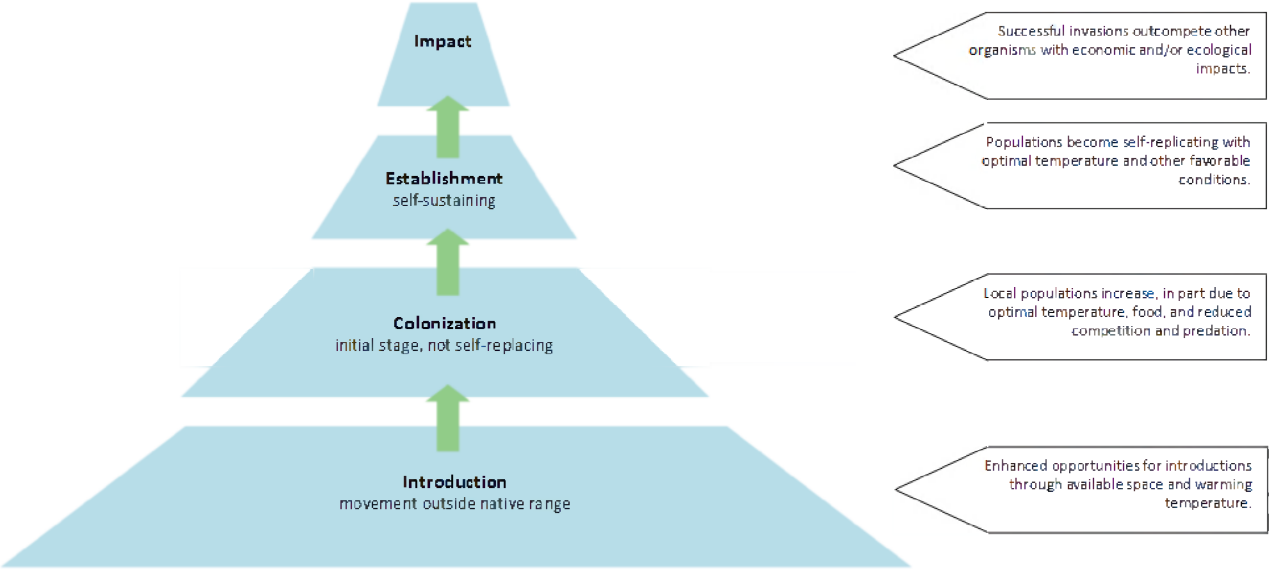


Figure 11.7. Stages in the sequential transitions of a successful invasion process. (Modified from Maggs *et al.*, 2010, and Walther, G. R., *et al.*, 2009.)

11.7 Future directions

Understanding the complexities of the impacts of multiple climate drivers on the invasion process requires an integrated approach, combining experimental and observational studies, which is currently not available for most invasions. One major challenge to documenting change is the need for data from many sampling sites over extended periods. This can be overcome to some extent by improving integration between research and monitoring projects across the Atlantic under a single umbrella. The Global Invasive Species Programme (GISP; closed March 2011) has applied an integrative approach by the centralized gathering of studies and information on non-native species from terrestrial, freshwater, and marine habitats (Wittenberg and Cock, 2001). This desk-based study highlights the problems currently facing countries with respect to the arrival of, and colonization by, non-native species, and it has produced a toolkit to assist nations in tackling invasive species problems. Such an approach demonstrates that international collaboration and integration of research programmes, including complementary standardized methodologies and data storage, centralized data archiving, data sharing, and dissemination to a wide international audience, can be achieved within a single, structured framework.

The new European Marine Strategy Framework Directive (MSFD) is a legislative framework for an ecosystem-based approach to environmental management that includes invasive species as a descriptor, with a requirement that "Non-indigenous species introduced by human activities are at levels that do not adversely alter the ecosystems" (Olenin *et al.*, 2010). Monitoring programmes and corrective measures have to be put in place to achieve "Good Environmental Status" by 2020. Potential increases in the spread of invasive species resulting from climate change, and the difficulty of sampling and controlling ballast-water treatment, will make it difficult to achieve the deadline of 2020. Furthermore, the 2004 International Convention for the Control and Management of Ships' Ballast Water and Sediments is still awaiting signature, so the spread of new species via shipping is likely to continue for some time.

In July 2010, the US adopted recommendations for an ocean policy that identifies coastal and marine spatial planning (CMSP) as a framework for meeting the goals of protecting, restoring, and maintaining coastal and ocean resources, and the Great Lakes. The CSMP effort is designed to integrate a wide range of services, including identifying impacts of invasive species and adopting methods for their control and prevention (http://www.whitehouse.gov/administration/eop/ceq/initiatives/oceans).

Canada supports an ocean policy that focuses on healthy coastal and ocean ecosystems and, in addition, supports the Canadian Aquatic Invasive Species Network (CAISN), with the goal of providing scientific information to "influence the implementation of government policy, ensuring the regulation of preventive measures to minimize the spread of AIS in Canada's aquatic ecosystems" (http://www.nserc-crsng.gc.ca/Partners-Partenaires/Networks-Reseaux/CAISN-CAISN_eng.asp).

Non-native micro-organisms and their potential invasive impacts are the most under-researched sector and must also be included in future non-native research programmes. In the past, their study and provenance have been complicated, owing to difficulties in determining their taxonomic status, but advances in molecular science are allowing progress in this field.

Long-term data on the presence and abundance of non-native species collected over large regions are necessary in order to determine what, when, how, where, and why colonization events occur, and to assess invasion risks across the North Atlantic. In addition, another option for increasing resources and gathering data on selected non-native species, especially near the limit of observed physiological ranges, is to employ "citizen scientists" to gather data (see box below). If networks of amateur naturalists are coordinated by professional organizations involved with the recording programmes for non-native species, and a robust quality assurance procedure is implemented, then citizen scientists provide a far larger network of observers and recorders than can be achieved within the scientific community alone.

11.8 Conclusions

The arrival of non-native species into the North Atlantic has, with rare exceptions, been independent of climate change until recently. However, evidence indicates that a few non-native species have expanded their range in response to rising temperature, although demonstrating the effects of climate change on the spread of non-native organisms in marine environments (cf. in terrestrial and aquatic habitats), and independent of spread during the invasion process, remains a challenge. Most of the studies in marine ecosystems focus on invertebrates and algae. A lack of techniques for defining speciation of native and non-native HABs and micro-organisms limits the understanding of impacts in the pelagic realm. Nevertheless, HAB species, one of the best-studied groups in the plankton, are not considered to be spread by humans and are only weakly associated with climate change.

Prior to the creation of *ICES Code of Practice* (ICES, 2005a) several non-native species were introduced to areas on the assumption that local temperatures were too low for reproduction and growth. For example, *Crassostrea gigas* and *Ruditapes philippinarum* are organisms that failed to reproduce well in areas that formerly experienced a colder climate and/or winter, but do so now. For example, the introduction of *Undaria pinnatifida* was based on an optimal temperature for growth rather than the range of temperature within which it survives. Determining a link between climate change and impacts may be tempered by the physiological responses of organisms; for example, *Codium fragile* subsp. *fragile* is a warm-water species that has adapted to cold waters and spread beyond its historically introduced range in the US.

Long-term community studies indicate that some non-native species appear to be benefiting from warmer temperature in the North Atlantic, with a shift in previously static distributions and an increase in the speed of range expansions. Compared with terrestrial species, marine species appear to be responding faster to climate change. In future, thermophilic non-native marine species are predicted to increase in biomass, density, and distribution within the temperate and southern boreal regions of the North Atlantic as warming continues, with the caveat that some native species will also increase and may retard the rate of change in non-native species. New invasions that would previously have been inhibited by temperature are also likely to increase in number.

As some species are driven northwards by rising temperatures, others in northern latitudes may experience local extirpation as temperatures become too high. Climate change may result in new pathways for the arrival of non-native species into the North Atlantic, with or without shipping as the vector of spread. Rising temperature and subsequent ice melt within the Northwest Passage will present a new route for vessel traffic and species migration through Arctic corridors.

At present, there is no evidence of any effects from ocean acidification on non-native species, but projected reductions in ocean pH are expected to affect many of them, with unknown consequences for their success, growth, or expansion/contraction.

Although there are several new national and regional policies and efforts directed at the prevention of new introductions, on-the-ground monitoring and enforcement of regulations remain understaffed and underfunded. An understanding of the role of anthropogenic influences as well as that of climate change is key to unravelling the primary drivers with respect to each species and invasion event. This information is essential to the development of the next generation of predictive ecological models which, by incorporating phenological responses and reproductive shifts to climate-driven environmental changes, can improve our understanding of the risks of non-native species in a changing environment. New tools are needed to translate the data collected from field studies and experimental observations, to identify species and country/region of origin through molecular probes, and to assess maps of past and present distributions, with information on vectors of spread, in order to identify which non-native species are enhanced or perturbed by climate change. Use of citizen scientists will benefit long-term studies for selected species and support scientific and taxonomic studies of non-native species and climate change.

More information is needed on the physiological responses of non-natives within their introduced range, together with knowledge of their potential for genetic adaptation. This will help us to understand why non-natives become an invasive problem in some areas but not others, and allow improved predictions of the scale of future impacts of established non-native species in response to increasing temperatures and decreasing pH levels in the North Atlantic. Only then will it be possible to prioritize confidently the invasive species that should be removed, and to implement the best methods to ensure biosecurity within coastal regions of the North Atlantic.

Climate change and non-native introductions are two primary drivers of change within marine ecosystems, but tend to be studied in isolation. At present, there is insufficient information available to allow the quantitative assessment of the responses of non-native species to climate change, or to attribute climate change as a causal driver in many colonizations. An increase in detected arrivals of non-natives, coupled with an acceleration of the impacts of climate change on native species and communities, requires an integrative approach in order to document interactions between these two drivers and subsequent alterations to native biodiversity.

Expanding non-native species surveys using citizen scientists

The detection of new non-native species arrivals has been improved by using naturalists, students, college field classes, and divers (Lodge *et al.*, 2006; J. T. Carlton and J. Pederson, pers. comm.). In the US, the use of citizen scientists to assist with collecting data is not new, and it has been successful in terrestrial and aquatic environments and, more recently, in marine ecosystems (Delaney *et al.*, 2008; Crall *et al.*, 2010). Several New England non-governmental organizations and state-led initiatives have recruited citizen scientists to help identify the presence, abundance, and spread of non-native species in the New England region and to supplement observations by researchers and agencies (Salem Sound Coast Watch, Massachusetts Coastal Zone Management; http://massbay.mit.edu/mitis/index.php). The data provide valuable information on the spread of selected species, such as the seaweed *Grateloupia turuturu* and the sea squirt *Didemnum vexillum*. These data can be used to support policy decisions and the development of plans for managing non-native species. A citizen-based project enlisted over 1000 participants to assess the distribution of the Asian shore crab (*Hemigrapsus sanguineus*), the European green crab (*Carcinus maenas*), and native crab species from Long Island Sound to Maine (Delaney *et al.*, 2008).

The Marine Biological Association of the UK runs the "Alien Invaders and Climate Change Indicators" schools project in the UK. This project engages schoolchildren in the search for and recording of non-native species and promotes awareness of climate change within the national curriculum (http://www.marlin.ac.uk/).

A UK-wide Marine Aliens project is monitoring seven species within marinas and ports, namely: two brown algae, wakame (*Undaria pinnatifida*) and Japanese wireweed (*Sargassum muticum*); the green alga *Codium fragile* subsp. *fragile*; Chinese mitten crab (*Eriocheir sinensis*); Japanese skeleton shrimp (*Caprella mutica*); leathery sea squirt (*Styela clava*); and a colonial sea squirt (*Perophora japonica*). Several other species are also being monitored: the slipper limpet (*Crepidula fornicata*); zebra mussel (*Dreissena polymorpha*); Pacific oyster (*Crassostrea gigas*); Australasian barnacle (*Austrominius modestus*); a Pacific bryozoan, *Tricellaria inopinata*; the southern hemisphere solitary sea squirt *Corella eumyota*; and the compound sea squirt *Botrylloides violaceus*. Marine Aliens is a research project but also has recruited "alien detectives" to assist with the surveys in relation to climate change. Results are entered into the MarLIN website (http://www.marlin.ac.uk/rml.php).

Canada has launched an Invasive Alien Species Partnership Programme (IASPP) to encourage and fund amateur enthusiasts in the recording of non-native species (http://www.ec.gc.ca/eee-ias/default.asp?lang=En&n=A49893BC-0). Transport Canada Marine, the Ontario Federation of Anglers and Hunters, and the Ontario Ministry of Natural Resources have joined forces to produce an information CD for recreational boaters entitled "Stop the Spread of Aquatic Invasive Species".

Although citizen monitoring programmes are not a substitute for bio-invasion research, the data provide the much-needed observations, over time and in numerous locations, that are required to document range expansions and to understand the relationships of such changes to climate variability. The efficiency and scientific validity of the data are supported from appropriately designed and executed citizen monitoring programmes (Delaney *et al.*, 2008).

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12 Summary and conclusions

Harald Loeng and Ken Drinkwater

12.1 Introduction

The physical, chemical, and biological properties and circulation of the North Atlantic undergo significant variability on time-scales from seconds to centuries. This report has focused on seasonal to multidecadal time-scales and has summarized our present understanding of the causes of this variability. The effects of anthropogenic forcing as well as natural climate variations have also been examined, although distinguishing the two is often difficult and a matter of ongoing research. Climate variability and change act to alter the characteristics of ecosystems, fundamentally affecting chemical and physical oceanography as well as ocean biota. Both phytoplankton and zooplankton have undergone climate related changes in production and distribution and are projected to undergo further modification under future climate change. Climate-related changes to fish can occur indirectly through the foodweb as well as directly through physiological processes. The report also contains information on ocean acidification, one of several other factors such as fishing, pollution, etc. that also can cause changes to ecosystems in addition to climate. Multiple forcing makes it challenging to establish unequivocal linkages between climate and observed changes in marine ecosystems.

This chapter is divided into four parts.

1) Main findings as outlined in the previous chapters
2) Gaps in knowledge that are important and need to be filled
3) Activities and research actions required to address the identified gaps in knowledge
4) How ICES should address climate issues in future

12.2 Main findings

12.2.1 Atmosphere

- Model results suggest that storm paths across the North Atlantic may shift northward under climate change, with fewer storms of higher intensity compared with today. This will result in a shift in the position and intensity of the Icelandic Low and Azores High, and may lead to increased strength of the NAO pattern.

12.2.2 Oceanography

- The general warming of the North Atlantic has been more intensive in northern regions and accompanied by changes in the amplitude (and in some cases, phase) of the seasonal cycle. Advection plays an important role in the temperature changes in several areas and, as such, contributes to the spatial variability around the North Atlantic.
- Arctic sea-ice extent has tended to decrease steadily since the late 1970s, reaching a record low in 2007, and has become almost 40% thinner over the past 20 years. This has led to projections that perennial ice areas may become seasonally ice-covered within 10–50 years.

- Sea level is rising through the world's oceans mainly caused by thermal expansion of seawater and melting of glaciers, ice caps, and ice sheets, but there is high spatial variability in the rate of rise. It is projected that global sea level will continue to rise by an extra 0.2–0.6 m by the end of this century.
- The waters in the North Atlantic and Arctic are rapidly becoming more acidic, causing aragonite and calcite saturation depths to rise at rates of 1–2 m year^{-1}. Continual reductions in ocean pH in future are expected to affect mainly those organisms that produce calcareous body parts, but the consequences to these and other organisms are currently unclear.

12.2.3 Plankton

- In most open-ocean regions at low to mid-latitudes, increased thermal stratification in recent years has decreased the nutrient supply to the upper mixed layer and lowered productivity. In contrast, in more northern latitudes with previous ice-covered regions, there has been enhanced primary production because of increased light and an extended growing season.
- Available observations suggest an overall increase in global oceanic phytoplankton biomass since the 1970s. Regional changes, however, vary from increases in subpolar and large upwelling regions to net decreases in the Subtropical Gyres. The oligotrophic central North Atlantic Gyre is expanding annually (almost 5% year^{-1}), primarily during winter because of increasing thermal stratification, consistent with global-warming scenarios.
- Analyses of plankton time-series reveal that, in the North Atlantic, important changes have occurred in the abundance, distribution, community structure, and population dynamics of phytoplankton and zooplankton. These planktonic events appear to be responding to changes in regional climate, caused predominately by warming sea temperatures and associated changes in hydrodynamics.
- Climate-induced change alters the relative abundance of permanent (holoplanktonic) and temporary (meroplanktonic) zooplankton species. In the North Sea, for example, a temperature-dependent-driven increase in the abundance of phytoplankton and meroplankton has changed the foodweb structure through competitive exclusion of the holozooplankton by the meroplankton, resulting in significantly diminished transfer of energy towards top pelagic predators (e.g. fish) and increased transfer to the benthos.
- Changes in zooplankton biomass and in the seasonal timing of plankton production attributed to climate variability have resulted in poor recruitment of several commercially important fish species and low seabird breeding success in recent years in some North Atlantic regions.

12.2.4 Fish

- Climate change is expected to have a major effect on fish abundance through its influence on recruitment via the match or mismatch between the timing of their spawning relative to either the production of larval food and/or the presence of predators, and on the connectivity (retention or transport) between spawning and nursery areas.

- There will tend to be a general northward movement of zooplankton and fish as waters warm and species follow their preferred temperature range. This will result in distributional shifts, geographic expansion, or both. This may change traditional biogeographical zones, community dynamics, and ecosystem resiliency as the overall movement and rate of change will vary with species.
- Synergistic effects of climate and fishing, as well as counteracting processes, can confound our perception of the effects of climate change.

12.2.5 Benthos

- Latitudinal shifts, generally northwards, in the distribution of benthic species of up to 50 km decade^{-1} have been detected. Such shifts in parasitic species, for example, can potentially produce either positive or negative effects on the ecosystem. Altered physics may affect the distribution and abundance of benthic species through changes in transport of larvae or juveniles, changes in stratification causing increases in anoxia and hypoxia, and through increased storminess. Together or individually, these responses might have a negative effect on benthic communities in intertidal and shallow areas.

12.2.6 Invasive species

- Warming in the North Atlantic has resulted in shifts in species distribution (plankton, fish, and benthos) causing the invasion of non-native species into certain regions. In future, thermophilic non-native marine species are predicted to increase in biomass, density, and distribution.

12.2.7 Future scenario building

- Impact studies of climate change are built upon climate projections forced by assumptions about future emissions of greenhouse gases and based on mathematical representations of the climate system expressed for atmosphere–ocean global circulation models (GCMs). Few climate projections are available from higher-resolution atmospheric or regional ocean models that are needed to capture many of the dynamic processes important for biology.
- The main sources of uncertainty in climate predictions of the physical system come from (i) uncertainties in future emissions of greenhouse gases, (ii) limited knowledge of the physical processes, and (iii) model uncertainties. Few quantitative measures of the uncertainties have been developed.

12.3 Gaps in knowledge

In order to reduce uncertainty in future climate and ecosystem scenarios, many aspects of the interaction between the atmosphere and the ocean, as well as their impacts, require improved understanding that will only be achieved through continued (and long-term) monitoring and increased research efforts. Some of the most important gaps include the following.

- Quantifying the processes controlling ocean temperature and/or salinity variability, especially the influence of (i) clouds; (ii) freshwater fluxes including condensation, evaporation, and precipitation; (iii) the variability in the depth of the upper mixed layer; (iv) interactions and feedback mechanisms between the atmosphere, sea ice, and the ocean; and (v) the relative role of advection compared with air–sea heat and freshwater exchanges;

- The availability of downscaled coupled atmosphere–ocean regional models to adequately resolve the physical processes of relevance to the biology, including mesoscale features such as eddies, fronts, upwelling, etc.;
- Understanding the interaction between climate variability (on annual to multidecadal scales) and climate change (longer-term scales) in marine ecosystems, in order to identify possible physical and biological tipping points;
- Understanding the nature of the physiological processes underlying direct climate–plankton–fish relationships and how these processes, acting on individuals, lead to changes at population, community, and ecosystem levels;
- Identification of potential bottlenecks at different life-stages of marine organisms (zooplankton, benthos, and fish) that limit growth, survival, and population persistence, and the potential role of climate in creating these bottlenecks;
- Determining the interactions between climate and fisheries and their combined effects on marine populations (growth, maturation, recruitment, survival, etc.), community resilience, and the ability of these marine populations to adapt to climate change;
- Understanding the processes responsible for distributional shifts of organisms, and the different rates of movement between species and the consequential impacts on ecosystem structure and function, and hence identifying when non-native species may invade and what effect they will have on the local ecosystem;
- Better understanding of interactions between pelagic and benthic communities and the influences of climate processes, such as temperature changes and the intensity and frequency of storms, on these interactions;
- Establishing the effect of ocean acidification on the flora and fauna of marine ecosystems, both calcareous and non-calcareous;
- Quantification of the consumption and production rates of marine organisms for use in end-to-end models.

12.4 Needed activities and research actions

To begin the process of filling the above gaps in knowledge, to assess ongoing changes in the marine ecosystem, and to make projections about future ecosystem scenarios, the following suggestions are proposed:

- Process and comparative studies need to be encouraged and undertaken in order to quantify biogeochemical, physical, biological, and biophysical processes.
- Initialization of global and regional climate models using present conditions is required, in particular for near future (decadal) predictions for which natural variability is expected to be more important than global climate change. Downscaling of GCMs to regional models is needed in order to make future regional projections at the spatial scales used in

regional models. The downscaling should be from several GCMs that are able to adequately hindcast the recent past.

- Spatially resolved end-to-end ecosystem models are needed in order to better represent synergistic effects of multiple drivers on ecosystems, including climate change, fishing, and other anthropogenic effects.
- Up-to-date knowledge from field studies should be used to improve the parameterizations of ecological processes in models. These parameterizations should be a collaborative work between modellers and knowledgeable field scientists.
- The effects of climate change are largely the outcomes of processes acting on individuals, but are generally observed at the population, community, and ecosystem levels. Therefore, increasing attention should be paid to the response of individuals to climate change to complement the responses of other levels of the ecosystem.
- There is a need for more rapid detection of the arrival of non-native species and an integrative approach to document subsequent alterations to native communities.
- A closer working relationship should be established between those studying climate impacts and those involved in fishery assessments. Marine resource managers need to develop approaches that maintain the resilience of individuals, populations, communities, and ecosystems under climate change.
- Better integration of ongoing environmental and biological monitoring is needed, not only to describe ecosystem changes but to attribute cause and effect. Long-term monitoring sites must be maintained and new sites established for regions, variables, and key species that are currently undersampled. Models should be used to determine locations for the establishment of new monitoring sites, if possible. Greater emphasis should be placed on the monitoring of phytoplankton and zooplankton. As well, improved integration between national research and monitoring programmes is required throughout the ICES Area, including standardization of methodologies and centralized archiving of data.
- Monitoring should be expanded to include CO_2, pH, and aragonite- and calcite-compensation depths. In addition, experiments on the effects of acidification should be carried out on various marine organisms under realistic and projected future CO_2 values with emphasis on long-term exposure under different temperatures to determine the combined effect of global warming and ocean acidification.
- New technologies and methods should be developed and/or used for monitoring and process-oriented field studies.

In summary, there is a need for a "three-track" approach for future studies of how climate change will affect the ecosystem. These key stages are (i) integrated monitoring, (ii) process studies involving fieldwork and experiments, and (iii) modelling.

i) There is a clear need for long-term, large-scale, integrated inventories and ecosystem monitoring in order to provide scientists with the background information necessary to strengthen our current hypotheses. Such data provide the classic descriptors of community structure, such as abundance and species richness, can be used for genetic studies to explore the connectivity between populations, and determine species–species and species–environment interactions. As such, they increase general knowledge of ecosystem functioning and provide information on the life cycle of key species in order to understand phenomena such as "match–mismatch".

ii) More field and experimental (both laboratory and mesocosm) studies are required in order to provide a broader understanding of the dynamical processes linking climate and marine biology.

iii) Monitoring, field studies, and experiments cannot provide us with the temporal and spatial resolution we would like or need to resolve physical and biological processes. For this, we require models, including end-to-end models, that contain realistic climate forcing, and cover biogeochemistry through to fish and fisheries. Models are also essential to develop future ecosystem projections. Of high priority is the development of regional ecosystem models including downscaling from GCMs in order to develop future ecosystem scenarios.

12.5 How should ICES address climate change issues in future?

Since its creation, ICES has played a pivotal role in the development of oceanography at an international level, providing mechanisms to guide and complement ongoing research by nation states. ICES and its Member Countries established, and have successfully maintained, monitoring programmes that have collected oceanographic data along coasts and in the open ocean over much of the North Atlantic since the early years of the last century (see illustration on the back cover). As a consequence, the North Atlantic has the most complete and longest oceanographic, plankton, and fisheries datasets of any ocean region in the world to research climate change. It is important that ICES continue to collect the data and maintain these datasets, which are made freely available to the marine community.

The 2008 *ICES Science Plan* states that there are two foci within the broad topic of climate change. One is to better understand ecological responses, such as the distribution, growth, and abundance of individuals and populations, to changes in temperature, pH, salinity, oxygen, turbidity, and other environmental variables. The second is the projection of oceanographic and ecological responses to selected future climate scenarios (as developed by IPCC). This will require regional models that focus on productivity, distribution of species, migration routes, and the possibility of regime shifts. It is anticipated that the ICES niche in climate-change studies will be in monitoring and research into ecosystem impacts to different physical oceanographic scenarios. ICES should continue to promote research into climate variability and change and their impacts through sponsoring symposia, workshops, and theme sessions. ICES should take the initiative to coordinate collaborative research that will improve the understanding of processes interacting between climate forcing and ecosystem impacts.

The Arctic is predicted to be ice-free during summer by 2030. This will impact the timing and magnitude of primary production and probably the composition of the zooplankton community, which will change the distribution area of various fish stocks. ICES should, together with PICES, take initiatives to lead studies on processes related to the consequences of a changing climate in the Arctic. ICES should also join with the International Arctic Science Committee (IASC) to initiate such studies in accordance with the Letter of Understanding between the two organizations.

Outside the ICES community, ICES is mainly known as a fishery organization, and relatively few know that it also deals with climate issues. If ICES wishes to be recognized as a significant contributor to climate-related research, we believe that it should take several active steps. With its unique datasets on hydrography, plankton, and fish stocks, ICES has an opportunity to be an important player in the climate field. It also has many scientists examining impacts of climate change. However, the organization needs to attract more physical oceanographers and even atmospheric scientists and climatologists if it wishes to be fully recognized as playing a significant role in climate-change research. The organization should use the opportunity in the relatively new field of ocean acidification to play a leading role in the monitoring and research into impacts of ocean acidification; for this, it will need to attract more chemical oceanographers into its fold. ICES should continue to contribute by facilitating and promoting studies on climate variability and change, and their impacts on marine ecosystems. Because one of the primary components of ICES science activities is coordination and synthesis, a way forward is to have an ICES Climate Coordinator responsible for overseeing and summarizing all climate-related work conducted within the expert groups and to promote ICES climate work in international meetings and other fora. The delivery process should follow the *ICES Science Plan* and include:

- leadership on climate issues within ICES at the scale of the North Atlantic including the effects of climate on fish populations (enhanced research coordination); and

expand ICES science capacity in climate-change matters to address specific knowledge gaps through engagement of ICES scientists and international partnerships (enhanced science capacity).

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