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TRANSREGIONAL LINKAGES IN THE NORTH-EASTERN ATLANTIC — AN 'END-TO-END' ANALYSIS OF PELAGIC ECOSYSTEMS

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Abstract This review examines interregional linkages and gives an overview perspective on marine ecosystem functioning in the north-eastern Atlantic. It is based on three of the 'systems' considered by the European Network of Excellence for Ocean Ecosystems Analysis (EUR-OCEANS was established in 2004 under the European Framework VI funding programme to promote integration of marine ecological research within Europe), the Arctic and Nordic Seas, North Atlantic shelf seas and North Atlantic. The three systems share common open boundaries and the transport of water, heat, nutrients and particulates across these boundaries modifies local processes. Consistent with the EUR-OCEANS concept of 'end-to-end' analyses of marine food webs, the review takes an integrated approach linking ocean physics, lower trophic levels and working up the food web to top predators such as marine mammals. We begin with an overview of the regions focusing on the major physical patterns and their implications for the microbial community, phytoplankton, zooplankton, fish and top predators. Human-induced links between the regional systems are then

considered and finally possible changes in the regional linkages over the next century are discussed. Because of the scale of potential impacts of climate change, this issue is considered in a separate section. The review demonstrates that the functioning of the ecosystems in each of the regions cannot be considered in isolation and the role of the atmosphere and ocean currents in linking the North Atlantic Ocean, North Atlantic shelf seas and the Arctic and Nordic Seas must be taken into account. Studying the North Atlantic and associated shelf seas as an integrated 'basin-scale' system will be a key challenge for the early twenty-first century. This requires a multinational approach that should lead to improved ecosystem-based approaches to conservation of natural resources, the maintenance of biodiversity, and a better understanding of the key role of the north-eastern Atlantic in the global carbon cycle.

Introduction

The European Network of Excellence for Ocean Ecosystems Analysis (EUR-OCEANS) was established in 2004 under the European Framework VI funding programme to promote the integration of marine ecological research within Europe. The network includes around 140 researchers based in 69 research institutes from 26 countries and deals with research on pelagic ecosystems. When the network was founded in 2004, seven 'systems' were defined to give geographical scope to the project. These were the Arctic and Nordic Seas, Baltic, Mediterranean, North Atlantic Ocean, North Atlantic shelf seas, Southern Ocean and Upwelling regions. Since many aspects of marine ecosystem functioning are related to latitude, bathymetry, and distinct climate regions, these ecosystems do display some internally coherent features (e.g., productivity in the Arctic Seas is typified by strong seasonality). However, marine ecosystems do not exist in isolation and this is particularly true for those systems with relatively open boundaries. The Arctic and Nordic Seas, North Atlantic shelf seas and North Atlantic share common boundaries and the processes occurring across their boundaries act to modify local processes in important ways. This review examines these interlinkages and gives a regional perspective to marine ecosystem functioning in the north-eastern Atlantic (Figure 1). Because of EUR-OCEANS' focus on pelagic systems, the review does not deal

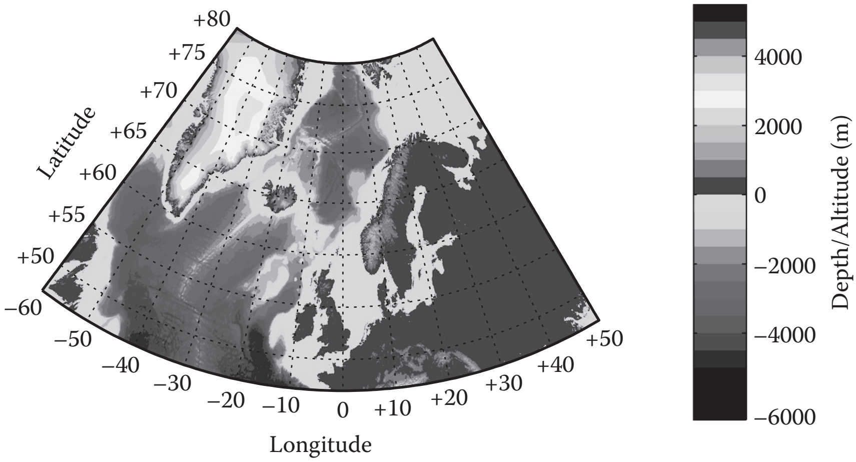

Figure 1 (See colour insert following page 52.) Overall topography of the north-eastern Atlantic, elevations in metres from mean sea level (MSL). (Prepared from ETOPO2v2 data.)

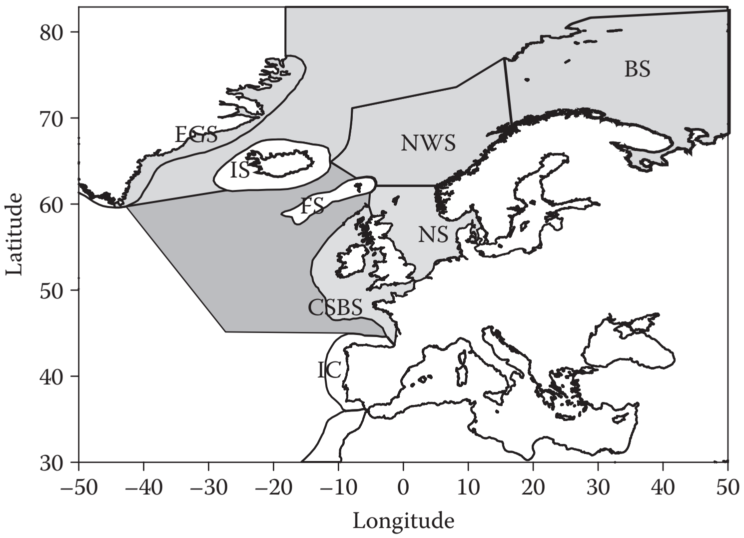

Figure 2 (See colour insert.) Large Marine Ecosystems (LME) boundaries within the north-eastern Atlantic. Colour coding refers to merging of LMEs and offshore regions to yield the three EUR-OCEANS systems: Nordic and Arctic Seas (blue), European shelf seas (yellow) and Atlantic Ocean (green). Processes occurring on the Icelandic Shelf and Faroes Shelf are not covered in this review. EGS = East Greenland Shelf; NWS = Norwegian Sea; BS = Barents Sea; IS = Icelandic Shelf; FS = Faroes Shelf; NS = North Sea; CSBS = Celtic Sea Biscay Shelf; IC = Iberian Coastal.

extensively with benthic ecology although the importance of benthic-pelagic coupling in nutrient recycling and the carbon cycle is acknowledged.

The system concept used in EUR-OCEANS is similar to the Large Marine Ecosystems (LME) introduced by Sherman et al. (1993). The aim of LME was to define sea areas on the basis of distinct bathymetry, hydrography, productivity and trophic interactions to promote coherent analyses of their functioning and health (Figure 2). The LME defined by Sherman did not extend into the deep oceans. However, as shown in this review, the linkages between the deep oceans and the LME cannot be ignored. Since then, reviews of ecosystem functioning in several defined areas within the north-eastern Atlantic have been undertaken (e.g., for the Nordic Seas; Skjoldal 2004) and the Regional Quality Status Reports produced under the auspices of OSPAR. However, all these approaches suffer from the delineation of somewhat artificial boundaries. Although some geographic features, such as the shelf break, do define genuine transition zones between areas where different physical and biological processes dominate (e.g., tidal mixing is dominant on the shelf seas but less important in the open Atlantic), other boundaries are more arbitrary and have been drawn in relation to national or management considerations. The aim of the present review is to consider the interlinkages in the north-eastern Atlantic, that is between the Arctic and Nordic Seas, European shelf seas and Atlantic Ocean.

This review is also structured using EUR-OCEANS' concept of 'end-to-end' analyses, which starts with a consideration of the physics and works up the food web to top predators such as marine mammals. For brevity, the review is also largely constrained to looking at those mechanisms 'linking' EUR-OCEANS' regions and not the internal processes occurring within them. Ocean currents, particularly downstream branches of the North Atlantic current, form the main physical link between the systems. Heat, dissolved nutrients and particulates are all transported by these currents. This has significant impacts within the regions themselves (e.g., the transport of heat by the North Atlantic current (NAC) is the reason why ice cover is more limited in the Nordic Seas compared to other areas at the same latitude). For pelagic biota, life-cycle duration tends to increase moving from lower to higher trophic levels. For example, individual phytoplankton cells, once in

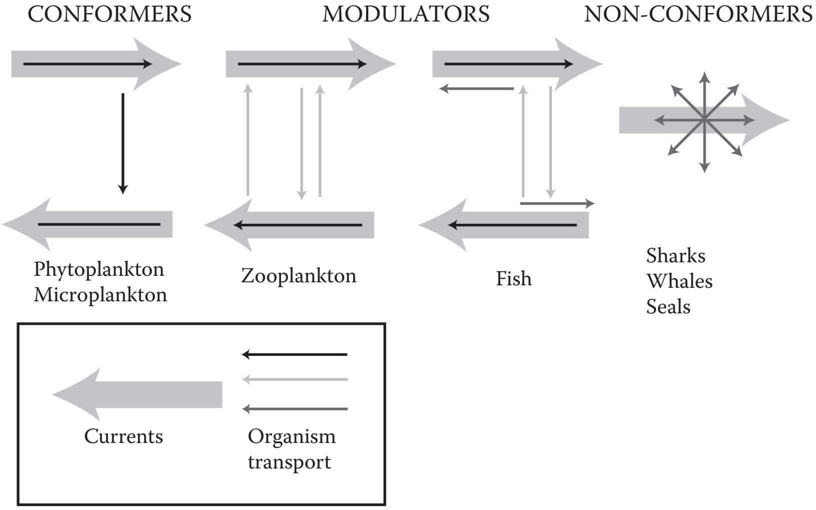

Figure 3 (See colour insert.) Role of water currents for individual dispersal options. *Conforming species* have insufficient motility to be anything other than passive to the general water flow. *Modulators* are primarily transported by water flow but can move vertically between flows to influence their trajectory. *Non-conformers* have sufficient mobility to overcome water flow. Some species, particularly fish, switch between conforming, modulating and non-conforming at different life stages.

a productive phase, can complete growth and division in a few days whilst many zooplankton take months to complete their life cycles. Consequently, longer-lived planktonic organisms can be dispersed over much larger distances compared with shorter-lived species. Although larger organisms such as fish are less directly affected by ocean currents, many have a planktonic larval phase. These can often exploit vertical differences in currents to influence their dispersal (Figure 3). In contrast, marine mammals can overcome flow velocities at all their life stages. Their life strategies and behaviour are therefore linked to the distribution patterns of their prey and predators. Moving from end-to-end we see that there is a transition from direct effects of oceanography on the dispersal of organisms to indirect effects via predator and prey distributions.

As well as direct oceanographic linkages between the regions, human activities are also increasing the exchange of materials between the regions. The most obvious example is the introduction of alien species ('alien species' refers to a species, subspecies or lower taxon introduced outside its natural past or present distribution whilst 'invasive alien species' means an alien species whose introduction or spread threaten biological diversity (Convention on Biological Diversity COP6 Decision VI/23), either via ships' ballast water, hull fouling or through aquaculture. Because of the regional connections many pollutants, introduced into one region, will spread through the north-eastern Atlantic. Finally, through industrial activities, humans are altering the concentrations of 'greenhouse' gases in the atmosphere and it is now almost certain that this is causing changes in climate that will persist over the rest of this century and beyond. In addition to affecting local temperatures, winds and precipitation/evaporation, this will lead to changes in some ocean currents, again affecting the whole north-eastern Atlantic. As our understanding of marine ecosystems improves we are beginning to appreciate how local-scale ecology is linked to the complete range of spatial and temporal scales ranging from regional to global, short term to long term and from the underlying physics to top predators. Appreciation of these interconnections by wider society is vital if we are to manage our activities in ways that promote the sustainable use and development of European marine resources.

Overview of the regions

The Nordic and Arctic Seas: general geography, size, bathymetry

The 'Nordic Seas' is used as a common name for the waters to the north of the Greenland-Scotland Ridge and between Greenland, Norway and Spitsbergen. This region forms the main connection between the North Atlantic and the Arctic Oceans. This area also includes wide shelf areas bordering the Arctic land masses. The International Hydrographic Bureau defines the Norwegian Sea as bounded to the east by the coast of Norway, on the north-east a line from North Cape over Bear Island to the south-west point of Spitsbergen (one of the Svalbard Islands). The western limit extends from this point along a line to Jan Mayen and further to the eastern tip of Iceland. The southern limit extends from there to the Faroe Islands and follows the 61st parallel to the coast of Norway. More recently, the oil industry has found it more practical to apply the 62°N parallel as the southern border of the Norwegian Sea. From an oceanographic point of view, it would be more correct to place the border to the north-east coincident with the shelf edge. The Barents Sea itself extends eastwards to Novaya Zemlya and northwards to the shelf edge between Franz Josef Land and Spitsbergen.

The main bathymetric features of the Nordic Seas are depicted in Figure 4. The Fram Strait, with a sill depth of about 2500 m, forms the main connection with the Arctic Ocean. To the south,

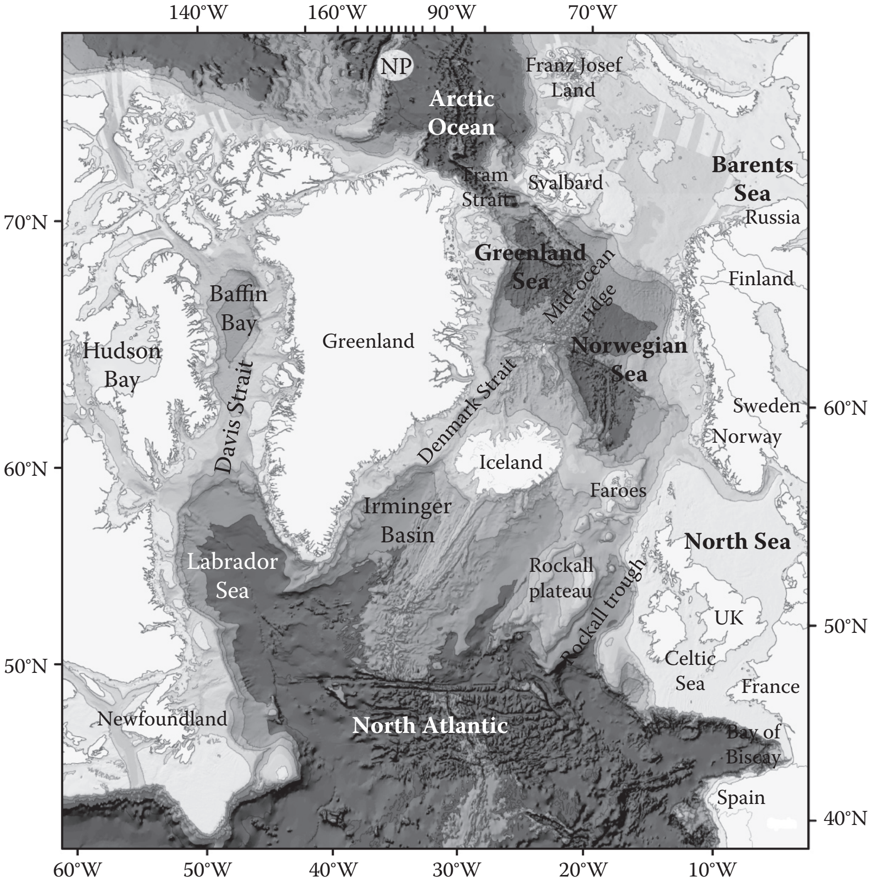

Figure 4 (See colour insert.) General bathymetry of the north-eastern Atlantic. NP indicates North Pole.

the Greenland-Scotland Ridge, with the deepest sills located in the Faroe Bank Channel (~850 m) and in the Denmark Strait (~620 m), forms the border towards the North Atlantic. Topographic features within the Nordic Seas divide the area into the Greenland, Iceland and Norwegian Seas. The most prominent of these features is the midocean ridge. Three main parts of this ridge system can be identified as the Kolbeinsey Ridge, Mohns Ridge and the Knipovich Ridge. The Kolbeinsey Ridge extends northwards from the North Icelandic shelf to the latitude of Jan Mayen where the Jan Mayen Fracture Zone cuts through it. Generally this ridge ranges in depth between roughly 400 and 1500 m, but to the west of Jan Mayen, some seamount-like features are shallower than 300 m, the shallowest only 25 m deep. The Mohns Ridge, between Jan Mayen and approximately 73.5°N, 8°E, has depths ranging between 1000 and 2000 m. Its rather complex topography is characterised by many isolated elevations. The shallowest peaks, the Myrseth and Boyd banks, are both about 600 m deep. The Knipovich Ridge stretches from Mohns Ridge to the Fram Strait, its shallower crests being at about 1000 m depth. Along the centre of both these ridges there is a rift valley with depths mainly greater than 3000 m. The topography along the southern side of the Jan Mayen Fracture Zone, between about 68°N, to the west of the Vøring Plateau, and 72°N off the East Greenland coast form a less-well-defined ridge system. Farther to the west, the area between Jan Mayen and Greenland is mostly shallower than 1500 m. Between 66.5°N and 68°N off the Norwegian shelf the Vøring Plateau has depths mainly between 1200 and 1400 m.

These bathymetric features divide the Nordic Seas into four major basins. To the west of the midocean ridge lie two deep basins in the Greenland Sea. The Greenland Basin is the largest of these, reaching depths from 3400 to 3600 m. To the north, the Greenland Fracture Zone separates it from the smaller and shallower Boreas Basin. Along its margins there are several shallower structures and seamounts, for example the Vesteris Bank (73°N, 9°W), which rises from the basin floor at approximately 3000 m to a depth of 130 m. Two deep basins are found in the Norwegian Sea, the Norwegian and Lofoten Basins, the former being the largest and deepest basin in the Nordic Seas. Its floor lies mainly between 3200 and 3600 m, but depths exceed 3800 m in a narrow trough around 65°N, 5°W. The shallower and somewhat smaller Lofoten Basin to the north of the Norwegian Basin reaches about 3200 m. The Iceland Plateau is the area between Iceland and Jan Mayen to the east of the Kolbeinsey Ridge. Along its eastern margin, which slopes into the Norwegian Basin, the Jan Mayen Ridge extends southwards from Jan Mayen. West of this ridge lies a small basin that is more than 2200 m deep but elsewhere, depths are mainly in the range 1200 to 2000 m. West of the Kolbeinsey Ridge the narrow Scoresby and Blosseville Basins (to the south) extend from the Jan Mayen Fracture Zone towards the Denmark Strait.

The Nordic Seas have been the subject of numerous national and international research programmes. Although many originated with a fisheries focus, they have now broadened to include studies on most aspects of the ecosystem (Skjoldal 2004). Since the Nordic Seas are experiencing particularly rapid changes linked with global climate, there has been a renewed emphasis on how these changes may affect biological productivity in the coming decades (Arctic Climate Impact Assessment [ACIA] 2004). There has also been a strong emphasis on the development of international programmes to measure the strength of ocean fluxes in the region because of their fundamental importance in climate control (Dickson et al. 2008).

The Atlantic: general geography, size, bathymetry

The Atlantic Ocean is the second largest of the world's oceanic divisions. It has a total area of about 106 million km^2 (41 million mi^2) and covers approximately one-fifth of the Earth's surface but this includes the southern Atlantic. The North Atlantic, which is the largest oceanic water mass associated with Europe, was not included in the original LME definitions as it is less productive than the adjacent shelf seas, but is included as a EUR-OCEANS' system. The North Atlantic Ocean is bounded on the west by North and South America whilst in the north and north-east, it is separated from the Arctic Ocean by the Canadian Arctic Archipelago, Greenland, Iceland, Jan Mayen, Svalbard, and mainland Europe. It connects to the Nordic Seas and Arctic Ocean through the Denmark Strait, Greenland Sea, Norwegian Sea and Barents Sea. To the east, the boundaries of the ocean proper are Europe and the Straits of Gibraltar (where it connects with the Mediterranean Sea). The average depth of the Atlantic is 3926 m but it reaches 8605 m in the Puerto Rico Trench. The principle bathymetric feature is a submarine mountain range, the Mid-Atlantic Ridge, which extends from Iceland in the north to around 58°S. The ridge has a maximum width of about 1600 km and a great rift valley extends along most of its length. The depth of water over the ridge is generally less than 2700 m.

The North Atlantic has been the subject of a number of major coordinated programmes at both the international (Joint Global Oceans Flux Study, World Ocean Circulation Experiment, Global Ocean Ecosystem Dynamics) and the European (Trans-Atlantic Study on *Calanus*) levels. Current relevant international programmes include the International Council for the Exploration of the Sea (ICES)/Global Ocean Ecosystem Dynamics (GLOBEC) Cod and Climate Change (CCC) programme, which is a North Atlantic regional component of GLOBEC. GLOBEC is a part of the International Geosphere Biosphere Program (IGBP) suite intended to evaluate the causes and consequences of global change. Another relevant IGBP programme is IMBER (Integrated Marine Biogeochemistry and Ecosystem Research), which is currently under development. Other international projects such as Climate Variability and Predictability (CLIVAR) and the Global Ocean Observing System (GOOS) are also relevant.

The European shelf seas: general geography, size, bathymetry

The European shelf seas within the EUR-OCEANS' context comprise the North Sea and the Celtic Sea/Biscay Shelf LMEs (Figure 2). The North Sea (including its estuaries and fjords) has a surface area of about 750,000 km^2 and a volume of about 94,000 km^3. It is relatively shallow in the south (including the Southern Bight and the German Bight) but becomes progressively deeper moving into the northern North Sea and the Norwegian Trench (Figure 5). The shallow Kattegat forms a transition zone between the North Sea and the Baltic. In the south, the North Sea is subject to strong tidal mixing, which prevents thermal stratification. However, significant freshwater run-off generates a series of salinity fronts and transient haloclines in this region. Water column structure in the central and northern North Sea is strongly affected not only by localised heating but also by significant inflows of Atlantic water, mainly through the Faroe-Shetland Channel and by outflow of freshwater through the Jutland Current, the Kattegat and the Norwegian Coastal Current. The English Channel is relatively shallow, and from a depth of about 30 m in the Strait of Dover deepens gradually to about 100 m in the west. The seabed topography shows extensive evidence of river valley systems that were carved during glacial periods when the sea level was lower (OSPAR 2000).

The Celtic Sea/Biscay Shelf LME covers 760,000 km^2. In the north it consists of the waters to the west of Scotland, including the Minch, between Scotland and the Hebridean islands. At this point the Rockall Trough separates the Rockall Bank from the western Scotland shelf with three significant seamounts, the Hebridean, Anton Dhorn and Rosemary Seamounts. The Rockall Trough follows northwards over the Wyville-Thompson Ridge into the Faroe-Shetland Channel and this topography is an important feature for interconnections between the Atlantic and North Sea (Baxter et al. 2008). Moving south, the shelf broadens forming the Malin Shelf and then follows the west coast of Ireland. The Irish Sea itself is semi-enclosed and relatively shallow (<60 m) in the east but with a deep channel (down to 200 m) in the west. The shelf continues as the Celtic Sea and narrows adjacent to the French coast forming one side of the Bay of Biscay.

The North Atlantic shelf seas are amongst the most productive in the world with respect to higher trophic levels. Despite overexploitation, this region still supports some of the world's major

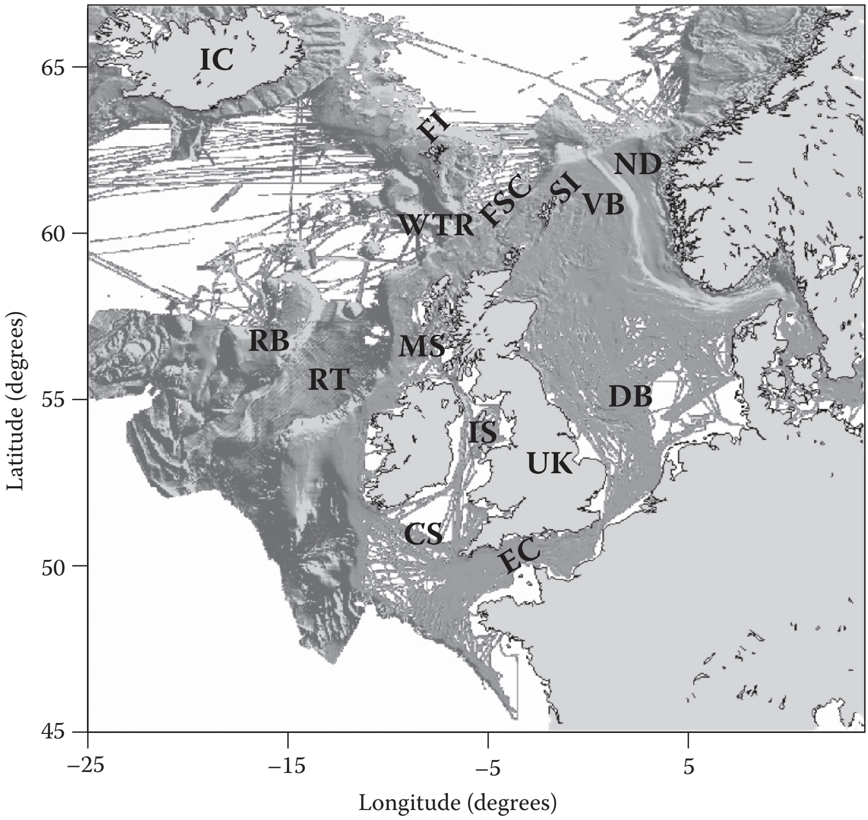

Figure 5 Many of the features of the shelf seas are revealed in this bathymetry compiled, processed and managed by Olex DS. Data are contributed voluntarily and merged into the central database; hence coverage is incomplete. IC, Iceland,; FI, Faroe Islands; WTR, Wyville-Thompson Ridge; FSC, Faroe-Shetland Channel; SI, Shetland Islands; VB, Viking Bank; ND, Norwegian Deeps; DB, Dogger Bank; EC, English Channel; CS, Celtic Sea; RT, Rockall Trough; RB, Rockall Bank; MS, Malin Shelf. (Reproduced with permission from Olex DTm, Edinburgh.)

fish stocks (e.g., herring and mackerel) whilst efforts are being made to rebuild other historically important stocks, such as cod (Horwood et al. 2006). Although the biological components of the shelf seas and the general physical conditions are fairly well described, the mechanisms responsible for interannual and longer-term variability in biological production are still poorly understood, and capturing the relative impacts of local and transregional processes is proving challenging. Nevertheless, understanding these couplings is crucial for sustainable resource exploitation in the North Atlantic shelf seas.

Over recent decades there have been many national research programmes in these shelf seas (e.g., the UK Natural Environment Research Council [NERC] North Sea programme and German GLOBEC). These have provided rich datasets for process understanding and for model development and testing. Since the 1960s, annual fisheries resource surveys have been coordinated through ICES and these provide some of the best multinational long-term datasets for evaluating the effects of environmental change and exploitation. The region is also generally well covered by Continuous Plankton Recorder (CPR) routes (www.sahfos.ac.uk), which extend over the last 70 years. However, in the context of understanding the impacts of long-term environmental change on the complete regional ecosystem, data availability and consistency over time remain problematic.

The major patterns across the wider region

The large-scale atmospheric and oceanic forcing that influences the north-eastern Atlantic

Overall environmental conditions in the north-eastern Atlantic are strongly influenced by three large-scale forcings: the global thermohaline circulation (THC), the freshwater balance in the north-eastern Atlantic and large-scale wind forcing which is strongly influenced by the North Atlantic Oscillation (NAO). In addition, the Atlantic Multidecadal Oscillation (AMO) exhibits as a long-term periodicity in sea temperatures covering the entire North Atlantic but the forcing mechanisms behind this phenomenon are poorly understood (Sutton & Hodson 2005). The global THC is driven by fluxes of heat and freshwater at the ocean surface driving density changes in the seawater, which in turn drives convective overturning (Rahmstorf 2006). Measurements of parts of the global THC have been made whilst the complete global picture is supported by theoretical and modelling results. The THC circulation arm in the Atlantic is relatively well observed and is alternatively termed the meridional overturning circulation (MOC). Changes in the THC have strong consequences for global climate; for example, a partial shutdown of the global overturning has accompanied abrupt shifts of the global ocean-atmosphere towards glaciation (Broeker & Denton 1989). The MOC helps to maintain the relatively warm climate of the North Atlantic compared with similar latitudes in the Pacific (Rahmstorf 2003) and in combination with wind-forcing and ice formation maintains the relative warmth of the north-eastern, compared to the north-western, Atlantic. Model experiments suggest that the impact of a hypothetical collapsed MOC would be an average cooling in the north-eastern Atlantic of around 1.7°C but with localised cooling of more than 15°C in the Norwegian and Barents Seas (Wood et al. 2003). Although it is now thought that a total shut-down of the THC is extremely unlikely, the results from Wood et al. (2003) do demonstrate the importance of the ocean circulation for regional climate in the north-eastern Atlantic. Precipitation and sea level would also be affected by a weakened MOC (Vellinga & Wood 2008). The impact of variations in the strength of the MOC on pelagic ecosystems are however relatively unstudied although see the work of Kuhlbrodt et al. (2009).

The large-scale balance of freshwater flux is important because of its impact on the MOC and because riverine inputs can strongly affect productivity in coastal areas (through water column stratification and nutrient supply). The major input of freshwater to the north-eastern Atlantic comes from rivers emptying into the Baltic and the eastern North Sea. The majority of this freshwater is carried into the Arctic by the Norwegian Coastal Current. On an annual timescale the whole of the north-eastern Atlantic benefits from an excess of precipitation over evaporation. This positive balance is particularly high to the south and west of Norway and over Iceland and south-east Greenland (Serreze et al. 2008) and is balanced by the southwards oceanic transport of ice and freshened seawater to regions where evaporation predominates.

The NAO is the dominant mode of atmospheric variability in the North Atlantic, accounting for 44% of the variance in winter (December–March) atmospheric sea-level pressure (SLP) in the last century (Hurrell 1995, Hurrell & Dickson 2004). The mode of SLP is manifest through changes in the relative strength of the Icelandic low and the Azores high pressure systems. Hurrell (1995) constructed a time series of the winter NAO index of SLP differences between Lisbon and Stykkisholmur, whilst Jones et al. (1997) used the SLP difference between Gibraltar and Reykjavik. These indices have the benefit that they can be extended as far as the 1800s allowing investigation of climate at multidecadel timescales. By using paleoclimate proxies the time series can be extended even further back but relating local conditions, such as surface temperature, to the NAO over these extended time-periods has proven problematic (Jones et al. 2001). These indices remain measures of SLP difference between two particular land stations and this may not account for long-term shifts in the centres of pressure. The oceans response to the NAO has been reviewed in detail by Visbeck et al. (2003) with changes identified including sea-surface temperature (SST), mixed-layer depth, heat content, extent of sea ice and currents. When the index is positive, winter westerly airflow of warm, humid air across the North Atlantic is enhanced and the shelf seas become warmer (Ottersen & Stenseth 2001, Hurrell & Dickson 2004). SST in the subpolar gyre is generally cooler through the enhanced heat flux generated by stronger winds and also northerly airflow at the western edge of the Iceland low. Positive NAO winters are also associated with a north-eastwards shift in storm activity and increased precipitation that is particularly evident along the Atlantic inflow pathway to the Nordic Seas.

The state of the NAO can also be linked to wider changes. Sundby & Drinkwater (2007) showed that the NAO influences the volume flux of water between the North Atlantic and the Arctic Oceans. A high NAO increases the flux of warm Atlantic water from the north-eastern Atlantic through the Nordic Seas to the Arctic Ocean. This increase is balanced by an increased flux of cold Arctic water from the Arctic Ocean into the north-western Atlantic. In contrast, a low NAO decreases the flux of warm Atlantic water in the north-eastern Atlantic, and again, this is balanced by less outflow of cold Arctic water. Hence the NAO forcing causes opposite decadal-scale ocean climate signals in the north-eastern and the north-western Atlantic. Moreover, it was demonstrated that these dynamics could explain the propagation of the great salinity anomalies in an alternative way (Dickson et al. 1988, Belkin et al. 1998, Belkin 2004).

During the last decades, it has become obvious that large-scale changes in atmospheric conditions over the open North Atlantic can be related to biological processes on both land and sea (Hurrell et al. 2003). For example patterns in phytoplankton (Irigoien et al. 2000), zooplankton (Piontkovski et al. 2006) and fish production (Stige et al. 2006) have all been correlated with the NAO index (but see Kimmel & Hameed 2008 for a counter-example). This suggests that atmospheric processes over the North Atlantic during winter–spring have an influence that extends over the whole region (Ottersen et al. 2001).

The role of atmospheric circulation for the transport of materials between the four systems: aerosol effects, iron particles, pollutants

North of about 60°N, the prevailing winds are westerly but in summer airflow can switch to easterly. This will transport Asian dust and smoke from boreal fires, and the area can suffer from the persistent presence of ‘Arctic haze’—aerosol derived from pollutants originating from anthropogenic emissions at lower latitudes (Tomasi et al. 2007). South of about 60°N the prevailing winds are the Westerlies. At the western boundary of the Atlantic Ocean, anthropogenic nitrogen sources have increased dramatically over the last 150 years and North American industry and agriculture contribute a major source of reactive (or fixed) nitrogen to the Atlantic atmosphere (Duce et al. 2008). This probably represents a considerable increase in flux of reactive nitrogen to the oceans compared with the 1860 baseline. The atmospheric nitrogen contributes to new production in the Atlantic and has an impact on primary production in areas that are nitrogen depleted (Moore et al. 2006, 2008). Concentrations of atmospheric nitrogen are reduced considerably by the time the air reaches the north-eastern Atlantic, but nevertheless concentrations in ‘clean’ background air in the eastern north Atlantic are approximately 4-fold higher than in background air over the South Atlantic (Baker et al. 2006). Although the prevailing Atlantic wind direction between about 60°N and about 40°N is from west to east, long-range aeolian transport also brings iron-bearing mineral dust to the Atlantic from the Sahara Desert, the largest global source of such dust. This is important for biological production as iron can be a limiting nutrient for phytoplankton (Jickells et al. 2005) due to the high iron requirements by these organisms in electron transport machinery and enzymes such as nitrate reductase and nitrogenase (Geider & LaRoche 1994). Although the major transport pathway from the Sahara is the north-easterly equatorial trade wind, which carries material westwards towards the Amazon and Florida, a less-frequent pathway sporadically ejects dust over the north-eastern Atlantic Ocean (Prospero et al. 2002). The supply of iron from Saharan dust is considered to control the distribution of nitrogen-fixing organisms in the (sub)tropical North Atlantic Ocean (Falkowski et al. 1998). Atmospheric concentrations of Saharan dust decrease with distance from the source (Mahowald et al. 2005), and consequently concentrations of dissolved iron in surface waters also decrease moving northwards in the Atlantic (Measures et al. 2007). Since the majority of dust found in the Greenland ice cap appears to originate from Asia (Grousset & Biscaye 2005) it seems likely that the waters of the north-eastern Atlantic also receive small inputs of dust from Asian sources.

Less-frequent transport events from sources in Europe can also be significant for the north-eastern Atlantic. For example, a brief episode of south-easterly flow from the United Kingdom and northern Europe contributed most of the atmospheric nitrogen, lead and zinc input into waters off the west coast of Ireland in May 1997 (Spokes et al. 2001, 2006). Similar high concentrations of nitrogen in European-origin air have been reported over other areas of the north-eastern Atlantic (Baker et al. 2006, Spokes et al. 2006) and might be important for local enrichment of iron (Choel et al. 2007, Jickells et al. 2008) and other pollutants. Back trajectory analyses have indicated that Saharan dust plumes moving into the North Atlantic have European airmasses mixed in, resulting in an enhancement of an anthropogenic signature (e.g., with nickel, lead, copper, zinc) of such plumes (Baker et al. 2007).

The oceanographic flows

The general circulation of the northern North Atlantic is heavily influenced by the complex topography of the region (Figure 6). The most obvious feature is the NAC, which brings warm Atlantic water from the south-west. The NAC splits south of Iceland, one branch heading north before splitting again at the Denmark Strait. The flow of Atlantic water along the west coast of Iceland, through the Denmark Strait and into the Nordic Seas has the weakest, although highly variable, volume flux of the NAC branches. However, this current is of great importance to the regional marine climate of North Icelandic waters. The average volume flux of Atlantic water in this curent is around 0.75 Sv* with little seasonal variation.

The other main branch of the NAC flows north-east around the Faroe Plateau carrying warmer water over the ridge between Iceland and the Faroes. North-east of this ridge, the water meets the colder and less-saline waters of the East Icelandic Current and becomes confined into a fairly narrow current flowing eastwards over the northern slope of the Faroe Plateau. On average, the Faroe branch transports volume flux of around 3.5 Sv of Atlantic water. The Shetland branch carries Atlantic water through the Faroe-Shetland Channel in addition to water recirculated from the Faroe branch. On average the Atlantic water flux has been estimated at 3.2 Sv with only a small seasonal amplitude of 0.2 Sv and maximum flow in November. The remaining warm Atlantic waters of the NAC flow through the Faroe-Shetland Channel thence northwards parallel to the Norwegian coast. The warm waters then split into a gyre-like circulation in the Barents and Greenland Seas. Some of its waters may deflect westwards into the northern Greenland Basin and the Boreas Basin, but most recirculation occurs in the Fram Strait. A smaller part of the West Spitsbergen Current eventually enters the Arctic Ocean where it flows eastwards along the Eurasian continental slope. The boundary current continues around the Arctic Ocean, although some of its water advects into the interior basins and forms the Atlantic Intermediate Layer. During this time, the Atlantic waters are subjected to seasonal cooling and mixing with cold, dense Arctic waters. The water of Atlantic origin is known as recirculating Atlantic water, and flows parallel with and partly underneath the cold and fresh polar surface waters, including sea

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[*] 1 Sverdrup = water volume transport 10^6 m^3s^{-1}.

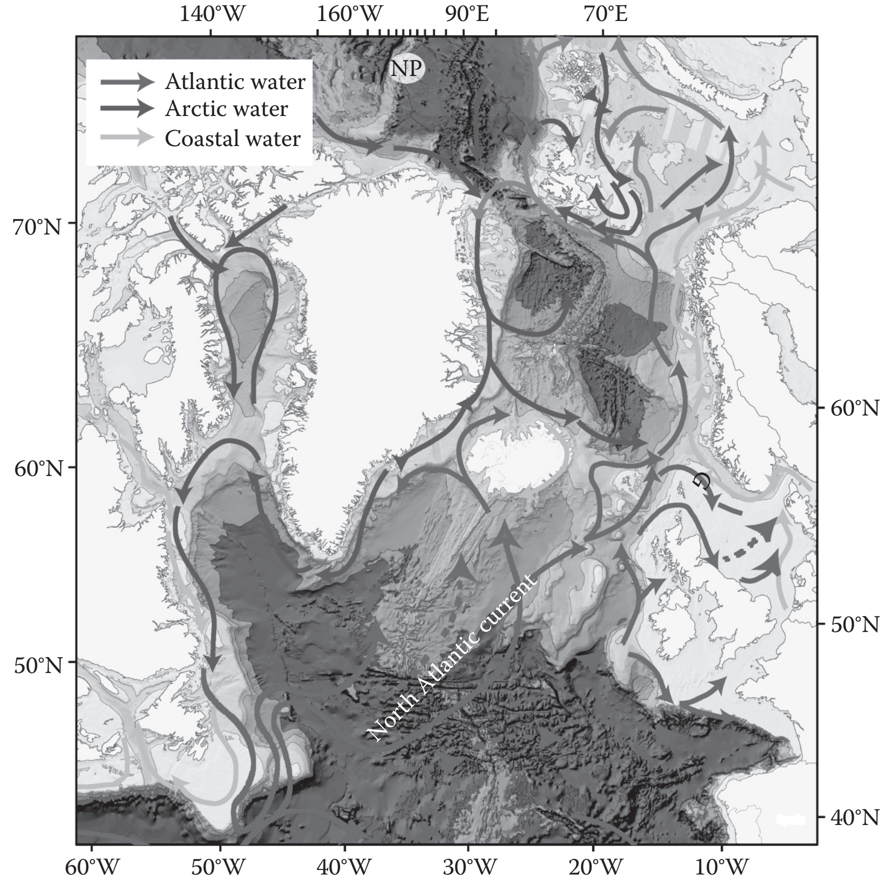


Figure 6 (See colour insert.) The general pattern of oceanographic flows in the north-eastern Atlantic.

ice. This generates the return flow via the East Greenland current. Just north of Iceland, a portion of the upper water masses and probably most of the bottom water in the East Greenland Current turns eastwards into the Iceland Sea. The remaining part flows out of the Nordic Seas through the Denmark Strait. It is important to note that Pacific water also enters the Arctic Seas through the Bering Strait and becomes mixed into the waters flowing south to the Atlantic.

Further south the most striking oceanographic feature is the strong northwards-flowing shelf-edge current, which acts to limit exchange between the Atlantic and the continental shelf. There are very few measurements of cross shelf-edge flows which tend to be episodic and mostly wind driven, either due to local forcing or large-scale pressure effects. Flows on to the shelves are particularly important for the influx of nutrients but because of their large-scale and episodic nature, the best estimates of direct transport come from modelling. Proctor et al. (2003) estimated that 0.7 Mt of nitrate entering the Celtic Sea region originated from across shelf-edge. Internal waves generated at the shelf edge can mix nutrients vertically and if coupled with surface wind flow can be responsible for transport on to the shelves. In reverse, cascading occurs when shelf waters cool and become more dense than adjacent waters over the slope and this is a potentially important mechanism for exporting biogenic material to the deep sea. Evidence of individual cascading events has been found during various studies including Shapiro & Hill (1997).

The mean currents of the North Sea form a cyclonic circulation (Figure 7). The bulk of this circulation is concentrated to the northern part of the North Sea due to major water exchange with

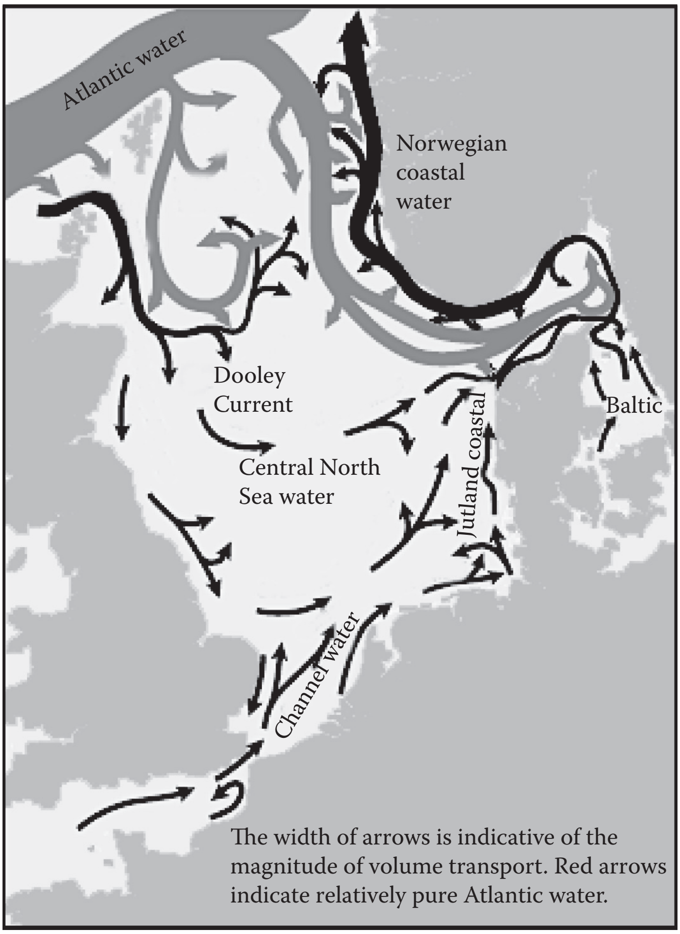


Figure 7 (See colour insert.) Schematic diagram of general circulation in the North Sea. (After Turrell 1992. Reproduced with Crown permission.)

the Norwegian Sea. The circulation in the northern North Sea can occasionally reverse into an anticyclonic pattern under persistent wind forcing (Dooley & Furnes 1981). The main inflow occurs along the western slope of the Norwegian Trench but significant inflows are also found around the Shetland Islands (Turrell 1992). Less than 10% of total inflow to the North Sea comes through the English Channel. All of these inflows are compensated by the northwards Norwegian coastal current. Because the western and southern regions of the North Sea are strongly mixed by the tides, vertical shear values are relatively low. However, the movement of North Sea bottom water has a strong seasonal signal in other parts of the North Sea, with large areas becoming almost motionless during the summer. These areas are usually marked by depressed oxygen levels (to a minimum of about 65% saturation) and by temperatures similar to those of the preceding winter. This typically occurs in large areas of the central and northern North Sea at depths greater than about 70 m. The situation is usually temporary as renewal of these deep waters occurs in the autumn. Areas permanently stratified by salinity have a generally slow bottom water exchange. In the Kattegat, the bottom water is renewed in 1–4 mo, the longest periods of stagnation occurring during summer. This slow renewal, in combination with eutrophication, frequently leads to periods of low oxygen content. The slowest movement of bottom water occurs in central parts of the Skagerrak where depths exceed 700 m. Here, waters are normally replaced at a much slower rate (every 2–3 yr), but rapid changes can occur in winter if bottom water cascades into the Norwegian Trench.

Major biological patterns across the wider region: primary production

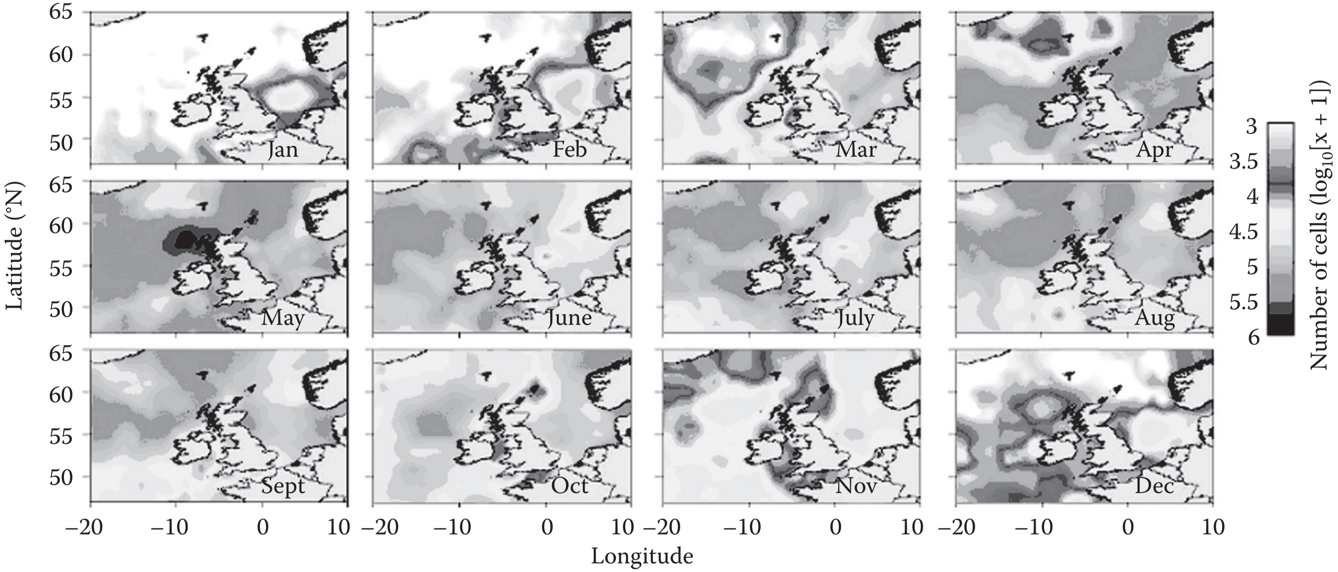
Primary production by phytoplankton fuels the majority of marine food chains and overall sets upper limits to both the activity of the pelagic food web and the quantity of organic carbon exported to the benthos (Mann & Lazier 2005). Phytoplankton community structure is strongly influenced by physical and chemical factors whilst the main losses are due to grazing (mostly by zooplanktonic organisms), sinking (Nielsen & Richardson 1989, Turner 2002) and viral infection (Suttle 2007, Brussaard et al. 2008). In the north-eastern Atlantic the growing season is strongly seasonal due to the annual light cycle and is accompanied by community successions as changing nutrient ratios favour particular phytoplankton groups (Colebrook 1979, 1982, Dippner 1998, McQuatters-Gollop et al. 2007a).

In midlatitude waters the classical picture is of a strong spring bloom dominated by diatoms, followed by a summer decline to a flagellate-rich community, followed by a smaller autumnal bloom as increasing winds mix nutrients back into the euphotic zone (Figure 8). This view has largely come from samples collected by the Continuous Plankton Sampler and latterly from satellite observations (Colebrook 1979, McQuatters-Gollop et al. 2007b). For those parts of the shelf seas subject to thermal stratification, the situation in summer is more complex as significant levels of primary production, not detected by surface sampling, take place just above the thermocline (Richardson et al. 2000, Weston et al. 2005).

However, despite the transient spring period of high biomass and hence productivity and export, in many regions of the open North Atlantic, including the Iceland and Irminger Basins, residual nitrate ($>2\ \mu M\ NO_3^-$) and phosphate ($>0.15\ \mu M\ PO_4^{3-}$) concentrations have been observed during the post-bloom summer period (Sanders et al. 2005). In addition these areas are characterised by consistently low chlorophyll concentrations during summer periods (Henson et al. 2003). The atmospheric supply of iron and the surface water iron concentrations in these regions are very low and recent biophysical and experimental observations have now shown that iron limitation of the phytoplankton community occurs in northern Atlantic waters (e.g., in the Iceland Basin following the spring bloom) (Moore et al. 2006). As a consequence there can be incomplete removal of nitrate and hence a reduced efficiency of the biological carbon pump in this region.

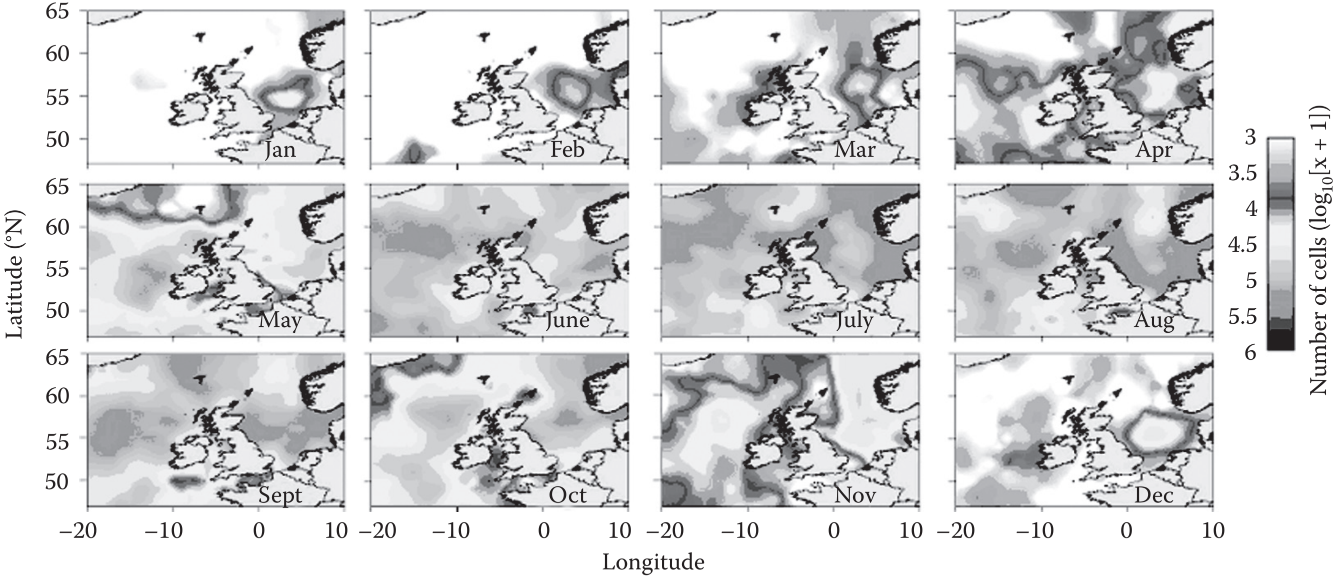
With increasing latitude, the growing season becomes progressively shorter due to changes in illumination (Mann & Lazier 2005). In the far north the bulk of production is concentrated into a single annual peak lasting only a few months. Again the spring bloom is diatom dominated (Hegseth & Sundfjord 2008) although in the Arctic Ocean proper, smaller flagellates are more common. Recent reductions in sea ice between 1998 and 2006 have led to increases in open water area at the rate of around 70,000 km^2 $annum^{-1}$ with the greatest increases in the Barents, Kara and Siberian sectors. Although pan-Arctic primary production averaged 419 ± 33 Tg C $annum^{-1}$ during 1998–2006, recent increases in open water area have led to higher rates of annual production, which reached a 9-yr peak in 2006 (Pabi et al. 2008).

Throughout the north-eastern Atlantic, spring blooms tend to be diatom rich whereas in summer the picophytoplankton (<3 µm in diameter) dominate as described above (McQuatters-Gollop et al. 2007a). Several species of the colonial Prymnesiophyte *Phaeocystis* (e.g., *P. pouchetii*) in the colder Nordic Seas and *P. globosa* in the temperate Atlantic shelf seas, regularly dominate the phytoplankton community (Schoemann et al. 2005, Long et al. 2007, Nejstgaard et al. 2007). Another important organism in the north-eastern Atlantic is the coccolith *Emiliania huxleyi*. This species forms massive summer blooms in the temperate and subpolar north-eastern Atlantic and associated shelf seas and plays key roles in the global carbon cycle (Hays et al. 2005). As well as squestering atomospheric carbon dioxide, *Phaeocystis* and *E. huxleyi* also play key roles in climate regulation through the production of dimethylsulphide (Strom 2008).



(A) Spatial distribution of diatoms

Figure 8 (See colour insert.) Mean monthly spatial patterns of (A) diatoms and (B) dinoflagellates in the north-eastern Atlantic during the period 1958 to 2003. (From McQuatters-Gollop et al. 2007a. With permission of Inter-Research Science Center.)



(B) Spatial distribution of dinoflagellates

Figure 8 (continued).

Under the right circumstances the formation of phytoplankton blooms is common. Algal blooms are loosely defined phenomena, generally used to describe the accumulation of monospecific phytoplankton cell biomass through enhanced primary production. What constitutes an algal bloom is, however, not simply a biomass issue, as illustrated by blooms of toxic species (Smayda 1997). Phytoplankton species with relatively low *per capita* growth rates can still bloom if they escape grazing (Strom 2008). Reduced edibility is often linked with size (Long et al. 2007) or the production of phycotoxins (Turner & Tester 1997). Interestingly, *Phaeocystis globosa* appears to be able to modify its morphology in response to the dominant consumers present (ciliates or copepods), a strategy that may reduce the level of grazing it suffers (Long et al. 2007). Blooms of phytoplankton differ in their magnitude and frequency with latitude and closeness to land. Furthermore, the Atlantic shelf seas are enriched with inorganic nutrients from terrestrial run-off, leading to concern about eutrophication (Andersen et al. 2006) and stimulation of harmful algal blooms (HABs) in these areas (Smayda 1997). A broad classification of HABs distinguishes two groups of organisms: the toxin producers that can contaminate seafood or kill fish and the high-biomass producers that are considered 'nuisance' algae, causing anoxia, clogging fishing nets and affecting tourism. Some HABs have characteristics of both. Many of the toxin-producing HABs are dinoflagellates. There are also concerns that, particularly in the shallow shelf seas, multiple stressors of climate change and anthropogenically altered nutrient ratios will lead to increases in the occurrence of HAB events (Peperzak 2005).

Evidence has also emerged that a significant change in the primary production cycle in the central north-eastern Atlantic and North Sea took place in the mid-1980s with an extended growth season and loss of the classic double peak in production (Reid et al. 1998). This is associated with a 'regime change' spanning all trophic levels and may have been caused by recent warming and changes in turbidity, altering phytoplankton community structure (McQuatters-Gollop et al. 2007b).

Major biological patterns across the wider region: secondary production

Zooplankton includes a wide range of organisms (e.g., ciliates, chaetognaths, hydrozoa, copepods and egg and larval stages of fish, bryozoans, echinoderms). Zooplankton communities are often dominated by copepods (Williams et al. 1994), which act as the key link between primary producers and higher trophic levels and as a critical food resource for early-feeding larval fish (Banse 1995). The population dynamics of individual zooplankton species is a product of their rates of reproduction, growth and mortality. Reproduction and growth patterns of zooplankton vary not only between species but also within species, reflecting regional dissimilarities in production cycles and thermal regimes. The timing of the zooplankton production cycle is an important factor for controlling phytoplankton growth (Fileman et al. 2007), for larval fish survival (Cushing 1990) and for benthic-pelagic coupling (Townsend & Cammen 1988). Much of our knowledge of large-scale zooplankton patterns has come from the Continuous Plankton Sampler (Barnard et al. 2004, Warner & Hays 1994) and the north-eastern Atlantic is unique globally in the long-term and broad spatial coverage of zooplankton distribution by this survey.

The regional patterns of secondary production generally follow those of primary production, with highest levels in North Atlantic shelf seas and the Arctic and Nordic Seas; production levels in the open ocean North Atlantic are generally lower. As mentioned previously the primary production season becomes shorter with increasing latitude and this in turn affects secondary production (Mann & Lazier 2005). Local features particularly mixing and stratification of the water column will also affect secondary production through their influence on phytoplankton growth (Cushing 1989). Frontal systems in shelf seas have been shown to be particularly significant in influencing regional-scale distributions and productivity (Perry et al. 1993, Thibault et al. 1994, Albaina & Irigoien 2004, Wishner et al. 2006).

Zooplanktonic metabolic responses to climate change, in particular warming, can be assessed using ecological metabolic theory. This considers how metabolic rates vary with body size and temperature (Brown et al. 2004). Although mainly applied to terrestrial systems, this approach is emerging as a powerful tool in marine studies. For example, the metabolic theory can be used to predict variations in production and respiration and to evaluate how the primary production/ respiration rate and implied changes in carbon flux will vary with different climatic scenarios (López-Urrutia et al. 2006).

Ocean currents as the major mechanism linking the regions in the north-eastern Atlantic

The role of ocean currents in the transport of nutrients

The traditional concept was that availability of nitrogen was the primary control on phytoplankton growth but for the North Atlantic, the general picture that is emerging is of a latitudinal gradient with nitrogen-deficient systems in northern parts and a shift towards phosphorus deficiency in the south. The present understanding is one of a biological control of the nitrogen/phosphorus balance in which the nitrogen content adjusts to the phosphorus content via the two opposing processes of nitrogen fixation and denitrification (Tyrrell 1999).

For the Arctic inflow around Greenland, the nitrogen deficiency seems at least partly to originate from the Bering Strait and Chukchi shelf regions, where high sedimentation rates combined with shallow depths produce low-oxygen environments that favour denitrification (Carmack & Wassmann 2006). Denitrification appears to function relatively efficiently at low temperatures, as illustrated by the detection of denitrification and an-ammox (anaerobic ammonium oxidation) activity in Arctic sea ice (Rysgaard et al. 2008). Adaptation to temperature appears to be a strong selective force among diazotrophs (nitrogen-fixing bacteria), as demonstrated by the distribution of different nifH phylotypes according to temperatures in the southern North Atlantic (Langlois et al. 2008). Despite evidence that low temperature *per se* is not inhibitory to nitrogen fixation (Karl et al. 2002), nitrogen fixers appear to be absent in cold marine waters (Staal et al. 2003). Presumably as a consequence of this, nitrogen deficiency is conserved in the Arctic and a low nitrogen/phosphorus signal is still a characteristic feature of water when it leaves the Arctic Ocean in the East Greenland current (Daly et al. 1999).

The first claims of phosphorus deficiency in the southern part of the North Atlantic came from the Sargasso Sea. Here, rapid turnover of orthophosphate leads to phosphate concentrations below 1 n*M* (Cotner et al. 1997, Wu et al. 2000). Iron is a critical cofactor for the nitrogenase enzyme (Karl et al. 2002), making iron availability an expected key controlling factor in marine nitrogen fixation. Based on this, aeolian input of iron via Saharan dust has been suggested to be a mechanism stimulating nitrogen fixation in the south-western North Atlantic (Walsh & Steidinger 2001, Jickells et al. 2005). In the western Central Atlantic, however, enzyme assays identified phosphate, rather than iron, as the main constraining nutrient for *Trichodesmium* N_2 fixation (Webb et al. 2007). There is an ecological argument that too efficient nitrogen fixers would destroy their own ecological niche if they load excess nitrogen into the system. Such 'overshoots' in nitrogen fixation do, however, seem to occur in nature (Nausch et al. 2004), driving the system into phosphorus deficiency. There is also evidence that the simple control model involving major nutrients is inappropriate, at least in some locations where regional differences in the availability of minor nutrients are significant in structuring the phytoplankton and microbial communities (Müller et al. 2005). Since climate change is likely to affect both sea-surface temperature (Walsh 2008) and iron input via aeolian dust (Mahowald et al. 2005), we can expect the latitudinal gradient in nitrogen/phosphorus balance in the Atlantic to be sensitive to climate change.

For the shelf seas, inflow from the Atlantic is crucial since it has been estimated that around 90% of nitrogen and phosphorus inputs to the North Sea come from this source (OSPAR 2000). However, much of this nitrogen is in the non-reduced form and so not readily available for primary production. In addition there are large intra- and interannual variations in the inflow.

The role of ocean currents in the transport of carbon between the four systems: shelf pump

According to the inventory of Sabine et al. (2004), the North Atlantic basin stores 23% of the global oceanic anthropogenic CO_2 despite covering only 15% of the global ocean area. The adjacent shelf seas are also efficient at drawing down atmospheric CO_2 and thus play a key role in the global carbon cycle. In the North Sea there is a separation in carbon processing of the shallower southern area from the deeper northern waters (Figure 9). Carbon export occurs in the deeper northern waters, particularly during the summer as particulate organic carbon from algal production sinks to the deeper, cooler waters. Heterotrophic respiration below the thermocline releases CO_2 into the water, where a substantial fraction is transported northwards by the subsurface circulation. According to Thomas et al. (2005), 90% of the CO_2 absorbed in the North Sea is exported to the North Atlantic. The Atlantic water entering the North Sea through the Orkney Shetland gap thus gains approximately 40 mmol C kg^{-1} before leaving the North Sea. During late summer the outward carbon transport via the Norwegian trench is approximately 2.2×10^{12} g C, while in the same period the North Sea absorbs approximately 15% from the atmosphere.

Export of carbon from the North Sea occurs because the thermal stratification of the northern section of the sea allows particulate organic carbon from algal production in the warmer surface waters to be exported down into the cooler subsurface layer. Most of the CO_2 that is subsequently released from heterotrophic respiration of this particulate organic carbon is transported northwards to the

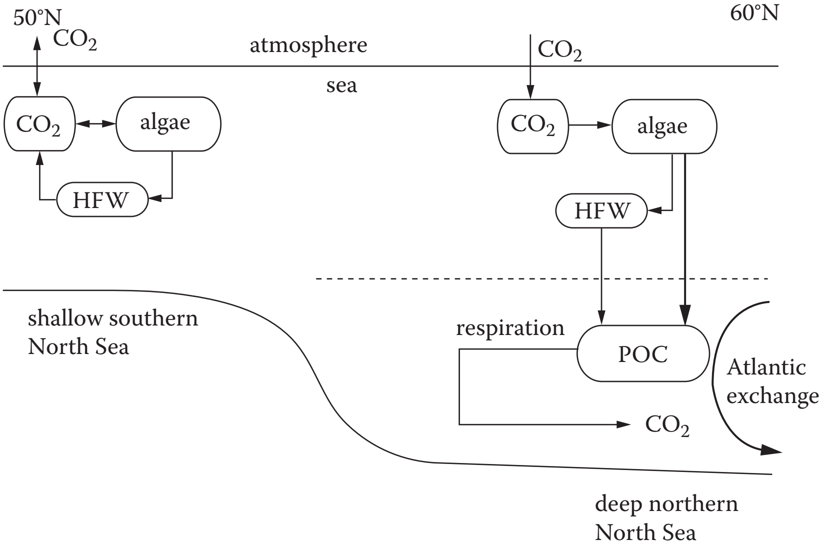


Figure 9 South-north section through the North Sea. In the shallower southern region production and respiration processes occur throughout the mixed water column whereas in the deeper northern North Sea seasonal stratification separates the production and recycling processes of CO_2, POC (particulate organic carbon), and HFW (high-level food web). (Modified from Thomas et al. 2004a. With permission of AAAS.)

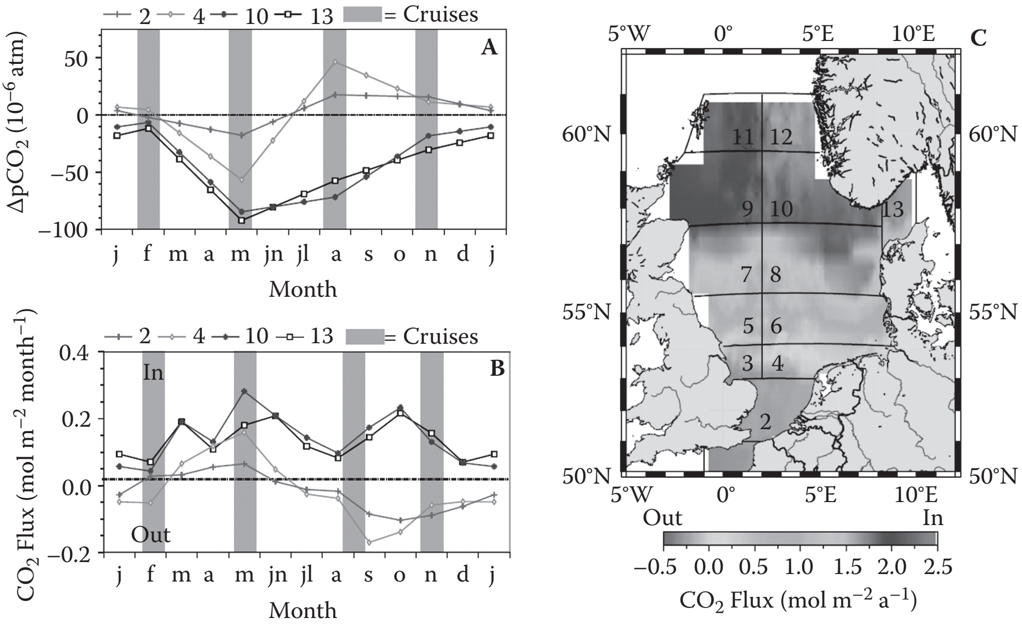


Figure 10 (See colour insert.) Annual cycles of air-sea partial CO_2 pressure differences (A) and calculated fluxes (B) for selected areas in the North Sea, with shading indicating periods of observation. The spatial pattern of air-sea CO_2 fluxes across the North Sea is shown in C. Note positive values for CO_2 flux indicate absorption from air to sea. (From Thomas et al. 2004a. With permission of AAAS.)

North Atlantic Ocean by subsurface ocean circulation (Figure 9). The shallower non-stratified southern section does not contribute to this carbon transport since both algal production and heterotrophic respiration occur within the year-round mixed water column, thus preventing significant exports.

The findings of Thomas et al. (2004a) were based on four cruises spread across a year to reveal seasonal and spatial patterns. The seasonal variations of partial pressure differences (Figure 10A) were measured and interpolated for 13 sectors of the North Sea (Figure 10C) and coupled with measurements of the seasonal variations in CO_2 flux (Figure 10B) to enable the spatial patterns in annual CO_2 flux to be calculated (Figure 10C).

This study showed that the North Sea as a whole acts as a CO_2 sink all year round. The only source is from the southern areas (sectors 1–4) during the late summer (Figure 10c). The greatest drawdown occurs in May during the spring algal blooms, and secondly in October, when storms force CO_2 uptake. Only about 1% of carbon captured by the algae is sequestered in the North Sea sediments; the majority, as described, is exported to the North Atlantic Ocean.

Based on these studies the significance of the North Sea shelf pump for the sequestering of carbon is well established. The effects of global warming on the efficiency of the shelf pump are, however, unclear. A longer stratification season due to warming may further reduce the flux of nutrients to the surface layer. As a result, primary production after the spring bloom and a restructuring of the phytoplankton community may occur. Furthermore, the increased stratification has the potential to increase the dominance of the microbial loop thereby recycling carbon in the surface layer and potentially resulting in a reduced flux of organic material to the deep layer. Thus, carbon outflows due to the shelf pump will probably be reduced, limiting the efficiency of the shelf pump and the contribution of this mechanism to the sequestration of carbon.

The role of ocean currents in the transport of phytoplankton and microzooplankton

The phytoplankton communities of the north-eastern Atlantic are strongly influenced by the inflow of Atlantic water into the North Sea and the Nordic Sea (Skogen et al. 2007). Wind conditions associated with the NAO also affect the development of the upper mixed layer and thus phytoplankton productivity. As demonstrated in freshwater lakes this may potentially affect their nutritional value to higher trophic levels (Diehl 2007). Modifications in vertical mixing and stratification may also alter species composition and the export of primary production to deeper waters.

As discussed on page 12 there is a large interannual variability in the flux of Atlantic water entering the shelf seas. Although this advection transports oceanic phytoplankton cells to different locations, it is the local conditions that determine whether these species can become established in new areas (Hegseth & Sundfjord 2008). In the north-eastern Atlantic there is a weaker latitudinal gradient in temperature compared to the north-western Atlantic. Nevertheless, this weaker gradient can still set barriers to the long-term survival of phytoplankton species but serial seeding can lead to significant temporary range extensions (Edwards et al. 2002). For example, Johnsen et al., (1997) described an advection event that resulted in a widespread bloom of the normally oceanic *Ceratium furca* that persisted over a 6-wk period and reached mid-Norway (63°N). However, blooms may propagate over wide distances without advection. Since many of these organisms produce resting stages or are present at very low population levels in seawater, blooms can initiate if environmental conditions become optimal. For example, a bloom of the coccolithophorid *Emiliania huxleyi* started in Norwegian coastal waters at 60°N and passed the Arctic Circle (70°N) 3 mo later (Hegseth & Sundfjord 2008). Because some bloom-forming species interfere with human activities such as aquaculture, more attention is now paid to monitoring their occurrence, particularly in coastal waters. Increased frequency of recorded HAB outbreaks may be related to factors such as enrichment of coastal nutrients but may just reflect increased monitoring and human activity in the coastal zone. Periodic incursions of warm-water phytoplankton into Norwegian waters have certainly been noted since the early 1900s (Smayda 1958).

The role of ocean currents in the transport of mesozooplankton

Mesozooplankton are of intermediate size, typically with body lengths between 0.2 and 20 mm (Harris et al. 2000). Although the number of mesozooplankton species in a region can be quite high there are usually a few dominant species in terms of biomass (Pitois & Fox 2006). In northern areas of the Atlantic, *Calanus finmarchicus* tends to be dominant, constituting up to 80% of mesozooplankton biomass but in the shelf seas smaller species such as *Pseudocalanus elongatus*, *Temora longicornis* and *Acartia clausi* are common. As with all plankton, the mesozooplankton have little direct control over their horizontal movements, relying on vertical behaviour to constrain dispersal (Backhaus et al. 1994, Aksnes & Blindheim 1996, Slagstad & Tande 1996, Speirs et al. 2004). Because of its ecological importance, *Calanus finmarchicus* has probably been the most intensively studied copepod species in the north-eastern Atlantic. The complex life cycle of *Calanus finmarchicus* strongly affects the extent to which different geographical regions in the north-eastern Atlantic are linked. Backhaus et al. (1994) first proposed that there was a line source of overwintering *C. finmarchicus* below the continental shelf jet (CSJ), which got transported into the North Sea when migrating to the surface in the spring. Deep counter-circulation flowing out of the North Sea would subsequently close the cycle, transporting the next overwintering generation to deep water off the continental shelf. Although there is little evidence for a truly ‘closed’ circuit of transport in the way originally imagined, it has become clear that the North Sea is essentially replenished on an annual basis from the oceanic population centres in the north-eastern Atlantic and the Norwegian Sea (Heath et al. 1999). During the winter, preadult fourth and fifth copepodite stage (CIV, CV) individuals are found at depths of 200–1500 m (Heath et al. 2004) and remain there in a suspended, diapause-like state (Hirche 1996) in which they subsist on stored lipids (Jónasdóttir 1999). In the spring they rise to the surface, moult to the adult stage, and begin reproduction (Heath & Jónasdóttir 1999). The number of generations per year varies between one and three depending on temperature. During the surface reproductive phase, *C. finmarchicus* is transported into the shelf seas. In these shelf regions the individuals of the species play a significant ecosystem role as grazers and as a major food source for larval fish (Heath & Lough 2007, Rowlands et al. 2008). This life cycle has two important implications in relation to regional interconnectivity. Firstly, although *C. finmarchicus* is ecologically important on the shelf, it is essentially an oceanic species. Secondly, its demography is fundamentally affected by circulation (and changes in circulation) in both surface and deep currents.

The ocean-shelf linkage is also potentially the key to understanding the relationship between the negative correlation between the winter NAO index and the abundance of *C. finmarchicus* and the weaker positive relationship with the abundance of its warmer water congener *C. helgolandicus* on the shelf seas (Fromentin & Planque 1996). Originally Fromentin & Planque (1996) attributed the relationship to the fact that more positive winter NAO years typically experience higher temperatures and westerly winds, both of which would affect primary production, and that this favours warmer water species such as *C. helgolandicus*. Subsequently, Stephens et al. (1998) suggested that periods of negative (low) NAO were associated with stronger inflows of Atlantic water to the North Sea, which would lead to increased transport of *C. finmarchicus* from the Norwegian Sea. This hypothesis was further developed to a basin-scale context by Greene & Pershing (2000). Sundby (2000) suggested that the variable advection of *C. finmarchicus* from the core production area of the Norwegian Sea to the North Sea and the Barents Sea is an important factor influencing the recruitment of cod stocks. However, Kimmel & Hameed (2008) have recently questioned the strength of the statistical link between *C. finmarchicus* abundance in the north-eastern Atlantic and the NAO.

Heath et al. (1999) showed that the Wyville-Thompson Ridge forms an effective physical barrier for overwintering *C. finmarchicus*, with much higher densities occurring in the Norwegian Basin and Faroe-Shetland Channel than to the south of the ridge. During winter, diapausing *C. finmarchicus* in the Faroe-Shetland Channel are concentrated below the pycnocline in Norwegian Sea Deep Water (NSDW). During negative winter NAO years winds tend to come from the north-west, favouring production of NSDW and advection of *C. finmarchicus* into the Faroe-Shetland Channel. However, the well-behaved negative relationship between the winter NAO index and *C. finmarchicus* broke down in 1996 and 1997 (Planque & Reid 1998). This appears to be because NSDW production also integrates climatic conditions on a decadal timescale. In 1996 the NAO was strongly negative but following an extended positive period; the abundance of *C. finmarchicus* in the North Sea remained small because although transport into the North Sea was favoured, the NSDW overflow remained small (Heath et al. 1999). The links between the atmospheric drivers and *C. finmarchicus* are mediated by responses to changes in both deep water (affecting the overwintering stages) and surface water circulations and these respond over different timescales.

Calanus finmarchicus has a large geographic domain extending from the Gulf of Maine to the southern Labrador Sea in the western Atlantic and from the North Sea to the Barents Sea in the eastern Atlantic. CPR data revealed that there are three main oceanic population centres in the Norwegian Sea, Irminger Sea and southern Labrador Sea. These population centres are associated with oceanic gyres, which may help to reduce advective losses to regions that are unfavourable for population growth. Aksnes & Blindheim (1996) examined this problem by estimating the advective renewal rate of the Nordic Sea gyre and the subpolar gyre and comparing them to estimates of the intrinsic rate of population increase under various assumptions of fecundity and the number of generations per year. Since the advective renewal rate is equivalent to a per capita loss from the region for a well-mixed population, this comparison provides a rough estimate of whether a region can independently sustain a population. In all cases the biological rate of increase was at least an order of magnitude greater than the advective renewal, and that less than 5% of the annual production in the Nordic seas was lost from the system.

The dominance of biological rates over physical ones is also apparent in modelling studies. Speirs et al. (2006) constructed a spatially explicit coupled physical/biological model of *C. finmarchicus* over its entire geographic range. Development rate and fecundity were driven by a yearly cycle of temperature obtained from the Ocean Circulation and Advanced Modelling Project (OCCAM) ocean circulation model (De Cuevas et al. 1998) and of phytoplankton carbon derived from bottle samples and SeaWiFS (Sea Viewing Wide-Field of View Sensor) satellite data (Clarke et al. 2006). Population control was achieved by density-dependent mortality, which they showed needed to be temperature dependent to match CPR data. The spatial transport of *Calanus* was calculated from the OCCAM flow fields together with an assumed horizontal dispersion. In one experiment Speirs et al. (2006) switched off transport entirely and then ran the model to a quasi-stationary state. The results indicated that transport had a relatively minor impact on the distribution of *Calanus* in the sense that the two major population hot spots in the Norwegian Sea and the subpolar gyre persisted. By contrast, transport was of major importance in extending the population range. The most dramatic impact is in the northern Norwegian Sea, where sea ice prevents sustainable populations in the absence of seasonal influxes of animals.

In a second experiment relating to large-scale transport, Speirs et al. (2006) simulated the propagation of *Calanus* inocula in the Norwegian Sea gyre and the subpolar gyre. Within 2 yr the individual gyre systems were populated. By the third year the Norwegian sea population had become entrained in the Greenland coastal current and was transported through the Irminger Sea and into the subpolar gyre. In both cases the model had nearly reached its fully populated steady state after 5 yr. This surprisingly short invasion timescale suggests a very high level of connectivity, despite the fact that the large-scale demographic impact of transport is limited. These two observations can only be consistent if the environmental factors driving the demographics show coherence over spatial scales at least as large as the distances travelled by individual *Calanus* during their generation time.

High-dispersal capacity coupled with the lack of physical barriers suggest that many marine species with pelagic stages should show weak population genetic structuring (Palumbi 1994). However, the very large scale of the geographic distributions of certain mesozooplanktonic species, together with the possibilities of gene-flow restriction mediated by gyre systems, introduces the potential for regional genetic isolation. To date the evidence for significant genetic differentiation in *C. finmarchicus* across the Atlantic is at best equivocal. Bucklin & Kocher (1996) reported the same mitochondrial 16S ribosomal DNA genotypes in both the eastern and western Atlantic but using the same markers found significant variation within the Georges Bank region. Using different markers, Bucklin et al. (2000) revealed differences between Atlantic and Arctic *C. finmarchicus* populations in Icelandic waters. More recently more sensitive microsatellite markers have been developed (Provan et al. 2007). Provan et al. (2009) used these together with a part of the cytochrome B (CYTB) gene to estimate gene flow across 14 sites in the Norwegian Sea gyre, the Irminger Sea gyre and the North Atlantic off Nova Scotia. They concluded, contrary to previous studies, that there was no evidence for genetic differentiation across the main population centres for *C. finmarchicus*.

From a population dynamics and ecosystem perspective such genetic studies are extremely important because if strong regional differences are found it may not be possible to understand local dynamics without an appreciation of local phenotypic adaptations. However, the present lack of evidence for differentiation within *C. finmarchicus* at the basin scale is in agreement with the high connectivity and short timescales predicted by Speirs et al. (2006). It is also worth noting that genetic differentiation (in the absence of selection) arises through the countervailing effects of population mixing and genetic drift. A full synthesis must await a new generation of coupled physical/biological models that include a genetic model. Although less intensely studied, oceanic transport into shelf seas is also likely to be a key factor in the ecology of other important mesozooplankton such as *Calanus helgolandicus* (Bonnet et al. 2005, Helaouët & Beaugrand 2007).

The role of ocean currents in the transport of macro- and megazooplankton

Macro- and megazooplankton are planktonic organisms larger than 2 cm (Harris et al. 2000). This diverse group includes tunicates, chaetognaths, euphausiids and gelatinous zooplankton and ichthyoplankton but because of its importance for fisheries, the transport of fish larvae is dealt with in a separate section.

It has long been known that marine organisms can be used to characterise water masses and many marine biological studies during the early twentieth century adopted this approach. At this time there was a marked warming of coastal waters associated with a positive phase of the NAO and AMO. Cushing (1982) has described how during this period (1920s–1930s) unusual numbers of surface-living and pelagic subtropical animals were transported to the western British Isles. In the waters off Plymouth (south-western England) it had been noted that the chaeotognath *Sagitta setosa* was characteristic of English Channel water whilst its congener *S. elegans* typified warmer Atlantic water. Changes in the relative abundance of these two species at the E1 observatory have been consistent with changes in sea temperature and with wider ecosystem effects (Hawkins et al. 2003).

Throughout the north-eastern Atlantic there are numerous records of periodic outbursts of gelatinous zooplankton. Whilst there have been several claims that the rate of outbursts may be increasing, due to climate change, overfishing or increases in the availability of hard surfaces required by the planulae larvae (Mills 2001), these claims are hard to verify. Macrozooplankton have generally been poorly monitored in the past, giving at best a fractured baseline to compare with modern observations (Purcell et al. 2007). In addition, these organisms are characterised by pulsed population dynamics (Boero et al. 2008). Most observations come from the shelf seas where species may either be endemic (e.g., *Aurelia aurita*) or oceanic or warmer water species advected into the shelf seas. As well as potential poorly understood impacts on overall food web structuring (Mills 2001), blooms of gelatinous zooplankton can have direct impacts on human activites such as fishing, fish farming and tourism. For example, Båmstedt et al. (1998) reported a mass outbreak of the siphonophore *Apolemia uvaria* along the western Norwegian coast that caused deaths of farmed salmon. This species has a near-global distribution being normally found in offshore waters down to depths of 800 m. *Apolemia* was therefore probably transported from the open Atlantic along the Norwegian coast (Figure 11). Mass invasions of oceanic species associated with increased influx of North Atlantic water on to the European shelf seas and into Norwegian coastal waters are not uncommon. In summer of 2007 a similar event was reported in the popular press involving the oceanic species *Pelagia noctiluca* (Heard 2005) that resulted in complete destruction of a salmon in a sea farm off northern Ireland.

The role of ocean currents in the distribution of fish across system boundaries

Transport of fish eggs and larvae

Dispersal of marine organisms during their planktonic stages is a crucial factor affecting the genetic structuring, recolonisation capacity and the ability of populations to respond to environmental change. The distances and pathways over which planktonic stages are transported are direct functions of the strength of residual currents and the duration of the planktonic stages (Shanks et al. 2003). Because the planktonic stages of many fish are relatively long lived, potential dispersal

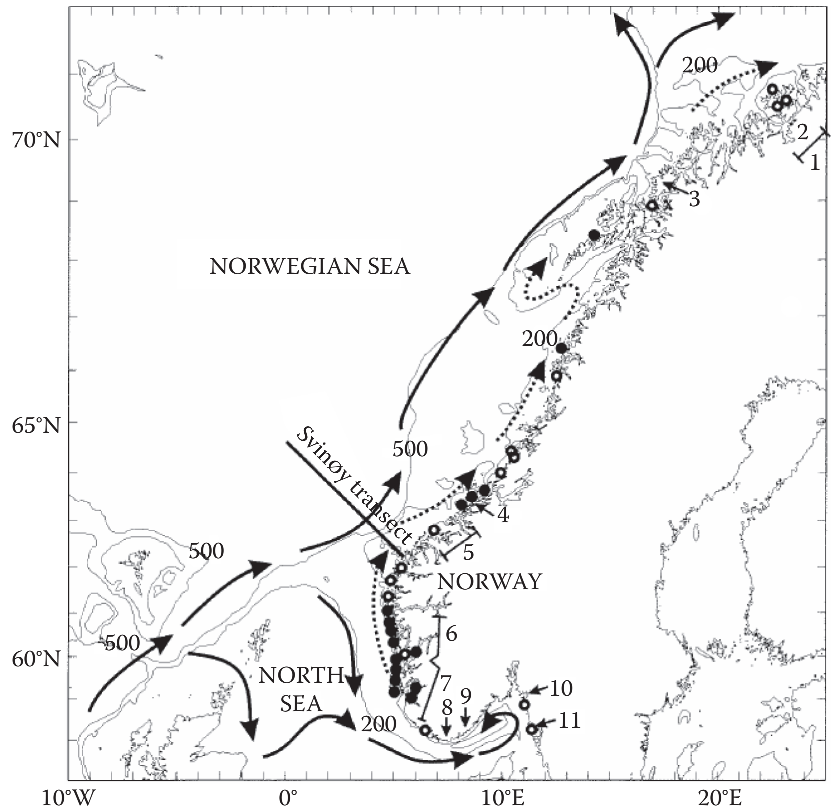


Figure 11 Reported occurrence of *Apolemia uvaria* blooms along the Norwegian coast in 1997 (Båmstedt et al., 1998). Solid circles indicate mass occurrences causing salmon farm problems, open circles indicate low abundance of *Apolemia*. Solid and dotted arrows indicate the main oceanographic flows. (Reproduced with permission of Taylor & Francis.)

distances for individuals will range from tens to hundreds of kilometres (van der Molen et al. 2007). However larval behaviour and oceanographic features can act to restrict dispersal so that a significant portion of offspring are retained close to their natal origins—potentially generating self-recruiting populations. Whilst self-recruitment has been most widely studied in tropical reef fish (Almany et al. 2007) it is also a feature for some temperate species. For example, Iles and Sinclair (1982) proposed that larval retention by oceanographic features, predominantly fronts, was a key mechanism for maintaining genetically discrete substocks of Atlantic herring (*Clupea harengus*). Because of their small size and extended planktonic durations there are few direct observations of fish larval dispersal except where population size and dispersal range are sufficiently small to allow observation or mass marking and recapture (Almany et al. 2007). Most estimates of dispersal distances have been inferred from knowledge of water currents potentially linking known spawning areas and nursery grounds. More recently coupling of oceanographic computer models with particle tracking has allowed more formal testing of these transport paths, including seasonal and interannual variability. Although such models may adequately simulate the dispersal of the essentially passive egg stages, incorporating responsive larval behaviour remains a challenge (Vikebø et al. 2007a). Even for well-studied species such as European plaice *Pleuronectes platessa* (Fox et al. 2006) or walleye pollack *Theragra chalcogramma* (Olla et al. 1996) there is limited understanding of how individual larvae react to environmental cues and trade off the risks of obtaining adequate food against predation (Vikebø et al. 2007a). Experimental studies of temperate fishes have also tended to focus on a limited range of commercially important species (Leis 2007). Because of this we probably underestimate the variety of behaviours, and thus transport pathways, utilised by the early life stages within fish communities as a whole (van der Molen et al. 2007). Despite these problems, particle-tracking models have provided important insights into the transport of early life stages of several fish species in European waters. Most examples suggest drift to be contained within EUR-OCEANS' systems. For example within the North Sea, the transport of plaice eggs and larvae across the southern North Sea is relatively well understood (van der Veer et al. 1998) whilst it is known that residual currents transport haddock eggs and larvae from spawning grounds off the north-west of Scotland, around the northern tip of the United Kingdom and into the northern North Sea (Heath & Gallego 1998). Off Norway the northwards drift of cod eggs and larvae from spawning grounds around the Lofotoen Islands, including aspects of larval behaviour has also been relatively well studied (Vikebø et al. 2007a). Here there is a clear influence of regional linkage since Vikebø et al. (2007b) modelled the impact on Arcto-Norwegian cod of a slowdown in the MOC. According to their model results, a 35% reduction in the MOC would result in a southwards and westwards shift in the distribution of cod year classes from the Barents Sea on to the narrow shelves of Norway and Spitsbergen, reductions in individual growth of the pelagic juveniles and in increasing numbers of larvae and pelagic juveniles being advected towards the western parts of Spitsbergen, and possibly further into the Arctic Oceans, where they are would be unable to survive.

As well as the indirect effects of regional linkages, some species cross between EUR-OCEANS' regions. One of the best-known examples is the European eel (*Anguilla anguilla*). Following spawning in the south-western Sargasso, the larvae (leptocephalii) drift across the open Atlantic (Wang & Tzeng 2000). When the leptocephalii reach coastal waters, they metamorphose into glass eels, which move into estuaries and rivers. Eel populations within European rivers have declined catastrophically since the 1980s and processes occurring in the open ocean, such as shifts in the track of the North Atlantic drift, may be behind this decline (Feunteun 2002, Bonhommeau et al. 2008). The importation of Japanese eels (*Anguilla japonica*) for cultivation trials has also introduced a parastitic nematode (*Anguillicola crassus*). This nematode is now widespread in Europe but its impacts on native eel stocks are not known (Kennedy & Fitch 1990). The European eel thus provides a strong example of where both life history linkages between the Atlantic and the shelf seas and the dispersal of alien species within the shelf seas are of key importance. In terms of transregional linkages, mackerel and blue whiting provide further examples of commercially important species. Starting in February, north-eastern Atlantic mackerel spawn progressively from the Bay of Biscay up the shelf edge and spawning ends around July off the west of Scotland (Bartsch & Coombs 2004). Model-based particle tracking suggested that although most of the larvae drift northwards in the Atlantic current, a smaller proportion are transported southwards and the location of the division that separates the drift routes varies interannually depending on the hydrographic conditions (Skogen et al. 1999).

Interannual variability in oceanographic flows can lead to pulsed recruitment in certain regions. A well-studied example is the western Greenland cod stock, which was historically sustained by periodic influx of cod larvae transported from Icelandic spawning grounds. The strength and timing of the transport are related to the NAO. Because the NAO index has recently been in a positive phase, both transport conditions and local conditions at Greenland have been less favourable for the cod and the western Greenland stock has declined (Dickson & Brander 1993, Stein & Borovkov 2004). Other long time-series exist for catches of Arcto-Norwegian cod and Norwegian spring-spawning herring and it has been shown that the state of these stocks can be linked with cycles of warming and cooling associated with the AMO (Toresen & Østvedt 2000, Sundby & Nakken 2008). Unfortunately, most records of fish distribution and abundance only relate to the adults so it is difficult to examine the responses of the early life stages to oceanographic and environmental variability. We know that there have been significant biogeographic and phenological changes in the plankton of the north-eastern Atlantic since the 1960s but whether similar shifts have occurred for fish larvae is less clear. Across the wider region, analysis of fish larvae in CPR samples was stopped in 1978 due to financial constraints (Coombs 1980) but samples are now being reanalysed and a re-evaluation of biogeographic patterns for north-eastern Atlantic ichthyoplankton should soon become available.

Movements of juvenile and adult fish

Many fish species undergo extensive migrations with the potential to move between EUR-OCEANS' systems. However, the life cycles of most appear to be contained largely within one of the three systems discussed in this review: European shelf seas, Atlantic or Arctic and Nordic Seas. An exception is the Atlantic salmon (*Salmo salar*). This species breeds in over 2500 rivers around the North Atlantic, from Portugal to Russia, and also in Iceland, Canada and the United States. A large number of these river stocks are currently in a depleted state and are considered to be outside safe biological limits (ICES 2008). The main reasons for these declines are thought to be declines in the quality of freshwater habitats and overexploitation, although the latter has been greatly reduced in recent years. However, processes occuring during the marine phase of the salmons' life cycle may also be critical. Salmon spawn in freshwater where their offspring spend from 1 to 7 yr before they emigrate to sea as smolts. They then remain at sea for a further 1 to 3 yr (and occasionally more) before returning to their river of origin to spawn. The precise migration routes of salmon smolts after they enter the sea are not known, but the fish appear to move rapidly away from the coast, and there is some evidence that they may follow major ocean currents. Thus smolts leaving rivers in the United Kingdom and Ireland, for example, move northwards into the Norwegian Sea within a few months of leaving freshwater (Holm et al. 2000, 2003). Subsequent movements are poorly understood but depend, in part, on how long the fish will remain at sea. Salmon of all ages have been caught in fisheries in the Northern Norwegian Sea that have operated during winter and spring months, and the majority of these fish are thought to be on their return migration. A fishery has also operated along the west coast of Greenland in the late summer and autumn; this fishery only takes salmon that would have spent at least 2 yr at sea, and a larger proportion of these fish originate from more southerly rivers. A similar pattern is seen for salmon from North American rivers. However, little is known about the movements and distribution of the fish between these points. Recent studies have shown that the condition of adult salmon returning to their home rivers has fallen as ocean conditions in the North Atlantic have become warmer, and underweight fish have been shown to have disproportionately low reserves of lipids (Todd et al. 2008). Such observations point to multiple trophic-level effects of environment-driven change in the north-eastern Atlantic (Beaugrand & Reid 2003).

Another wide-ranging species is the North Atlantic bluefin tuna (*Thunnus thynnus*), which can travel up to 8000 km in 50 days. The eastern stock has its main spawning areas in the Mediterranean and after spawning they migrate through the Straits of Gibraltar and follow the NAC northward, sometimes into Norwegian waters (Metcalfe et al. 2002). Significant annual variations in migration routes exist but these are not fully understood. The feeding migrations into Norwegian waters, particularly during the 1950s, were found to provide these individuals with access to abundant prey (herring, mackerel, saithe, squid and crustaceans). The condition factors of the bluefin tuna feeding along the Norwegian coast were significantly higher than the condition factors of specimens feeding in the mid-Atlantic. Catches of bluefin tuna in Norwegian waters declined markedly during the 1960s and this species is now more or less absent from these areas. The bluefin tuna stock is, according to the International Commission for the Conservation of Atlantic Tunas (ICCAT), at a critically low level and this is probably the main reason for the absence of this species in the Norwegian Sea.

Several species are largely confined to one of the EUR-OCEANS' systems but components of the population range into adjacent systems. For example, Atlantic mackerel (*Scomber scombrus*) are distributed from Morocco to northern Norway, including the North Sea, the Norwegian Sea and the entrance of the Barents Sea (Iversen 2004). Three main spawning areas are recognised: southern,

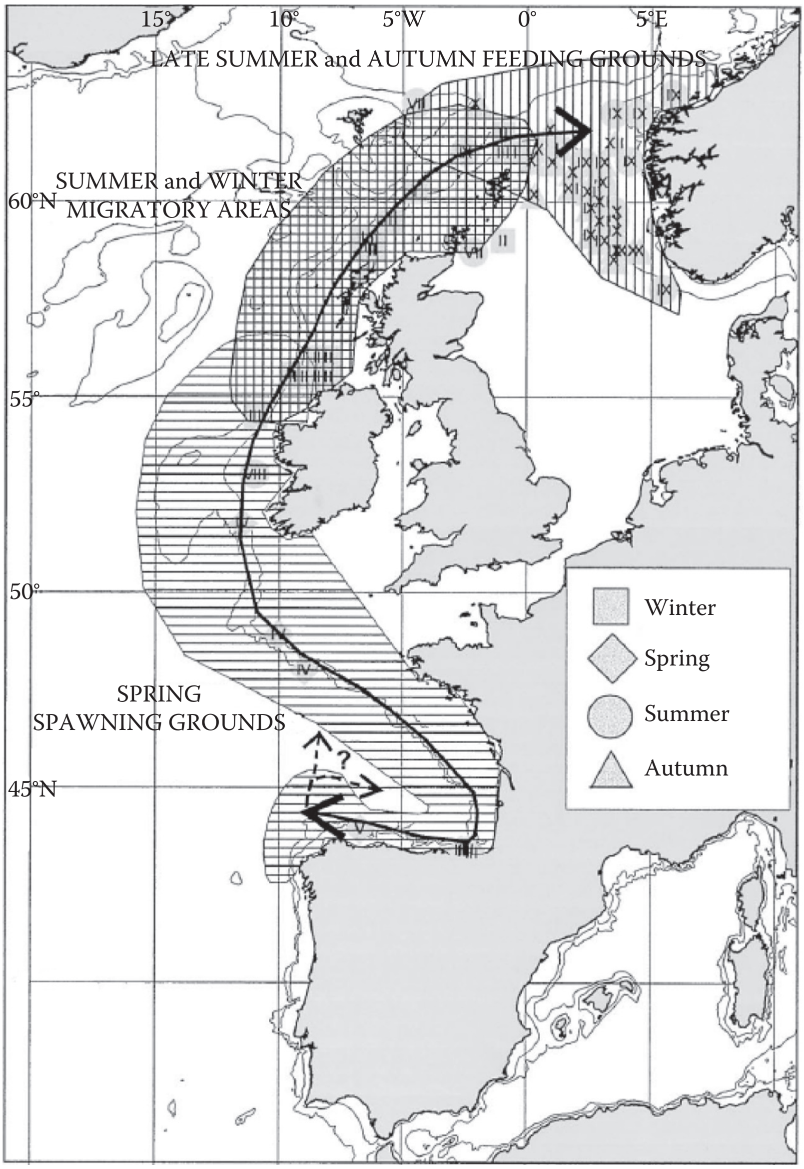


Figure 12 Pathways of mackerel tagged as mature or spawning fish off the Spanish Basque coast. (From Uriarte & Lucio 2001. With permission of Elsevier.)

western and North Sea. However, tagging data raise some doubts over whether the southern component is a truly separated stock (Uriarte & Lucio 2001). After spawning, mackerel from the southern and western areas migrate into the Norwegian Sea and the North Sea to summer feeding grounds (Figure 12). During the autumn most of the mackerel are found in the North Sea where they stay as late as February–March of the following year before migrating back to their spawning areas. Walsh and Martin (1986) found that while the timing and pattern of the post-spawning migration has been relatively stable, the migration routes back to the spawning areas have changed significantly from late summer in the 1970s to January in the 1990s. Walsh et al. (1995) found that the migration pathway of mackerel towards the spawning areas was linked to a tongue of warm water along the

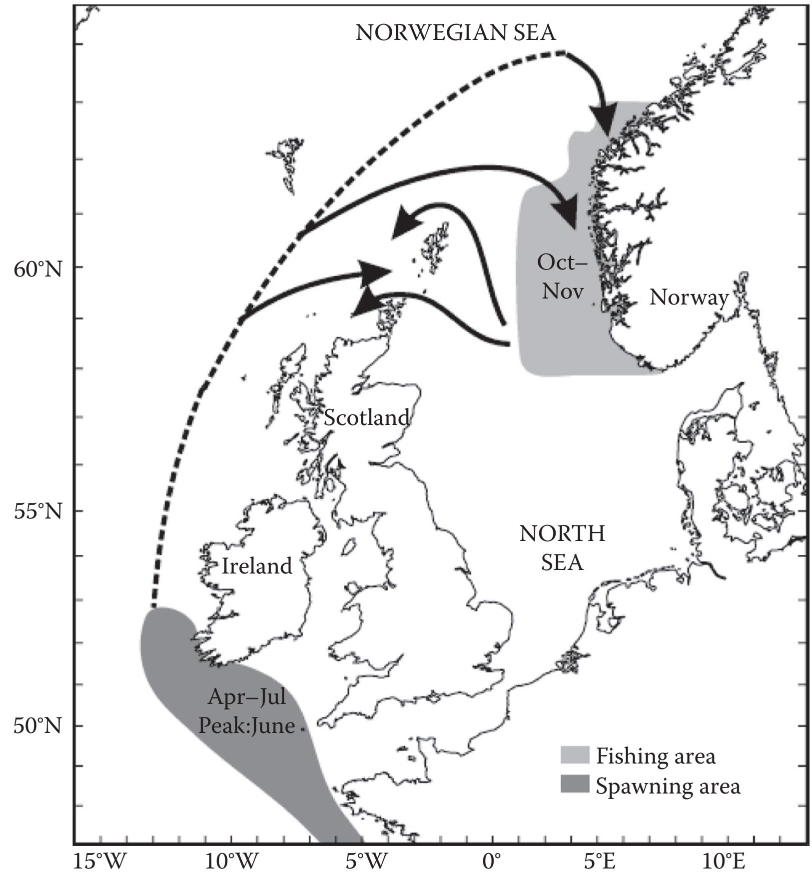


Figure 13 The spawning area, migration route and Norwegian fishing area for western horse mackerel. (From Iversen et al. 2002. With permission of Blackwell.)

shelf edge. Subsequently, Reid et al. (1997) suggested that the migration back to the spawning areas was regulated by temperature; when the sea temperature falls below 9°C, it triggers the migration. In contrast to the prespawning migration, mackerel actively feed post-spawning and because prey availability may be the more important driver, the relationship with water temperature is not so clear during this phase of the life cycle.

Horse mackerel (*Trachurus trachurus*) are also widely distributed, with three spawning components in the north-eastern Atlantic: in the southern, western and North Sea (Iversen 2004). Parts of the western stock, which spawn west of Ireland and in the Bay of Biscay during May–July subsequently migrate into the North Sea and Norwegian Sea (Figure 13). There is a strong correlation between modelled flux of Atlantic water into the North Sea in winter and catches of horse mackerel 6 mo later (Iversen et al. 2002). It was hypothesised that increased temperatures and food production during years with high inflow explained the increased catches.

Blue whiting (*Micromesistius poutassou*) is an important industrial species in the north-eastern Atlantic. Its distribution extends along the continental shelf from the Canary Islands to Spitzbergen, with smaller populations in the north-western Atlantic and the Mediterranean Sea (Was et al. 2008). Adults reach maturation at 2–7 yr old, and undertake long annual migrations from feeding grounds to spawning grounds and back again (Bailey 1982). It has recently been suggested that observed variability in the migration route of blue whiting from the spawning grounds to feeding areas in the Norwegian Sea can be explained by the influence of the subpolar gyre on the westwards extension of the spawning area (Hátun et al. 2007). According to these authors, the spawning areas are shifted eastwards due to colder conditions farther west during periods of strong subpolar circulation. This would lead to a post-spawning migration through the Faroe-Shetland Channel. In contrast, a weak subpolar gyre would lead to warmer conditions spreading farther west and consequently improved conditions for blue whiting spawning in these areas. During such periods the post-spawning migration route will be shifted westwards of the Faroe Islands. The authors suggested that this last condition would lead to improved conditions for recruitment and could explain the relatively high recruitments observed from the late 1990s until 2005. The position of the Arctic front in the Norwegian Sea varies according to the strength of the East Icelandic Current and the Atlantic Current. Since blue whiting do not appear to enter Arctic waters such oceanographic changes will greatly influence their distribution.

The role of ocean currents in the distribution of higher predators across regional boundaries

Large marine organisms such as basking sharks, turtles and whales are all active swimmers capable of travelling large distances. Consequently the major influences of oceanographic flows on their movements are indirect (Figure 3). Population distributions are bounded by physical and biological constraints such as topography, temperature, predators and prey. Of these, the distributions of target prey are probably the most significant.

Archival pop-up tags have recently been used to reconstruct the movements of basking sharks (*Cetorhinus maximus*) around the European continental shelf (Figure 14). These data showed extensive movements of up to 460 km between distinct centres in the shelf seas and along the shelf edge (Sims et al. 2003, 2008). Basking sharks spent most of the time in areas characterised as tidal or shelf break fronts. It was noticeable that individuals foraging along fronts off the south-western peninsula of England moved to three main areas: the Celtic Sea front, the Goban Spur and into the Atlantic at the shelf edge in Biscay (Figure 15). Individuals also moved northwards from these areas

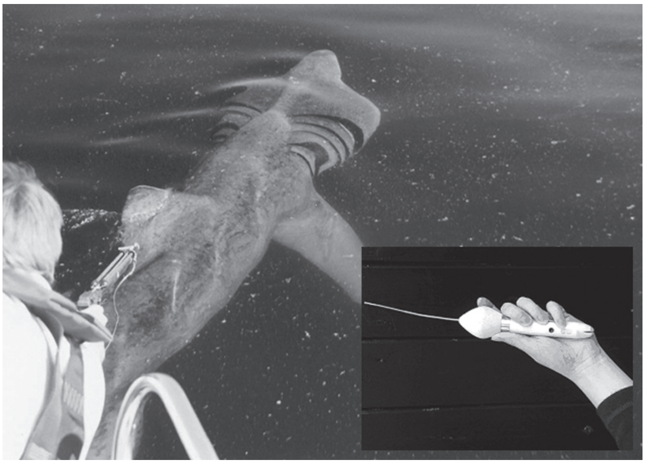
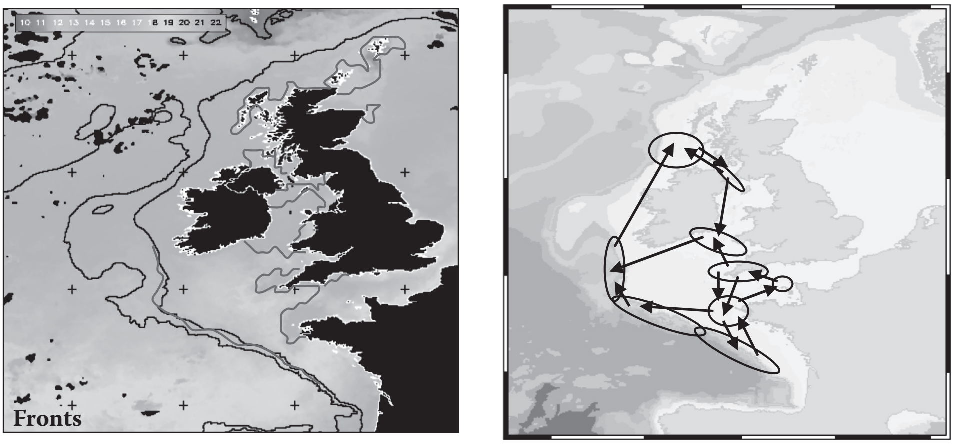


Figure 14 Tagging a basking shark (credit David Sims, Marine Biological Association, United Kingdom) and inset, a pop-up archival tag (Wildlife Computers, Redmond, WA 98052, USA) suitable for attachment to such large marine organisms. The tag records environmental data such as depth, temperature and ambient daylight for at least a year. A release mechanism then operates, the tag floats to the sea surface and the data are transmitted to shore via satellite (Service Argos).



(A) (B)

Figure 15 (See colour insert.) (A) Tidal and shelf break fronts (red lines) on the European shelf and (B) the generalised movement patterns of "tracked" basking sharks between these productive regions. Remote-sensing image is a monthly composite of sea-surface temperature during August 2002 from AVHRR on National Oceanic and Atmospheric Administration (NOAA) satellites. (From Sims et al. 2005. Reproduced with Crown permission.)

along the shelf edge into rich feeding areas in the Hebridean Sea (Sims et al. 2003). Frontal areas are probably targets for basking sharks since they are often associated with enhanced primary and secondary production (Le Fèvre 1986). Interestingly, no sharks tagged off south-western England in spring moved through the Irish Sea during summer, whereas sharks tagged in the fjord-like Clyde Sea in summer travelled relatively rapidly southwards through the Irish Sea to areas off south-western England. Overall, it appears that during summer, basking sharks move between centres of high zooplankton abundance in fronts, tending towards a northwards movement of variable distance (from Plymouth to the Celtic Sea or Hebridean Sea). In winter, some individuals remained or moved into shallow coastal waters, generally in the southern region of the shelf but there was no evidence to support the hypothesis that basking sharks hibernate overwinter in deep waters.

While several species of turtle (loggerhead, *Caretta caretta*; Kemp's ridley, *Lepidochelys kempii*; green, *Chelonia mydas* and hawksbill, *Eretmochelys imbricata*) have been recorded in the north-eastern Atlantic this is probably the result of accidental straying from more southerly waters. Leatherback turtles (*Dermochelys coriacea*) are however regularly encountered in the region. Coastal nesting takes place in the Caribbean, Central and South America and western Africa but feeding occurs over wide areas of the North Atlantic (Hays et al. 2004). Soft-bodied macroplanktonic invertebrates, particularly jellyfish, make up the main component of the diet. Tracking studies of leatherbacks suggests a combination of locomotive strategies that are at times independent of oceanographic processes (Hays et al. 2004) but at others times strongly correlated with them (Luschi et al. 2003). Thus it is probable that the occurrence of leatherback turtles in the open ocean system west of Europe and their subsequent invasions into shelf waters to the west of the British Isles and Norway represents the foraging behaviour of a non-conformist species (Figure 3) focusing on patches of conforming prey (Sims et al. 2008).

The mysticete (baleen) whales are highly mobile and the majority of species are not restricted to any particular region. Species such as minke (*Balaenoptera acutorostrata*) and humpback (*Megaptera novaeangliae*) focus their summer foraging in shelf waters but others like the fin (*Balaenoptera physalus*) and sei whales (*B. borealis*) occupy both offshore and shelf waters. All species typically feed at higher latitudes in summer and migrate towards the tropics to breed in winter. The location of these breeding areas and the paths taken to reach them are poorly known but these migrations represent significant transregional movements. From what is known it is clear that most species do not follow ocean currents (Townsend 1935) although minke whales may track the NAC (Clark 1995). The reason why breeding takes place at low latitudes is unknown but may be a strategy to avoid predation by killer whales (*Orcinus orca*), which have ranges that focus on the productive shelf and polar waters (Corkeron & Connor 1999).

Odontocete (toothed) whales (with the exception of sperm whales *Physeter macrocephalus*) have life histories that are less spatially and temporally compartmentalised, with breeding and feeding occurring in the same areas. As a taxonomic group they are widespread with the majority of species showing distinct habitat preferences by latitude and water depth. For example, bottlenose (*Hyperoodon ampullatus*) and beaked whales (*Mesoplodon* and *Ziphius* spp.) are primarily distributed off shore (>200 m water depth) whilst harbour porpoises (*Phocoena phocoena*) are found almost entirely in shallower waters. Different dolphin species also show segregated distributions, although some, such as bottlenose dolphins (*Tursiops truncatus*), display alternative population strategies (possibly ecotypes as in the western Atlantic with populations at or beyond the shelf break and other populations restricted to localised areas in coastal waters) (Hersh & Diffield 1990). Female sperm whales, like other odontocetes, show preferences for specific habitats, favouring off-shelf waters south of 55°N. In contrast, subadult and adult male sperm whales range north from temperate into Arctic waters and thus straddle offshore latitudinal boundaries for distinct breeding and feeding life-history activities (Rice 1989).

Pinnipeds such as grey and harbour seals (*Halichoerus grypus, Phoca vitulina*) are primarily restricted to shelf waters close to haul-out sites. However species such as harp (*Pagophilus groenlandicu*s), bearded (*Erignathus barbatus*) and ringed seals (*Phoca hispida*) that are associated with ice may forage into deeper waters while hooded seals (*Cystophora cristata*), which are typically considered to be Arctic species, forage in off-shelf waters as far south as Ireland (Folkow & Blix 1994). In addition to the regular seasonal movements of individuals across ecosystem boundaries, others occur more episodically. In particularly harsh winters, harp seals may shift their range southwards from Greenland and northern Norway to southern Norway and the northern North Sea (Nilssen et al. 1998). These seal "invasions" can have wider impacts as these polar seals are thought to be vectors for the introduction of phocine distemper virus (PDV) to populations of harbour and grey seals in the North Sea (Dietz et al. 1989). The first well-documented seal epizootic resulting from this viral infection killed an estimated 18,000 common seals in 1988 and resulted in significant impacts on indigenous seal numbers, ranging from 40 to 80% population mortality. A second PDV outbreak occurred in 2002. Similar viral interspecies jumps may occur in odontocete cetaceans (Kennedy 2000) and it has been suggested that offshore pilot whales *Globicephala* spp. may act as a reservoir of morbillivirus infection for cetaceans, including those in coastal waters (Duigan et al. 1995).

Even less predictable, but with some potential for implications over longer time scales, are the extralimital movements of individual animals out of their normal ranges. The occurrence of emaciated, usually juvenile, polar seal species on beaches in southern Europe is an almost annual event and is usually considered a result of straying of young or ill individuals. However the chance discovery that a ringed seal that had been tagged and released off Brittany, France, had made its way back to the population's normal range off Iceland (Ridoux et al. 1998) suggests that there may be an ecological role as a mechanism to allow colonisation of new areas (Wilson 2008). One highly predictable extralimital occurrence is the appearance in late winter and early spring of male sperm whales in the North Sea. As described above, this species typically feeds and breeds in the deep waters off the continental shelf. The annual occurrence of small numbers of male sperm whales in an area without feeding or breeding opportunities is therefore mysterious. The majority of whales that are identified in this area usually eventually perish through starvation or beaching. There have been a variety of explanations proposed for this phenomenon and perhaps the most convincing is the notion that the geography of the North Sea conspires to form a large sperm whale trap (Jauniaux et al. 1998). Whales feeding in seas west of Norway migrate south to breed and some may miss the shelf edge and instead turn into the northern North Sea. Continuing south leads the whales to the shallow, narrow and for this deep water species, potentially impassable English Channel.

Being active swimmers, living marine mammals usually exhibit precise habitat preferences and only indirect ecological coupling to the movements of water masses. However, ocean currents influence the ecosystem impacts of marine mammals after their death. *Post-mortem*, most marine mammals float, either immediately or after some putrefaction. The carcasses are then subject to passive transport by surface currents. Relatively little research on the fate of marine mammal carcasses has been performed and the majority of studies have focused on the impacts of large carcasses landing on the abyssal seafloor. However, seasonal pulses of beach-cast dolphins originating from offshore fisheries (Kuiken et al. 1994) suggest that transport of biomass across regional boundaries could be at times appreciable. Whilst the actual quantity of this biomass will be dwarfed by other processes, the impacts of the delivery of biomass in highly localised areas of the seabed can cause hot spots of sediment oxygen demand and bioaccumulated anthropogenic contaminants as the blubber of marine mammals often contains accumulated lipid-soluble pollutants such as PCBs (polychlorinated biphenyls; Stockton & DeLaca 1982). Historical changes in marine mammal abundance, disease epizootics and the legacies of discards from whaling may add further temporal aspects to the magnitude of this effect (Whitehead & Reeves 2005).

Human-induced links between the regional systems

Introduction

Human activities have resulted in significant changes in the state and functioning of the ecosystems of the north-eastern Atlantic. The physical and biological links previously described provide pathways for the 'products' of these activities, such that initial local- or subregional-scale phenomena may have much wider influence. In addition, the links described in previous sections may be short-circuited by human intervention (e.g., trade). In some cases these products or 'state changes' (in the context of the driver-pressure-state-impact-response [DPSIR] framework) may have negligible deleterious effects, but observing and modelling their behaviour can provide useful insights about the transport mechanisms involved. For example, radionuclides released from nuclear fuel reprocessing operations in north-western Europe have been used extensively as tracers of water circulation throughout the north-western European shelf seas, the Nordic Seas, the Arctic Basin and the Labrador Sea from the 1970s to the present day. On the other hand, anthropogenic activities may have significant direct or indirect impacts on the nature and functioning of the ecosystem, causing ecosystem degradation, or some other undesirable disturbance. In some cases these may be the result of a deliberate action, such as dumping unwanted materials (e.g., munitions) or using rivers to dispose of chemical wastes. However, in many cases the observed changes follow the 'law of unintended consequences'. For example there are now many non-indigenous species that have become widespread following accidental or deliberate introduction (Hulme et al. 2008, IMO 2004).

Alien species introductions

There are many potential pathways for the introduction of non-indigenous species in the marine environment (Hulme et al. 2008) but the principal vector has been shipping (Gollasch 2002). Once a species has been introduced locally it can often be spread further by human vectors or oceanographic pathways. Alien species have been inadvertently transported on ship's hulls since the earliest seafarers. For example, the shipworm *Teredo navalis* was introduced to Norway about 300 years ago in the hulls of wooden vessels, and the barnacle *Balanus improvisus* became established in the early

1800s, probably from North America (Hopkins 2002). In the North Sea, alien species were present in around 98% of samples taken from commercial ship hulls (Gollasch 2002). The introduction of antifouling coatings may have had some impact on this pathway but use of tributyl tin (TBT) has, in turn, led to problems with induction of imposex in certain organisms (especially gastropods) along major shipping routes and in ports (Terlizzi et al. 2001). The other main shipping vector for alien introductions has been the inshore exchange of ballast water, increasingly by large bulk carriers (Ruiz et al. 2000). Between 3 and 5 billion tonnes of ballast water are transferred annually (http://globallast.imo.org). The recognition that this provides a vector for the introduction of non-indigenous species has led to the provision of good practice guidelines by the International Maritime Organisation (IMO) and the adoption of the *International Convention for the Control and Management of Ships' Ballast Water* in 2004 (http://www.imo.org/conventions/mainframe.asp?topic_id=867).

Species introductions have affected all European regional seas, with the most devastating consequences to date being observed in the Black Sea (e.g., comb jelly, *Mnemioposis leidyi*). Such invasions may represent a component in broad-scale regime shifts combined with the effects of overfishing leading to trophic cascades (Daskalov et al. 2007). So far the north-eastern Atlantic has not experienced a similar scale of change although several hundred non-indigenous species have been identified in the region (Gollasch 2002). These include members of the Chlorophyta, Dinoflagellata, Phaeophyta, Rhodophyta, Cnidaria (Hydrozoa), Nematoda, Chordata (Tunicata, Osteichthyes), Crustacea (Copepoda, Cirripedia, Mysidacea, Isopoda, Amphipoda), and Mollusca (Gastropoda, Bivalvia). The scale of introductions has been documented by member states of the OSPAR Commission (www.ospar.org) and the results summarised by Leppäkoski et al. (2002). These actions have culminated in the establishment of the European Research Network on Aquatic Invasive Species (ERNAIS) whose role has been recognised in the European Strategy on Invasive Alien Species (Genovesi & Shine 2003). However, the picture is not static and new non-indigenous species are constantly being recorded; for example, *Mnemioposis leidyi* was observed for the first time in the Baltic Sea in 2006 and in the southern North Sea in 2007 (Boersma et al. 2007).

An example of a phytoplankton introduction with potential nuisance effects is the diatom *Coscinodiscus wailesii*, native to the Indian and Pacific Oceans. This species was observed in the waters off the south-west of the United Kingdom in 1977 and has since spread along the French Atlantic and southern U.K. coasts. It is now being recorded in Helgoland and south-western Norway. *Coscinodiscus wailesii* forms dense, mucilaginous blooms (up to 1400 µg carbon l^{-1}) but is inedible to most zooplankton, causes anoxia near the seabed and clogs fishing gears (Laing & Gollasch 2002). A number of dinoflagellate species have also been introduced in ballast water that are capable of causing HABs. These include *Alexandrium catenatumi* and *A. tamarensis*, which can cause paralytic shellfish poisoning (PSP), and *Karenia mikimotoi* (formerly *Gyrodinium aureleolum)*, which has caused major fish kills in caged sea trout (Goulletquer et al. 2002, Hopkins 2002). Ballast water is also considered the vector responsible for the introduction of the Chinese mitten crab *Eriocheir sinensis* to Germany in 1912. It has spread widely since and can cause significant damage to river and estuary banks, as well as competing with native fauna (Nehring 2002).

Another vector for introductions is aquaculture (Minchin 1996, Hégaret et al. 2008). For example, the Japanese (or Pacific) oyster *Crassostrea gigas* was introduced to France in the 1970s to sustain the oyster industry. This is considered to be a commercially 'successful' introduction but the species may have provided a vector for parasites that have since infected native species (Goulletquer et al. 2002). In contrast, the slipper limpet *Crepidula fornicata*, accidentally introduced along with the oyster imports, can have a negative impact on oyster beds. It has a high reproduction rate and tends to deposit mud on the underlying oysters. Another example is the parasitic nematode *Anguillicola crassus* introduced in a consignment of Japanese eels in the 1980s. The parasite infects the swim bladder of native eels (Køie 1991). Some non-indigenous species have been deliberately introduced for sports fishing (e.g., rainbow trout *Oncorhyncus mykiss*), others as discarded pets or surplus to the restaurant trade (e.g., American lobster *Homarus americanus*, carrying a bacteria [*Aerococcus viridans*] that causes 100% mortality in the European lobster *H. gammarus*). An unusual vector was the carriage of drinking water barrels from southern Australia, resulting in the introduction of the gastropod *Potamopyrgus antipoarum* to the United Kingdom in the 1850s, since spreading widely in coastal waters as far as Norway (Hopkins 2002). Rafting of organisms on a variety of natural materials (e.g., pumice, timber, macroalgae) is recognised as another significant transport mechanism, with evidence demonstrating that human activities have increased this phenomenon with the introduction of plastic debris (Thiel & Gutow 2005) and the occurrence of tar balls (Minchin 1996). Such rafts will follow the surface ocean currents described in previous sections, providing a vector for transregional transport.

Contaminants

Indirect sources of contamination

Plastic debris is now almost ubiquitous in the marine environment and is an extensive literature detailing the impacts of this debris on marine organisms (Derraik 2002). Disposal from shipping has come under increasing control (although this is difficult to enforce) so that most of the recent introductions have a terrestrial origin. Plastics degrade by breaking into smaller fragments and even 'biodegradable' plastics leave a legacy of microparticles. In addition, thermoplastic resin pellets (the 'feedstock' of the plastics industry) are ubiquitous in the world ocean and can act as vectors for organic pollutants such as PCBs, DDT (dichloro-diphenyl-trichlorethane) and PAHs (polyaromatic hydrocarbons) (Rios et al. 2007). Plastic microparticles can become incorporated into the cells of organisms, with potential toxic effects, and can increase the intake of some organic contaminants, such as phenanthrene (Teuten et al. 2007). Examination of archived samples from the CPR has revealed the presence of plastic microfragments on both the Aberdeen–Lerwick and Iceland–Scotland routes (Thompson et al. 2004). The fragments were more numerous on the former route, but for both there was a significant increase in abundance in the 1980s and 1990s compared with the 1960s and 1970s. This indicates that plastic microfragments are increasing in quantity and are being redistributed widely in the north-eastern Atlantic by the ocean currents.

Since the late 1960s there has been concern about the long-term impact of several classes of chemicals in widespread use that are considered to be persistent organic pollutants (POPs). These chemicals have a variety of effects on marine organisms, including endocrine disruption and immunosuppression. They can also affect people by becoming concentrated in marine food webs, with potentially dangerous levels appearing in marine bioresources consumed by humans. Although levels of consumption of marine products in Europe are generally too low for this to be a major concern, peoples in certain European countries, particularly in northern Europe, tend to have much higher per capita consumption rates. PCBs, DDT, PBDEs (polybrominated diphenyl ethers), dioxins and other POPs are known to accumulate in lipid-rich fish, with much higher levels in the Baltic and North Atlantic than in the Southern Hemisphere and elevated concentrations have been recorded in fish oils and farmed salmon fed on these oils (Jacobs et al. 2002). Bioaccumulation of POPs has also been linked to problems in top-level predators such as thyroid dysfunction in seals (Sørmo et al. 2005), immunosuppression leading to *Brucella* infection in hooded seals and impaired reproduction in polar bears (Sonne et al. 2006). It has also been suggested that the stress caused by the presence of POPs in the body may reduce the ability of mammals and seabirds to respond to additional environmental stress, for example from increased temperatures (Jenssen 2006). The PBDEs are part of the group of brominated flame retardants and increasing recognition of their possible ecosystem effects is leading to increased constraints on their manufacture and use (Betts 2008). Another group of chemicals found extensively in the north-eastern Atlantic are the perfluorinated acids (PFAs). These compounds have a wide variety of uses, including surfactants in water- and stain-resistant materials. Their production is being curtailed but there is less regulation on related chemicals that can degrade to PFAs (Jensen & Leffers 2008). They are stable in seawater and have been detected throughout the North Atlantic, including the Denmark Strait overflow and the Labrador Sea, leading to a proposal to utilise their presence as a tracer of ocean circulation (Yamashita et al. 2008).

In the North Sea, offshore oil and gas operations have resulted in some measurable environmental impacts. Routine operations release large volumes of produced water (partly formation water and partly injected for greater oil recovery), which may contain elevated concentrations of heavy metals, chemical additives (e.g., biocides), dissolved oil components (e.g., PAHs, alkyl phenols, toluene, naphthalene) and naturally occurring radionuclides (e.g., ^{226}Ra) (Meier et al. 2004). The quantities of produced water tend to increase as the oil field matures. Concern has been expressed that produced water may have an impact on fish populations, prompting studies on potential hormonal effects of alkyl phenols on fish reproduction (Meier et al. 2004, Martin-Skilton et al. 2006). Routine operations also produce drill cuttings comprising a mix of rock fragments, oil- and water-based drilling mud and a variety of other materials used operationally. Although there are clear local impacts, these tend not to extend more than a few kilometres from the platform (Lepland et al. 2000). However, contamination from this industry can be widespread. Perhaps the best-known example is the transport and accumulation of barium, as particulate barite, in the sediments of the Skagerrak, with a depth distribution in sediment cores correlating with the development of the North Sea oil fields (Lepland et al. 2000). One ecological benefit of the industry has been the provision of artificial reefs in otherwise rather barren environments, with complex depth-dependent ecosystems being observed on the platform substructure, including iconic species such as *Lophelia pertusa* on structures in the northern North Sea (Gass & Roberts 2006). The absence of a resident population suggests recruitment via the Atlantic water inflow east of Shetland carrying larvae from known populations west of Scotland. Man-made subsea structures, particularly in the shelf seas, may therefore act as stepping stones facilitating the range expansion of benthic species.

The industrialised nature and high population density of much of western Europe means that concentrations of many pollutants in north-western European coastal and shelf waters are significantly higher than in other ocean basins. These direct and indirect sources (including significant atmospheric transport) result in widespread contamination by organic and inorganic compounds, remote from the immediate sources, via the oceanographic links described in earlier sections of this review, with the Nordic Seas and Arctic receiving a disproportionate burden (Barrie et al. 1992).

Deliberate point-source releases

In most cases the deliberate dumping of wastes may have significant localised impacts but these do not generally extend to a broader regional scale. Dumping of sewage sludge and industrial wastes were common practices in coastal waters but this has now ceased under the OSPAR Convention. At present, most dumped material consists of dredged spoil, with much smaller quantities of fish wastes, and the chemical content and potential impact appear to be rather limited. However, large quantities of conventional and chemical munitions were dumped in the Baltic Sea and North Sea at the end of WWI and WWII and at other sites such as Beaufort Dyke, at the exit of the Irish Sea. Altogether it is estimated that 300,000 tonnes of WWII chemical munitions such as mustard gas have been dumped in European waters (Kaffka 1996). The potential long-term impact of this source and its spatial extent remains unclear as the original containment (e.g., shells, cases, ships' holds) continues to deteriorate and the contents become exposed to seawater.

Covert dumping of radioactive wastes by the former Soviet Union (FSU) and the Russian Federation took place over several decades in the Barents and Kara Seas. Liquid wastes were disposed of in the Barents Sea between 1959 and 1991 and solid wastes in the Kara sea from 1964 to 1991. The latter included objects containing spent nuclear fuel. The total amounts dumped are estimated at 38 PBq (Bq is disintegration s^{-1}) (International Atomic Energy Authority [IAEA] 1999a), but environmental contamination appears to be limited spatially and does not appear to have been exported to other regions in significant quantities (IAEA 1999b). Many of the radioactive components of solid wastes are not particularly soluble in seawater but long-term monitoring remains a priority.

Accidental releases

Accidental releases include conventional and chemical weapons lost, as opposed to deliberately dumped, as well as shipwrecked vessels containing fuel oil and potentially hazardous cargoes. In addition, two nuclear-powered submarines from the Russian Northern Fleet have foundered in northern European waters. The Kursk sank in 2000 in the Barents Sea, in 116 m, with the loss of 118 crew. The reactor was shut down and no significant leakage has been detected (Amundsen et al. 2001). The vessel was subsequently recovered in stages during 2001 and 2002. The Komsomolets sank in 1989 in about 1600 m of water, with many of the crew being lost. The vessel was carrying two nuclear-tipped torpedoes. The hull was damaged and some leakage was detected during a series of expeditions to monitor and repair the damage. Given the remote location and lack of vertical mixing it was not considered to represent a significant source of contamination to shallower waters. Much of the warhead plutonium was expected to be adsorbed by seabed sediments and not to become mobilised.

A further potential source of radioactive contamination is represented by a large number of redundant reactors from submarine and surface vessels located in bases on the Murmansk Peninsula, with very limited facilities for decommissioning after many years of underinvestment. The situation prompted an international response, with several countries arranging bilateral agreements with Russia to provide specialist advice and assist in improving storage and decommissioning facilities. It is not thought that there has been significant contamination of the wider region to date.

Useful tracers of ocean circulation and interregional transport

As discussed, a wide variety of contaminants has been introduced into the waters of the north-eastern Atlantic, from both diffuse and point sources. Many of these do not pose a direct threat to ecosystem functioning but have proved to be useful tools with which to study ocean processes. These transient tracers have been used—singly or in combination—to study pathways, transport rates, residence times, ventilation rates; to provide validation of model simulations; and to understand the fate of other contaminants (e.g., Heinze et al. 1998, Schlosser et al. 1995). The tracers have included stable chemicals from industrial production, such as chlorofluorocarbons (CFCs) and radionuclides released by human activities such as atmospheric nuclear weapons testing, routine discharges from the nuclear fuel cycle and accidental inputs, providing both diffuse and point-source signals. The production of CFCs for a variety of industrial applications (e.g., refrigerants), since the 1930s, has provided well-defined source terms, with inputs increasing steadily until the early 1990s. CFC-11 and CFC-12 concentrations and ratios (time-varying production rates) have been used to derive mean residence times in the Greenland and Norwegian Seas (Rhein 1991). More recently the tracers F-113 and CCl4 have extended the timescales that can be addressed (Haine et al. 1995). CFCs, in combination with $^{3}H/^{3}He$, have been used to estimate the residence times for surface and intermediate waters in the Eurasian Basin (Franke et al. 1998), the Greenland Sea (Bönisch et al. 1997) and the Makarov and Canada Basins (Smethie et al. 2000), and CFC-11 has been used to calculate the rate of North Atlantic Deep Water formation (Smethie & Fine 2001).

Radionuclides released from nuclear reprocessing facilities in the United Kingdom (Sellafield) and France (La Hague) have provided a useful set of tracers to study transport from the shelf seas into the Nordic Seas and the Arctic Ocean. The most widely used have been ^{90}Sr, ^{99}Tc, ^{125}Sb, ^{129}I, ^{134}Cs, ^{137}Cs, and isotopes of plutonium (Dahlgaard 1995, Kershaw & Baxter 1995, Gueguenia t et al. 1997). An additional radiocaesium signal was provided by the Chernobyl accident in 1986, with highest concentrations being recorded in the Baltic Sea, subsequently being transported into the North Sea and Norwegian Sea (Povinec et al. 2003). Substantial decreases in the direct discharge of most nuclides since the 1980s have reduced the quantity of such tracers entering the environment.

However, the discharges of ^{129}I and ^{99}Tc have increased due to changes in waste management practices and increased fuel throughput. Both are relatively conservative in seawater and have been used to demonstrate transport pathways and mixing processes over much of the North Atlantic. The use of AMS (accelerator mass spectrometry) has allowed ^{129}I analysis on very small samples (<1 l), permitting shared use of conventional water samplers (conductivity, temperature and depth sensor-rosette array) and submarines (US Navy Scientific Ice Expeditions [SCICEX] 1995 and 1996 described in Smith et al. 1999). These authors demonstrated that the boundary between Pacific and Atlantic origin water lies over the Mendeleyev Ridge and showed the flow of Atlantic water along the Lomonosov ridge on the basis of ^{129}I distributions. They included ^{137}Cs to estimate transit times and dilution factors for Atlantic water from the Norwegian coastal current (60°N) to the continental slope of the Makarov Basin and the Kara and Barents Seas (Smith et al. 1999). As the ^{129}I signal has propagated, measurements have been extended to estimate the ventilation times of North Atlantic waters from a single tracer (Edmonds et al. 2001, Tanhua et al. 2005) and in combination with CFC-11 (Smith et al. 2005) to follow the passage of Denmark Strait overflow water. Increased ^{99}Tc release in the mid-1990s was the result of an increased throughput of stored actinide-rich wastes (through the Enhanced Actinide Removal Plant). This reduced the concentrations of plutonium isotopes and ^{241}Am (of radiological concern) but ^{99}Tc was unaffected. Technetium is readily taken up by certain biota such as the algae *Ascophyllum nodosum* and *Fucus* spp. and lobster (*Homarus gammarus*), allowing the progress of the 'plume' along the U.K. and Norwegian coasts to be readily followed (Kolstad & Lind 2002, Nawakowski et al. 2004, Oliver et al. 2006). Observations of ^{99}Tc in seawater and biota have also been used to look at variability in transport rates from the Irish Sea to the Nordic Seas (Figure 16) in relation to regional and basin-wide transport processes (Kershaw et al. 2004, Orre et al. 2007) and to validate the North Atlantic/Arctic Ocean sea ice model (NAOSIM) developed by the Alfred Wegener Institute for Polar and Marine Research (Karcher et al. 2004).

Future trends for human-induced links between the regional systems

The volume of regional and intercontinental shipping is likely to increase with the potential for further shipping-related ecosystem impacts. However the *International Convention for the Control and Management of Ships' Ballast Water* is due to be implemented in 2009, and a number of active ballast water treatment systems have been, or are due to be, evaluated for their efficacy and safety (http://globallast.imo.org). The recent pattern of decreased summer ice in the Arctic is expected to continue, raising the prospect of new shipping routes (discussed more fully on page 54). This will likely be accompanied by increased military activity and exploration and exploitation of oil and gas and other natural resources (ACIA 2004). The impacts of these activities will certainly affect more southerly regions due to increased transportation of oil and other commodities from or through the Arctic with potential trans-shipment at new or existing facilities (e.g., Shetland) and increased potential for accidental spills in the shelf seas (Department for Environment, Transport and the Regions [DETR] 2001). Changes in energy production will be accompanied, under existing plans, by the decommissioning and removal of the oil and gas industry steel structures, presently providing a habitat for *Lophelia pertusa* and associated organisms. Removal of these structures may lead to undesired biodiversity impacts. New structures for renewable energy capture (wind, tidal) will tend to be in coastal waters due to the costs of transferring electricity along undersea cables and these will provide a different set of 'stepping-stones', allowing range shifts for benthic organisms. Although deliberate dumping at sea is now banned, we will continue to input an enormous range of chemicals into the waters of the north-eastern Atlantic, either as aerosols or through run-off and accidental discharge. Unfortunately we have rather limited knowledge of their long-term impacts, either singly or cumulatively. Moves towards an integrated European Marine Strategy should eventually provide stronger protection of the marine environment of the north-eastern Atlantic but ultimately future trends will depend on the socioeconomic development paths that Europe and the rest of the world follow (Pinnegar et al. 2006).

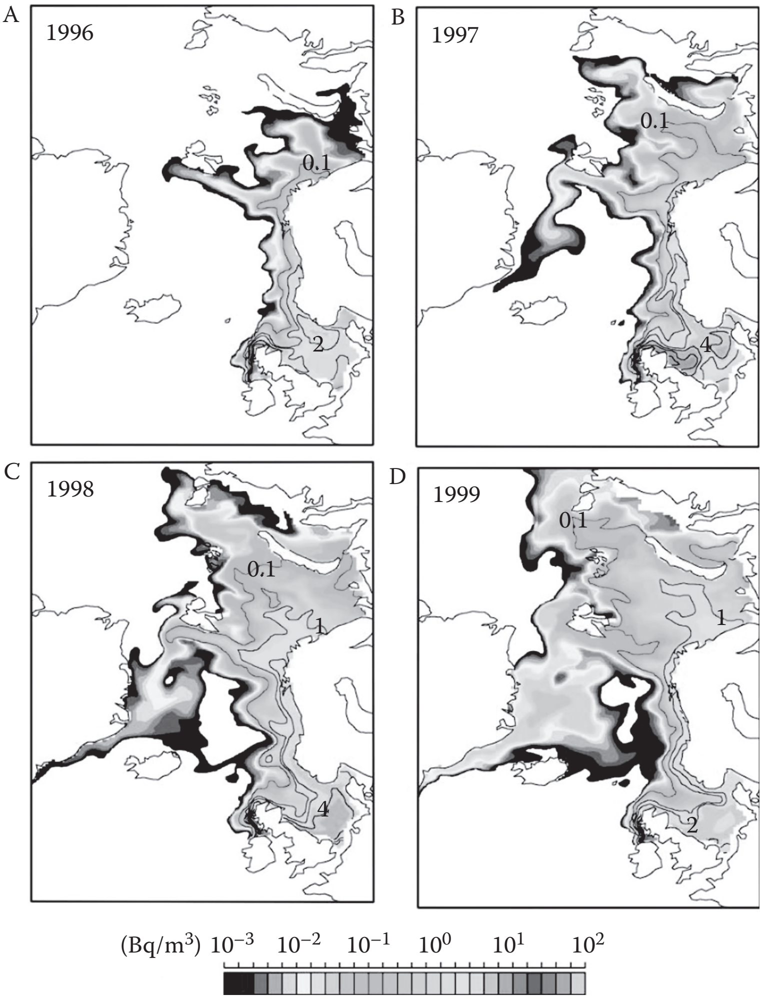


Figure 16 (See colour insert.) Simulated distribution of ^{99}Tc (Bq m^{-3}) in surface water, from the North Atlantic/Arctic Ocean sea ice model (NAOSIM), in September (A) 1996, (B) 1997, (C) 1998 and (D) 1999 (isolines: 0.1, 1.0., 2.0 and every 2.0 Bq m^{-3}). Model simulations were broadly in agreement with observed concentrations. Elevated releases from the Sellafield nuclear fuel reprocessing plant into the Irish Sea began in 1994 due to the startup of the enhanced actinide removal plant (EARP) facility. (From Karcher et al. 2004. With permisson from Elsevier.)

Possible changes in the regional linkages over the next century: the potential impacts of climate change

The background of climate change

The Intergovernmental Panel of Climate Change (IPCC) Fourth Assessment report concluded that most of the observed increase in global average temperatures since the mid-twentieth century is very likely (over 90% certainty) due to the observed increase in atmospheric greenhouse gas concentrations, with most of this increase due to burning of fossil fuels (Solomon et al. 2007). Observations since 1961 show that the average temperature of the global ocean to depths of at least 3000 m has increased and that the ocean has been absorbing more than 80% of the heat added to the climate

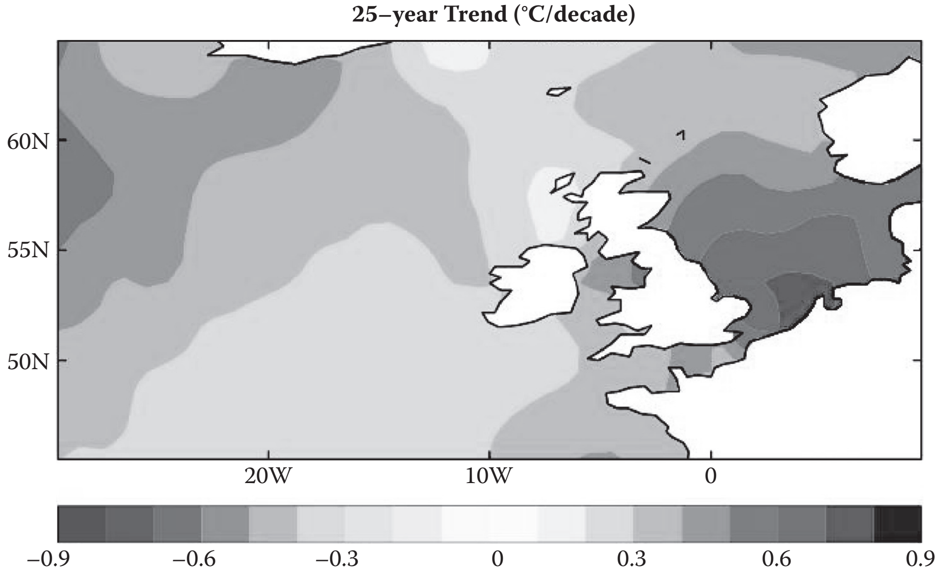


Figure 17 (See colour insert.) The 25-year trend in sea-surface temperature (°C decade-1, 1982–2006) for the north-eastern Atlantic. (From Holliday et al. 2008. Reproduced with Crown permission.)

system (Barnett et al. 2001, Hansen et al. 2005, Bindoff et al. 2007). These global patterns however mask strong regional variability (Pierce et al. 2006) and for the north-eastern Atlantic, observed sea-surface temperatures still remain within the historical envelope (Hobson et al. 2008).

The sea temperature in the north-eastern North Atlantic has shown an increasing trend over the recent three decades and this is probably an indication of climate change caused by emission of greenhouse gases (Figure 17). However, in addition to long-term climate change induced by anthropogenic activity, there is natural variability. Long-term variations caused by solar and tectonic factors and short- and midterm variations related to atmospheric and oceanic conditions exist and have to be separated from the long-term climate change even though it is difficult to distinguish between them. The longest time-series on ocean climate is from north of Kola (Figure 18). It goes back to 1900 and shows a slightly increasing trend over the entire time series. However, on top of this trend several longer- and shorter-term periods are displayed. An approximately 60-yr cycle is evident with

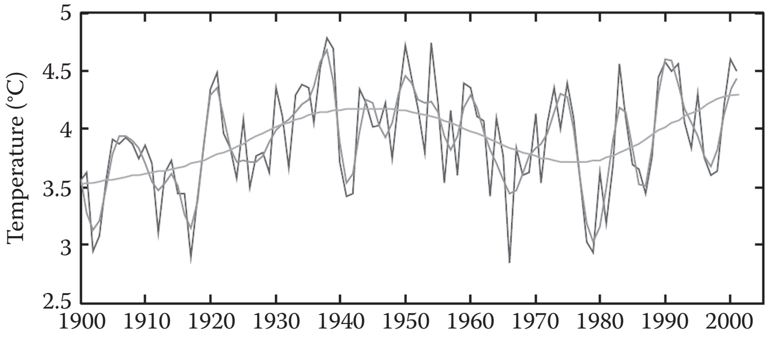


Figure 18 Sea temperature (averaged over 0- to 200-m depth) at the Kola section in the Barents Sea showing the annual mean, 3-yr moving average and long-term smooth. (From Stenevik & Sundby 2007. With permission from Elsevier.)

a maximum in the 1930–1940s and a minimum in the 1960–1970s. Another period displayed in the Kola time series is the 18.6 yr cycle due to the nutation of the earth. In addition, there are decadal-scale periods associated with the NAO, and there is also a clear biannual signal. At present we do not have sufficient knowledge to make predictions of these periodicities in regional climate. The IPCC stated that, ''Although progress has occurred, it is still not possible to assess regional responses to shifts in climate trends, and it is unknown if a general warming will increase or decrease the frequency and intensity of decadal-scale changes'' (Stenevik & Sundby 2007).

Observations to date suggest that there has been a general increase in wind speeds and the frequency of occurrence of storms in the north-eastern Atlantic; whether this is linked to increased atmospheric greenhouse gas levels is unclear as increased storminess is also associated with a positive mode of the NAO (Hurrell & Dickson 2004, Osborn 2004). Many global climate models do reproduce a general trend towards a positive NAO in the twenty-first century (Terray et al. 2004) although other analyses based on regional downscaling predict weaker trends for wind speeds and storminess (Hulme et al. 2002). Typically, climate models predict a decrease in the total number of extratropical cyclones but an increase in the number of intense wind events (Lambert & Fyfe 2006). Predictions of future climate also indicate that there may be an increase in rainfall at high latitudes associated with a polewards shift of the high-latitude storm tracks. This may have an impact on the distribution of atmospheric inputs to the north-eastern Atlantic region because wet deposition more efficiently removes particulate material from the atmosphere than does dry deposition.

Although the characteristics of key oceanic water masses are changing there is no clear evidence for changes in ocean circulation. Weak warming has been noted in the NAC but long-term cooling is also observed in the North Atlantic subpolar gyre. Since 1995, the upper waters of the North Atlantic subpolar gyre have become warmer and more saline (Bindoff et al. 2007). However, at regional scales, natural climate variability is relatively large, making it difficult to distinguish anthropogenic forcing. In particular, multidecadal changes in the AMO may reflect a 50- to 80-yr pattern of North Atlantic coupled ocean-atmosphere variability (Sutton & Hodson 2005). A major uncertainty in the North Atlantic is the future behaviour of the NAO and North Atlantic MOC (Meinke et al. 2003).

Suggestions that the THC has slowed by 30% since the early 1990s (Bryden et al. 2005) are controversial as recent longer-term observations have shown large natural varibility in flow (Cunningham et al. 2007). Simulations of twentieth century THC strength in a suite of atmosphere ocean general circulation models (AOGCMs), whilst being within the range of observational uncertainty for most models, show periods of higher and lower values and a few show substantial differences (Figure 19). Such variability in model outcomes for this particular oceanographic feature makes intepretation of short-term MOC observations particularly difficult (Houghton et al. 2001). However, all the models suggest some decrease in the strength of the MOC in coming years although none projects a complete switch off (Bindoff et al. 2007). A reduction in MOC strength should lead to temporary cooling in the north-eastern Atlantic (although this reduction would not be enough to offset future warming beyond 50 yr).

Since the third IPCC assessment, there have been significant advances in climate modelling, providing a stronger quantitative basis for assessing the likelihood of future change. However, uncertainty in regional-scale projections remains high. In particular there are uncertainties about changes in wind-induced ocean mixing and sea-level rise. In looking at annual, mean zonally averaged SSTs, the largest individual errors are found at mid- to high latitudes (Figure 20), where the model simulations are frequently negatively biased (Rayner et al. 2003). This bias appears to be associated with poor simulation of the path of the NAC (Solomon et al. 2007).

Although increasingly sophisticated models coupling atmospheric and oceanic processes (AOGCMS) are being used for projection, it can be argued that the representation of marine biological processes within them is still too simplistic. It is clear that changes in biological processing, such as the shelf sea pump described on page 19, have the capacity to significantly modify the future

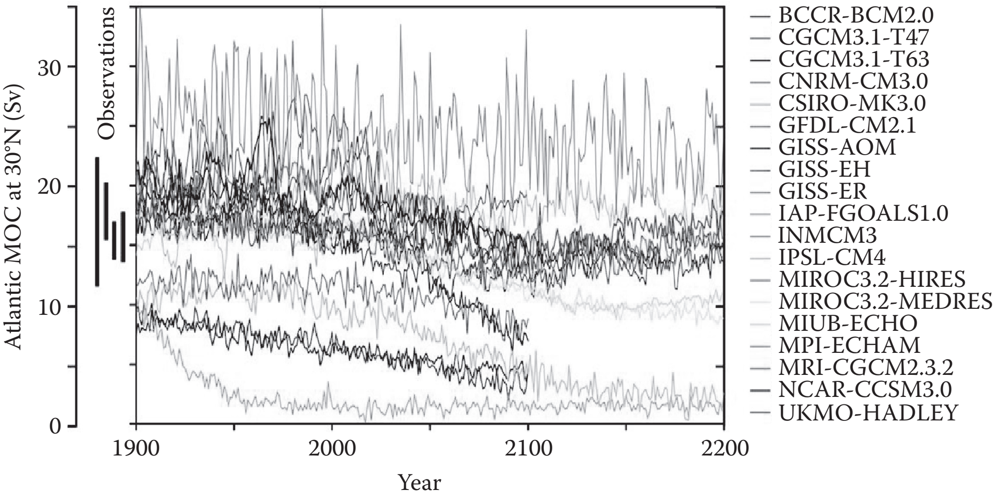


Figure 19 (See colour insert.) Evolution of the Atlantic meridional overturning circulation (MOC) at 30°N in simulations with the suite of comprehensive coupled climate models. (From Meehl et al. 2007, Figure 10.15, p. 773. With permission.)

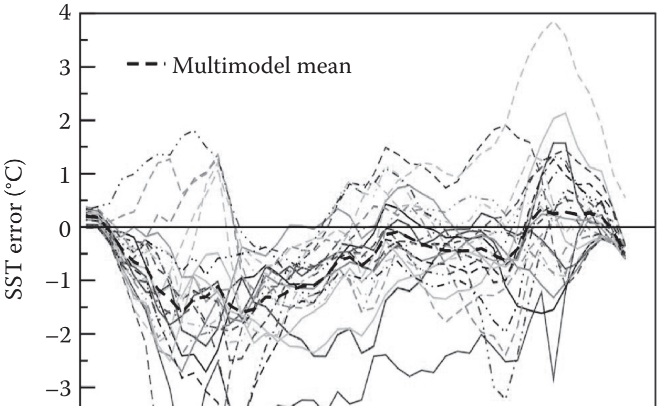


Figure 20 (See colour insert.) Annual mean, zonally averaged SST error, simulated minus observed climatology for a number of atmosphere ocean general circulation models (AOGCMs). The Hadley Centre Sea Ice and Sea Surface Temperature (HadISST; Rayner et al. 2003) observational climatology for 1980 to 1999 is the reference used here, and the model results are for the same period in the twentieth century simulations in the MMD at PCMDI. In the presence of sea ice, the SST is assumed. (From Randall et al. 2007, Figure 8.8, p. 614. With permission.)

global environment (Schmittner et al. 2005b, Bindoff et al. 2007, Schneider et al. 2008). For this reason, EUR-OCEANS has supported the development of improved global, plankton models such as PlankTOM in which a wider range of planktonic organisms are represented as functional groups (Le Quéré et al. 2005).

Impacts on regional linkages

Within the north-eastern Atlantic, potential changes in the Arctic have probably received most analysis through the work of the ACIA (2004). This group has produced a number of projections on how the marine environment might be affected by climate change (Tables 1 and 2). These projected changes arise from the combined impacts of local processes and changes in regional linkages such as large-scale atmospheric forcing.

Within the Arctic, a northern high-latitude maximum in surface air warming is consistently found in all AOGCM simulations and at the end of the twenty-first century the projected annual warming is 5°C with a range of 2.8 to 7.8°C. The annual mean temperature response at the end of the twenty-first century under the A1B scenario is characterised by robust and large warming over the central Arctic ocean (5–7°C) particularly in winter/autumn and associated with reduced sea ice. In terms of regional linkages, reduced warming in the North Atlantic (<2°C and even a slight cooling in some models) is consistent with a weakening of the MOC (Bindoff et al. 2007).

In comparison with air temperature modelling, potential climate change in Arctic waters has received less attention, although changes in the THC have been studied but primarily with low-resolution, uncoupled models. Due to the lack of coordination among modelling studies, few definitive projections can be made about changes to such variables as Arctic Ocean temperatures and salinities, stratification and circulation (including the THC). In light of this, future modelling efforts

Table 1 Changes in surface and boundary forcing based on model projections or extrapolation of observed trends

	2020	2050	2080
Air temperature			
Annual mean	+1 to 1.5°C	+2 to 3°C	+4 to 5°C
Winter	+2.5°C	+4°C	+6°C central Arctic
Summer	+0.5°C	+0.5 to 1°C	+ 1°C
Seasonality		Reduced seasonality (warmer winters compared to summers)	
Interannual variability		No change	
Wind			
Means	While changes in winds are expected there is no general agreement on basis of AOGCM results regarding likely magnitude of changes in speed or direction		
Storm frequency	Possible increase in storm intensity regionally (Labrador, Beaufort and Nordic Seas), in general winter storms will decrease slightly in intensity because the pole-to-equator temperature gradient decreases		
Storm tracks	Possible northward shift from present average tracks		
Regional effects	In areas of sea ice retreat there will be an increase in wind-driven effects (currents and waves) because of longer fetch		
Precipitation			
Mean	+2%	+6%	+10%
Seasonality	Decreased seasonality in run-off due to earlier snowmelt, changes in seasonality in precipitation uncertain		
Snow on ice	+1 to 2%	+3 to 5%	+6 to 8%
Sea level	+5 cm	+15 cm	+25 cm
Cloud cover			
General	+3%	+5%	+8%
Spring, autumn	+4 to 5%	+5 to 7%	+8 to 12%
Winter, summer	+1 to 2%	+3 to 5%	+4 to 8%

Note: AOGCM = atmosphere ocean general circulation model.

Table 2 Summary of changes projected in ocean conditions according to the five Arctic Climate Impact Assessment (ACIA)-designated models relative to baseline conditions

	2020	2050	2080
Sea ice			
Duration	Shorter by 10 days	Shorter by 10–15 days	Shorter by 20–30 days
Winter extent	6–10% reduction	15–20% reduction	Probable open areas in high Arctic
Summer extent	Shelves ice free	30–50% reduction	50–100% reduction
Export to North Atlantic	No change	Reduction beginning	Reduced
Type	Some reduction in multiannual ice	Significant loss of multiannual ice	Little or no multiannual ice
Landfast ice	Possible thinning and retreat in south	Possible thinning and further retreat in south	Possible thinning and reduction in extent in all Arctic marine areas
Sea surface temperature			
Winter/summer (outside MOC regions)	Increase of about same magnitude as in air temperatures in ice-free regions No change in ice-covered regions		
Seasonality	All Arctic and Nordic shelf seas undergo seasonal changes	30–50% of Arctic Ocean to Undergo seasonal changes	50–100% of Arctic Ocean to undergo seasonal changes
Mixed-layer depth	Increase during summer in areas with reduced ice cover and increased winds		
Currents	In regions affected by MOC, modifications to MOC will change strength of the currents		
Ocean fronts	Fronts are often linked to topography but changes in ocean current speeds may cause some to move		
Light exposure	With decreasing ice extent and duration, more areas exposed to direct light		
Nutrient levels	Substantial increases over shelf regions due to retreat of sea ice beyond the shelf break	High levels on shelves and in deep Arctic basins; higher levels due to deeper mixed-layer depth in areas of reduced ice cover	

Note: MOC = meridional overturning circulation.

should attempt to more fully address the range and uncertainty of potential changes in Arctic waters (Figure 21).This will require better resolution in the ocean models and improved coupling between the dynamic atmosphere and dynamic ocean components, particularly in the presence of sea ice (ACIA 2004). Summer sea ice is probably already thinning throughout much of the Arctic with 2007 showing one of the most dramatic declines in the extent of sea ice yet observed (Stroeve et al. 2007). However, once again there is debate about the relative roles played by changes in ice circulation associated with the NAO and Northern Annular Mode and direct warming caused by atmospheric greenhouse levels (Serreze et al. 2007).

The shelf seas pump

Global change, the result of natural and anthropogenic activities will affect directly or indirectly all components of pelagic marine ecosystems. Particularly susceptible to the impacts of global change are the services provided by shelf sea and coastal ecosystems. Despite their small areas, shelf seas play a key role in the global ocean carbon cycle, thereby providing feedbacks to global climate. Tsunogai et al. (1999) extrapolated their results from the shelf pump of the East China Sea to the world shelf areas, assuming that they functioned in the same way. They estimated that the pump would account for a net oceanic uptake of CO_2 of 1 Gt C/yr if the world continental shelf zone would absorb the atmospheric CO_2 at the rate observed in the East China Sea. Without resolving the shelves explicitly, Yool & Fasham (2001) calculated a net pumping rate of 0.59 Gt C yr^{-1} for the

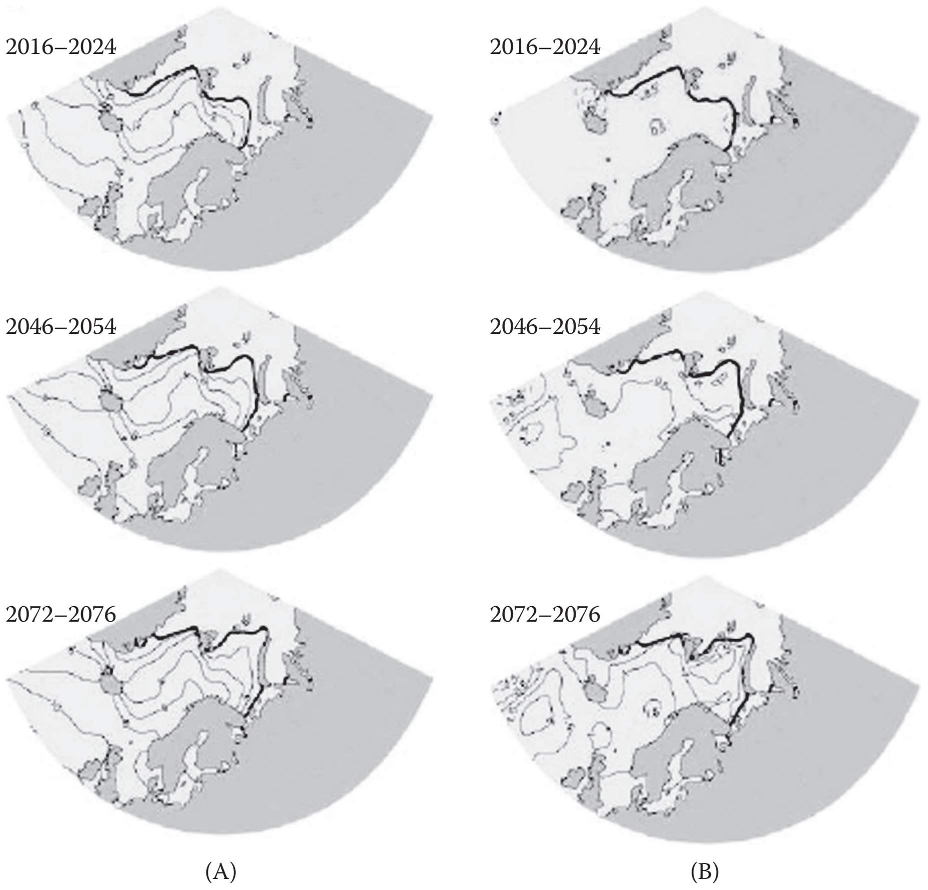


Figure 21 Evolution of the sea-surface temperature and sea-ice edge (heavy black line) in the BCM CMIP2 integration (modified from Furevik et al. 2002). (A) March SST and sea-ice distributions; (B) shows change since 2000.

shelf seas. Their arguments were supported by the investigations undertaken by Kempe & Pegler (1991) in the North Sea. This amount is smaller than the one calculated by Tsunogai et al. (1999), possibly because the effect of shelf carbon outgassing was included in the latter approach. Thomas et al. (2004b) in their study of the North Sea shelf pump estimated that about 8 million tonnes of carbon are exported each year from the North Sea to the North Atlantic Ocean—representing about 93% of the CO_2 that the North Sea takes up from the atmosphere. Extrapolating across the world's coastal and marginal seas suggests that these areas (just 7% of the world's oceans) may account for around 20% of the global oceanic annual uptake of anthropogenic CO_2, much higher than previously thought.

Based on these studies the significance of the North Sea shelf pump for the sequestering of carbon is well established but the effects of global warming on the functioning and efficiency of the shelf pump are unclear. Longer periods of stratification should reduce the flux of nutrients to the surface layer in those areas not subject to strong tidal mixing. As a result, restructuring of the post-bloom phytoplankton community is likely to occur. Furthermore, more intense stratification has the potential to increase the dominance of the microbial loop increasing the amounts of carbon recycled in the upper mixed layer and potentially resulting in a reduced flux of organic material to the seabed. If this happens, carbon outflows due to the shelf pump could be reduced, reducing the efficiency of the shelf pump and the contribution of this mechanism to the global sequestration of carbon to the deep ocean.

Biogeographical patterns and phenology

Over the course of the last few decades compelling evidence has emerged from the north-eastern Atlantic that biogeographical boundaries have shifted northwards. In particular there have been large distributional changes in the plankton (Beaugrand et al. 2002, Edwards et al. 2002). Such changes are probably also occurring in other oceans but the north-eastern Atlantic is unique in having good coverage with CPR survey routes that have been running for over 70 years (Warner & Hays 1994, Hays et al. 2005).

Using CPR data, both phenological changes (i.e., the timing of life-cycle events on an annual basis) and geographical distribution changes have been recorded (Beaugrand et al. 2002, Edwards & Richardson 2004). Poikilothermic organisms are especially sensitive to temperature changes which impact most aspects of their physiology (Lindley & Daykin 2005). Species will respond to temperature changes over time by moving towards their optimum position within their thermal envelope. This occurs both temporally as in seasonal succession (manifested as a phenological response) or geographically as a geographical movement of the range of the population. These responses can be particularly rapid in planktonic organisms due to their short life cycles. In the study by Beaugrand et al. (2002) large northerly movements of calanoid copepod species typical of the southern shelf edge were detected over the last 50 years. This has been accompanied by a northerly retreat of colder water species. This geographical movement is much more pronounced than any documented in the terrestrial environment being accelerated by advection in the shelf-edge current. For example, while surface isotherms have shifted approximately 100–200 km north, the southern species association has extended its range by more than 10° latitude (>1000 km). In recent years, the warmer water, shelf-edge species have been recorded in the northern North Sea, entering via the Faroe-Shetland Channel (Figure 22).

In other regions of the north-eastern Atlantic, northerly movements of plankton species have been more modest but still significant. Recently in the waters to the south of Iceland, subarctic species have decreased fairly rapidly, to be replaced by cold-temperate mixed-water species and in the Bay of Biscay an increase in subtropical and warm-temperate species has paralleled a reduction in continental and warm-temperate pseudo-oceanic species (Beaugrand et al. 2009). Lindley and Daykin (2005) also showed that the abundance of two subtropical zooplankton copepod species *Centropages chierchiae* and *Temora stylifera* has increased in the Celtic Sea over the last few decades.

These large-scale biogeographical shifts observed in the plankton have also seen paralleled latitudinal movements in fish species distribution in the Bay of Biscay (Quero 1998), North Sea (Perry et al. 2005) and wider north-eastern Atlantic (Brander et al. 2003, Harris et al. 2007). Northerly geographical range extensions have also been documented along the European Continental shelf edge (Beare et al. 2004a, b, Genner et al. 2004). It is noteworthy that fish with northern distributional boundaries in the North Sea have shifted northwards at rates up to three times faster than terrestrial species (Perry et al. 2005). This may reflect the more fragmented nature of the terrestrial environment where range shifts may be limited by the availability of suitable habitat. While these observations have described surface geographical changes in pelagic organisms it is worth remembering the 3-dimensional nature of the marine environment. Recent research has observed not just changes in fish biogeography but also changes in the depth distribution of fish species in response to recent warming (Dulvy et al. 2008). This change can be seen as analogous to the upwards movement of terrestrial organisms in alpine environments.

Further evidence that these distributional changes are genuine responses to environment comes from the western Atlantic. Here cooling and the freshening of the north-western Atlantic over the

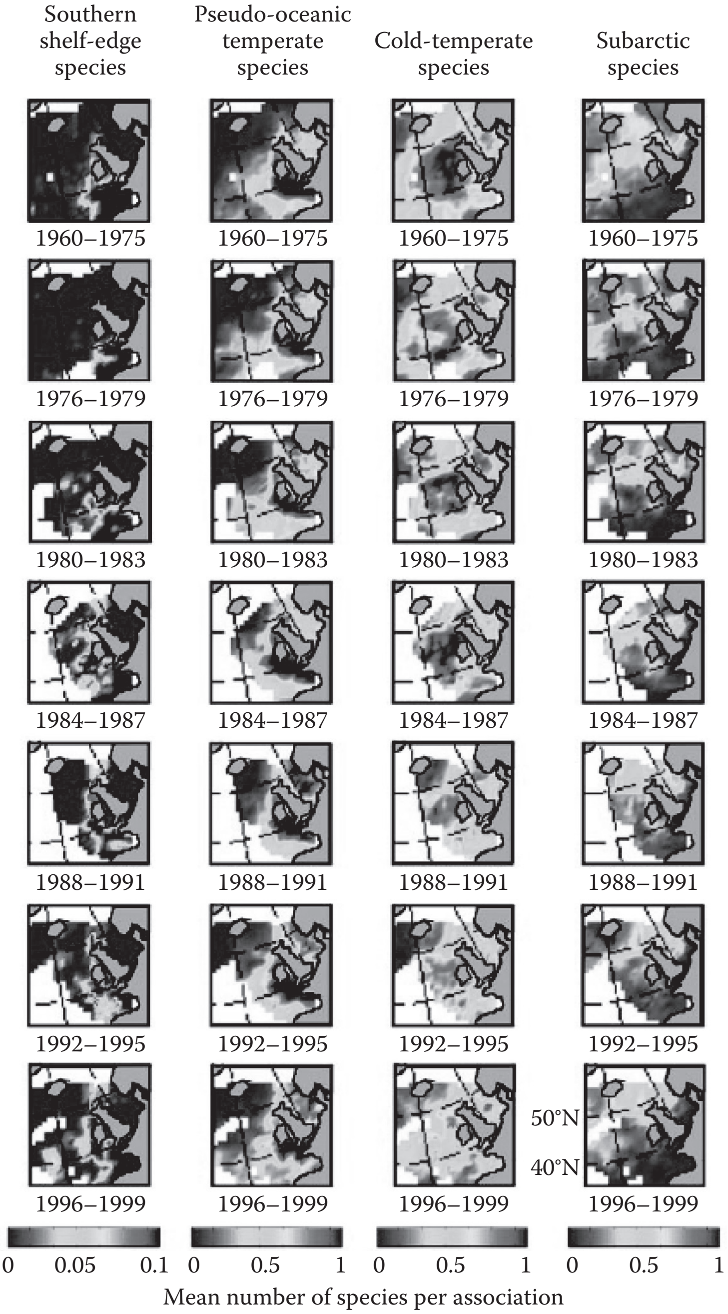


Figure 22 (See colour insert.) Long-term changes in the mean number of calanoid copepod species per association from 1960 to 1999 from Continuous Plankton Recorder (CPR) records. (From Beaugrand et al. 2002. With permission of AAAS.)

last decade have had an opposite effect, with some groundfish species (cod) and their prey (capelin) moving further south. However both Rose (2005) and Dulvy et al. (2008) cautioned that we know too little about the interrelationships between the environment, plankton, fish distributions and exploitation to draw definite cause-and-effect conclusions.

Primary production in the north-eastern Atlantic

In well-mixed waters, the timing of the onset of the spring phytoplankton bloom is largely controlled by available light. In these waters climate change should not have a strong impact on the onset of the spring bloom (Sommer & Lengfellner 2008) excepting that lag effects (Wiltshire & Manly 2004) or altered turbidity due to increased precipitation and terrestrial run-off may cause contrary effects (McQuatters-Gollop et al. 2007b). In deeper waters, bloom initiation occurs when phytoplankton cells are constrained above the compensation depth by a shallowing thermocline (Sverdrup 1953, Mann & Lazier 2005). In these areas increased sea temperatures may lead to earlier stratification and an advanced bloom but increased wind mixing, also predicted under climate change, may counter this effect. Once initiated, phytoplankton growth (light-saturated production) is temperature sensitive and mesocosm experiments have shown that increased temperatures during this phase lead to decreased peak biomass, decreased mean cell size and decrease in the proportion of diatoms (Sommer & Lengfellner 2008). All these changes may lead to increased carbon cycling within the pelagic microzooplanktonic community, poorer feeding conditions for copepod zooplankton and thus to a less-efficient energy transfer from primary to fish production under a warmer climate. The increase in overall growing season in the North Sea already observed (Reid et al. 1998, McQuatters-Gollop et al. 2007b) has been associated with an increase in abundance of smaller flagellates that favour warmer and more stratified conditions seen under the current ocean climate conditions.

The thermal responses of bloom-forming phytoplankton coupled with their short generation times means that it can be predicted, with some confidence, that the frequency of HABs will increase. In some areas of the North Sea, warming has already been associated with an increase in certain HAB species (Edwards et al. 2006). However temperature is not the only factor controlling these blooms. Uncertainty about how phytoplankton communities, and the food webs dependent on them, will react to combined changes in temperature and nutrients underlies the controversy surrounding the suggestion that deliberate fertilisation of large areas of the ocean to stimulate primary production might sequester atmospheric carbon dioxide to the deeper ocean (Buesseler et al. 2008, Glibert et al. 2008).

Shifts in algal abundance and species composition will also affect the quality of food available to grazers (Sommer & Lengfellner 2008). Another crucial aspect influencing predator-prey relationships is the degree of temporal overlap. There is evidence that phytoplankton may respond to increased temperatures by shifting the timing of their bloom more radically than their zooplankton predators (Stenseth & Mysterud 2002, Edwards & Richardson 2004). Such differing responses from previously coupled components of marine food webs could lead to trophic uncoupling. This might in turn lead to reductions in the efficiency with which energy is transferred to higher trophic levels and increased sedimentation to the benthos (Turner 2002). Such changes could explain recent increases in some benthic species in shelf seas (Kirby et al. 2007). However, these increases in benthic productivity may not be entirely environmentally driven since commercial fisheries, particularly in the shelf seas, have also altered benthic predation patterns (Heath 2005).

Secondary production in the north-eastern Atlantic

Richardson (2008) gave a recent and comprehensive review of the potential effects of climate change on zooplankton populations globally. Many of the examples were taken from the North Atlantic and included major effects within the region such as latitudinal range extensions and changes in timing of the seasonal cycle. As previously mentioned the north-eastern Atlantic is one of the most comprehensively surveyed regions globally for zooplankton through the CPR programme. However, most analyses of CPR data have concentrated on changes in distribution and phenology rather than productivity per se (Beaugrand et al. 2002, Edwards & Richardson 2004). An additional problem is that the CPR undersamples smaller species of zooplankton and so may have overemphasised the recent observed decrease in total copepod biomass in the north-eastern Atlantic (Pitois & Fox 2006). Beyond largely descriptive studies, predicting how zooplankton communties will respond to future environmental changes from first principles (i.e., physiology) is much more challenging (Helaouët & Beaugrand 2007).

Physiological processes, such as respiration, growth, development and reproduction in zooplankton are highly sensitive to temperature so even small changes in temperature can affect population dynamics. Durbin and Durbin (1992) suggested that warming, through effects on winter temperatures, will have a particularly strong effect on species developing under cold temperatures. For example, a rise of 2°C did not have a major effect on the maturation rate of the copepod *Acartia hudsonica* during spring and fall, whereas there was a larger cumulative effect during winter due to the slower development rate at the lower temperatures. Hence, these authors suggested that those zooplankton which complete a major part of their life cycle during the winter will be the first to be affected by climate warming. The short life-cycle of many zooplankton species can lead to a tight coupling between environmental effects and plankton dynamics. Few zooplankton species are commercially exploited so observed changes in productivity and abundance at lower trophic levels may be more easily attributed to climate change (although in some cases 'top-down' control, which can itself be affected by fisheries, may be important) (Reid et al. 2000). There are a number of key species, for example, copepods of the genus *Calanus*, that occur throughout the North Atlantic systems under review (Heath et al. 1999, Helaouët & Beaugrand 2007). Changes in their distribution and their species composition or trophic interactions resulting from shifts in geographic range undoubtedly will affect overall ecosystem structure and productivity (Beaugrand et al. 2002, 2007, Bonnet et al. 2005, Head & Sameoto 2007, Helaouët & Beaugrand 2007, Valdes et al. 2007). However, since multiple factors vary over different timescales, from seasonal to multidecadel, it has proven difficult to predict the relative impact of any single process on regional dynamics (Helaouët & Beaugrand 2007). It has been shown that climate-induced changes in advection and stratification affect both circulation and transport and vertical processes all of which are important for controlling zooplankton population dynamics. Discriminating between the impacts of local and remote forcing will require coordinated studies of key species across the three North Atlantic systems. Comparative studies between regions should also lead to better understanding of the mechanisms controlling the appearance and spread of new species that have extended their biogeographical ranges. It is likely that changes in the eastern and western Atlantic will occur on different time- and space scales because of differences in the physical drivers in these regions (Pershing et al. 2005, Kane 2007).

Fish in the north-eastern Atlantic

Interest in studying the relationships between environmental factors and the availability of fish to fisheries is not new (Cushing 1982). The earliest attempts at scientific investigation relate to long-term market records such as that of the Bohuslan (Swedish) herring (Ljungman 1882). As time series have built up for more species, especially over the last century, a large literature has evolved on correlations between climate and fish abundance (e.g., Alheit & Hagen 1997, Planque & Fox 1998, Planque & Frédou 1999, Fox et al. 2000, Stige et al. 2006). However, a significant criticism of most of these studies is the lack of physiological or ecological mechanisistic underpinning (Pörtner et al. 2001), increasing the likelihood that a significant portion of reported correlations are artefactual (Myers 1998). Furthermore, most studies have concentrated on commercial species, making it difficult to separate environment causes from the effects of exploitation. Because species at their northerly and southerly range limits are most likely to be exposed to damaging environmental conditions, it may be more sensible to look for shifts in boundaries rather than centres of distribution (Perry et al. 2005, Dulvy et al. 2008). Range shifts may result directly from movements of adult fish away from areas with detrimental conditions but can also be the consequence of differential survival of early life stages towards the edges of a species distribution. With regard to climate change, differing phenomenological shifts between early life stages and their prey may alter the degree of temporal overlap and thus lead to changes in survival (Hays et al. 2005). An ideal study would therefore examine changes for all fish species close to their latitudinal limits; consider non-commercial, as well as commercial species; use time-series covering periods of cooling as well as warming (Dickson et al. 1974) and bear in mind that seasonal conditions affecting certain life stages may be more critical than annually averaged conditions (Cushing & Dickson 1976). Unfortunately there are few time-series for fish that fulfil all these criteria.

Over the last 30 years sea temperatures in the north-eastern Atlantic have been increasing but, as pointed out by Hobson et al. (2008), this is not unprecedented. Analysis of previous warming periods may therefore give indications of how fish populations in the north-eastern Atlantic should respond in the short-to-medium term. During the 1920–1930s there was a marked period of warming in the north-eastern Atlantic. Unfortunately, apart from a few isolated observatories (Hawkins et al. 2003), standardised fishery surveys were not being conducted at this time. Biological responses must therefore be inferred from available data, mostly anecdotal or commercial landings. These records do indeed indicate that boreal species such as cod and haddock shifted northwards (Drinkwater 2006) and in addition there were increased sightings of warm-water species such as bluefin tuna (*Thunnus thynnus*) (cited in chapter 5 of Cushing 1982). In the north-eastern Atlantic century-long time-series exist for both Arcto-Norwegian cod and Norwegian spring-spawning herring. Toresen and Østvedt (2000) showed that the spawning stock biomass of herring has varied with the multidecadal climate signal. In addition Sundby and Nakken (2008) have demonstrated that the spawning locations of Arcto-Norwegian cod propagated northwards and southwards in tune with the AMO throughout the twentieth century. During the warming from the 1920s to the 1930s and 1940s the spawning areas were displaced northwards along the coast, while the cooling from the 1950s to the 1960s and 1970s resulted in a return to the locations favored during the cool 1900s to 1920s. During the recent warming, after the mid-1980s, the spawning areas were displaced northwards again. Also the spawning stock biomass of cod has displayed a similar long-term oscillation as the herring, the stock being large during warm periods and smaller during cold periods (Hylen et al. 2008). Particularly in the English Channel (Stebbing et al. 2002, Hawkins et al. 2003) and North Sea (Perry et al. 2005), recent changes seem to be similar to the historical responses observed to warming and cooling but we have also seen new interactions with the Atlantic through increased abundance in shallower waters of oceanic species such as the snake pipefish (*Entelurus aequoreus*) (Kirby et al. 2006, Kloppmann & Ulleweit 2006). Increasing abundance of snake pipefish in shelf seas may in turn be linked with reduced seabird fledging success as they are nutritionally inferior to sandeel (Harris et al. 2007). Environmental changes in regional connections can therefore have consequences that affect the whole food chain.

The main problem with interpreting such observations is that most of the time-series, except for some of the Norwegian fisheries records, only cover a few decades and relate to a period of almost continual warming (Hobson et al. 2008). If the NAO index reverts to a negative phase this may lead to temporary cooling in the north-eastern Atlantic. but climate models predict overall continued warming against these oscillations, which will lead to sea temperatures that eventually will exceed historical observations. Since most attempts to predict what may happen have taken a ‘climate envelope’ approach in which future distribution is predicted based on current thermal limits for a species, we may have limited ability to predict future trends once the environment moves outside the historical framework (Sharp 2003). Furthermore, rather than ‘smooth’ changes over time we may see abrupt realignments (‘regime shifts’) as communities reorganise in response to changing environmental conditions (Beaugrand 2004). Predicting how marine communities will respond under these conditions is a major challenge but has serious implications for the design of marine reserves, fisheries policies and biodiversity conservation. Among the potential future changes are an increase in production of marine fisheries in the northern North Atlantic (Alcamo et al. 2007) as well as an influx of more southerly species to areas like the North Sea. Reduced sea-ice in the

Arctic and Subarctic Seas may lead to increases in primary and secondary production south of the ice edge to the benefit of important commercial fish stocks in Arctic and Subarctic Seas, for example, cod (*Gadus morhua*) and herring (*Clupea harengus*), species that currently comprise about 70% of the total catch in these areas. An increase in water temperature of 1–2°C in the Atlantic part of the Norwegian and Barents Sea is very likely to result in a change in the distribution of several fish species (ACIA 2004). Capelin (*Mallotus villosus*) is likely to extend its feeding area north and north-eastward. During summer it might begin to feed in the Arctic Basin and migrate to the Kara Sea. Whether capelin will maintain their present spawning grounds along the coast of northern Norway and the Kola Peninsula is unclear. Extensions eastwards may also occur and capelin might begin spawning along the west coast of Novaya Zemlya. Cod is also likely to expand its feeding area eastwards and northwards (Stenevik & Sundby 2007). As cod is demersal it is not likely to migrate north of the Barents Sea and into the Arctic Basin proper. Haddock will probably follow the same pattern as the cod but at present it is likely to remain further south. In the Norwegian Sea, herring is likely to return to feeding and overwintering areas in use prior to 1964 but spawning grounds along the Norwegian coast may be maintained. Mackerel and blue whiting are likely to migrate north-east to the Barents Sea. These species may then compete for food with other pelagic species in the area (Figure 23).

It is notable that the recruitment success of many fish stocks shows an immediate response to interannual environmental changes (Planque & Frédou 1999). Although sea temperatures during the egg and larval periods have been most often linked with year-class success, temperature is likely a proxy for other processes such as prey availability (Sundby 2000) or predation pressure (Fox et al. 2000). Since healthy stocks of potentially long-lived species such as cod contain a spread of age-classes (Longhurst 1998), the spawning stock biomass tends to integrate these high-frequency variations towards the multidecadal environmental patterns (Sundby & Nakken 2008). Climate variations such as decadal-scale trends in the NAO therefore appear to influence fish stocks by increasing the probability of a run of strong or weak year-classes that gradually accumulates in the spawning stock (Stige et al. 2006). This is a somewhat different response to those of short-lived

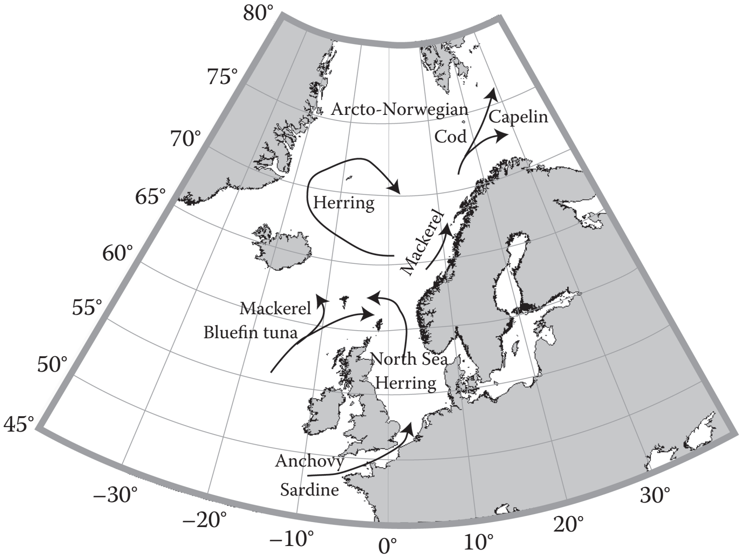


Figure 23 Likely extensions of the feeding areas for some of the main commercial fish populations in the north-eastern Atlantic under climate change. The extent of the movements is for illustrative purposes only and is not based on modelling results. (Reproduced with permission of Cambridge University Press.)

species such as anchovy for which there is a much more immediate and apparent response to interannual variations in stock biomass. It should also be pointed out that the temperature amplitude of the multidecadal oscillation is considerably smaller than the temperature amplitude of the decadal-scale oscillation. For the north-eastern Atlantic, the amplitude of the interannual and decadal-scale sea-temperature variations are typically around 2°C, while the amplitude of the multidecadal signal though the twentieth century is about one-third of that (i.e., 0.7°C) (Figure 18). Nevertheless, this moderate multidecadel climate signal has had a dramatic influence on the marine ecosystem with responses in the distribution of both zooplankton (Beaugrand et al. 2002) and fish stocks (Toresen & Østvedt 2000, Sundby & Nakken 2008). It can be concluded that it is not only the amplitude of the climate signal but also its persistence that affects marine ecosystems. The effects of multidecadal climate oscillations during the twentieth century can provide us with some important clues about how marine ecosystems may respond to anthropogenic climate change. However, temperature increases predicted for the twenty-first century are considerably greater than the AMO change of 0.7°C seen during the twentieth century. This implies a substantial extrapolation beyond our observations and we should expect to see potentially abrupt and non-linear responses.

Higher predators in the north-eastern Atlantic

As discussed on page 30, predictable movements of marine mammals over ecosystem boundaries can be direct (e.g., the annual north-south and inshore-offshore migrations of baleen whales) or incremental, such as the influx of oceanic dolphins into shelf and coastal waters of north-western Europe during the summer (e.g., common dolphin *Delphinus delphis* and striped dolphin *Stenella coeruleoalba*) (Goold 1998). For these southern dolphin species sea temperature appears to be a limiting factor (MacLeod et al. 2005) although this is probably a result of more complex relationships between temperature and prey distribution. As seasonal isotherms continue to move northwards it is conceivable that these summer dolphin migrations will become more exaggerated. However, other long-term climate-related impacts may be more subtle (e.g., changes in social structure of odontocete populations in the north-eastern Atlantic and Pacific have been linked, with a 2-yr lag, to the North Atlantic and Pacific Decadal Oscillations). It is thought these relationships are mediated through links between the atmospheric forcing and the recruitment success of salmon, which are a major prey item for the whales (Lusseau et al. 2004). Within the Arctic region, marine mammals that feed predominantly offshore may benefit from increased primary and secondary production due to reduced ice cover whilst inshore feeders may suffer as primary production is reduced due to increase coastal turbidity linked with increased terrestrial run-off (Bluhm & Gradinger 2008).

Ecosystem effects in relation to the regional linkages in the north-eastern Atlantic

Climate change related effects in the regional linkages of the north-eastern Atlantic will be mostly the results of changes in the atmospheric patterns and ocean currents. As shown on pages 47 and 28 the spread of warmer water species into the North Sea has been strongly associated with the inflow of warm slope shelf water into the North Sea via the Faroe-Shetland Channel (Beaugrand et al. 2002, Beaugrand 2004). The biota of the European shelf seas may therefore show rather rapid responses to climate change, over and above what might be expected from a consideration of the changes in isotherm location.

Similarly, the role of the ocean currents connecting the Atlantic and shelf seas to the Nordic and Arctic Oceans is a key factor in the regional ecology of the Arctic itself (Hegseth & Sundfjord 2008) and it is in the Arctic that the potential impacts of climate change on marine ecosystems have been most thoroughly considered (ACIA 2004, Vikebø et al. 2007b). The changes in physics described in this review will affect all levels of the marine food web (Table 3). Of most concern to humans will be changes at higher trophic levels, which will likely include alterations to the distribution and migration patterns of fish, possible higher growth rates and productivity in some areas, northwards spread of species from more southern areas and a retreat northwards of true Arctic fish species.

Table 3 Potential long-term ecological trends due to climate warming for the Arctic

	Phytoplankton	Zooplankton	Benthos	Fish	Marine mammals and seabirds
Distribution	Increased spatial extent of areas of high production in the central Arctic Ocean	Boundary for colder water/warmer water species moves northwards	Boundary for colder water/warmer water species moves northwards	Boundary for colder water/warmer water species moves northwards Timing and location of spawning grounds and feeding migrations to alter	Polewards shift in species distributions
Production	Increased production in central Arctic Ocean and Barents Sea	Difficult to predict	Difficult to predict, depends on phenological responses of phyto-plankton and zooplankton	Wind-driven advection patterns of larval drift may change, phenological responses may cause mismatches with prey for early life stages	Strong declines in populations of ice-associated mammals, increases in temperate species, seabird responses hard to predict
Biodiversity	Dependent on mixing depth: shallow mixing favours diatoms, intermediate mixing favours *Phaeocystis*, deep mixing may favour nanoflagellates	Adaptable Arctic species such as *Calanus glacialis* may be favoured	Cold water species likely to decline over much of the area, warmer water species (e.g., polychaetes and blue mussel) should increase	Cod, herring and some flatfish likely to move north and become more abundant; capelin, polar cod and Greenland halibut likely to decline	Declines in polar bear and ringed, harp, hooded, spotted, ribbon and possible bearded seals. Increased distribution of harbour and grey seals. Possible declines in bowhead, narwhal, grey and beluga whales. Ivory gulls and several of the small auk species likely to decline; response of other seabirds hard to predict

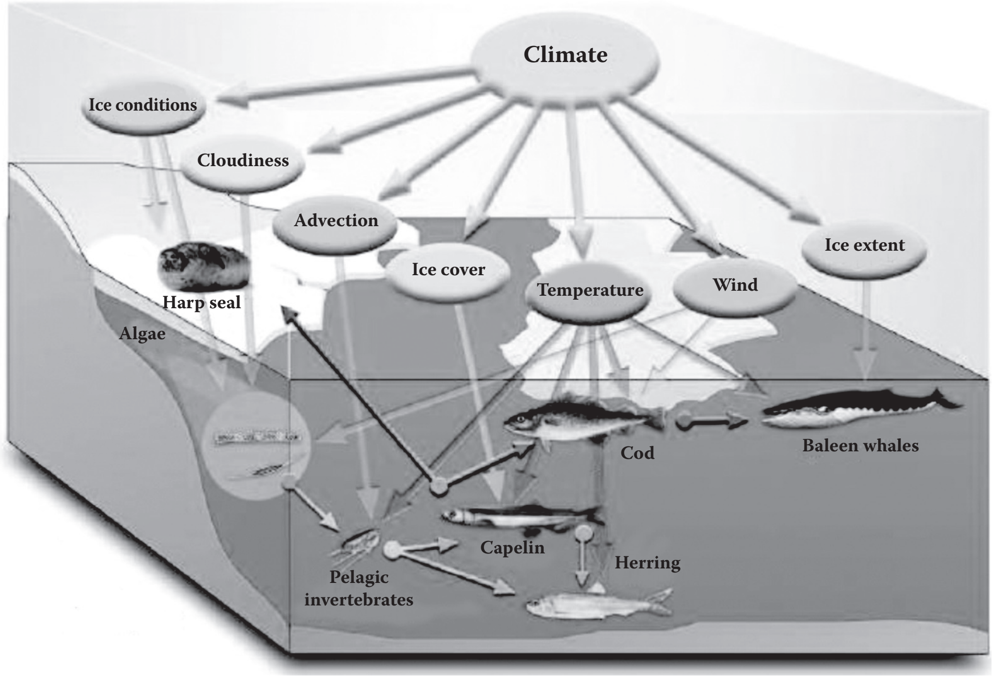


Figure 24 (See colour insert.) Interactions of climate change factors with biological components of the Nordic and Arctic Seas ecosystem. (Reproduced with permission of Cambridge University Press.)

In turn this will affect marine mammals (Figure 24). For some organisms, such as polar bears (*Ursus maritimus*), the extensive loss of sea ice will lead to reduced breeding success and population declines (Derocher et al. 2004) whilst for others, such as the bowhead whale (*Balaena mysticetus*) increased offshore productivity may prove beneficial (Bluhm & Gradinger 2008).

As noted in ACIA (2004) Nordic and Arctic Seas are likely to be heavily affected by increased human activity as summer sea ice reduces. There are strong indications that this is already happening with extensive prospecting for oil and minerals in newly accessible areas. Not only will this increase the risks of pollution incidents and introduction of non-indigenous species but also loss of sea ice during the summer will open new ocean connections to the Pacific (Figure 25). Indeed there is some evidence that this has already led to the spread of Pacific species into the north-western Atlantic, as shown by the occurrence of the Pacific chain-forming diatom *Neodenticula seminae* in the Labrador Sea (Reid et al. 2007).

The spread of non-indigenous species

The warming of north-eastern Atlantic waters is likely to increase both the dominance of existing non-indigenous species and the number of successful new invasions, but it is unclear how this will impact ecosystem functioning (Sax et al. 2007). Climate change is likely to promote earlier recruitment and faster growth rates and initiate reproduction in non-indigenous species already established in the region. Stachowicz et al. (2002) found that the initiation of recruitment of non-indigenous sessile marine invertebrates in the United States was strongly correlated with winter water temperatures. The pelagic larvae of these species arrived earlier in the season compared with native species when winter seawater temperatures were warmer. In addition, experiments demonstrated that non-indigenous ascidians were able to outgrow native species when seawater temperatures were raised higher than normally experienced in the region. In the European shelf seas, increases in seawater temperature have led to species, such as the Pacific oyster (*Crassostrea gigas*), naturally

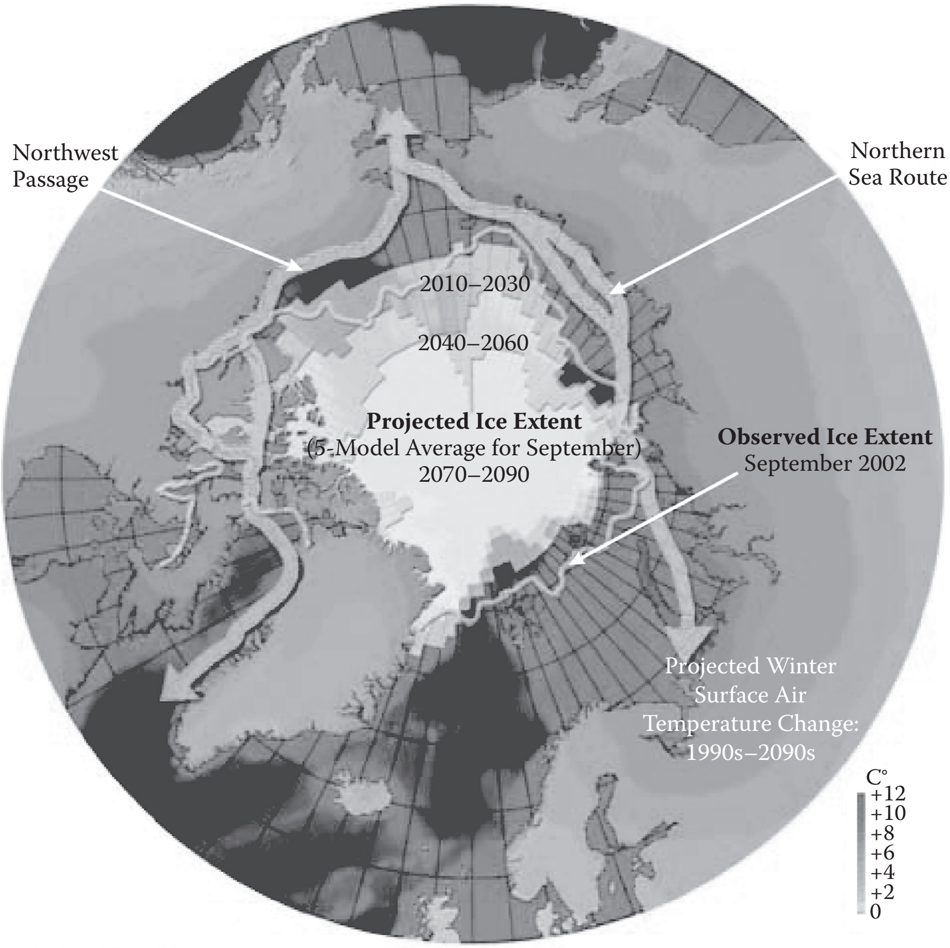


Figure 25 (See colour insert.) Potential navigation routes in the Arctic. (Arctic Council 2006. With permission.)

recruiting to regions beyond its zone of introduction (Nehring 2003, Diederich et al. 2005, Cardoso et al. 2007). *Crassostrea gigas* has been shown to cause significant changes in community structure, sediment porosity, bioturbation activity and biogeochemical cycling in areas where it has become established (Ruesink et al. 2006).

Increased storm intensity within the north-eastern Atlantic may also increase the rate of unintentional release of organisms from aquaculture installations (Naylor et al. 2001). This is a significant problem as it is estimated that up to 80% of adult salmon entering rivers in Norway are escapees (Fiske & Lund 1999). When aquaculture escapees breed with natural populations, hybridisation and subsequent introgression can lead to a reduced fitness in the hybrids, with the F2 generation hybrids suffering from higher mortality rates and increased susceptibility to infectious disease (Skaala et al. 2006). With an increasing dependence of aquaculture on non-indigenous species to meet the growing global demand for seafood, it is likely that the industry may become an even more significant pathway of introduction (Cook et al. 2008).

Climate change is also likely to increase the number of new invasions to the north-eastern Atlantic through northwards range expansions (see pages 45 and 53) and increased survivorship of species introduced from warmer ocean basins. The arrival of new species will accelerate over the next few years with the increasing use of the Arctic Ocean as a shipping route between Asia and Europe (Minchin 2006, Reid et al. 2007). In addition, the implementation of the total ban on TBT in antifoulants in 2008 is likely to increase the likelihood of non-indigenous species surviving as hull fouling on commercial vessels.

The introduction of non-indigenous species is widely recognised as a major threat to biodiversity (United Nations 1992, Worm et al. 2006), potentially leading to habitat modification, changes in ecosystem functioning, extinction of native fauna and flora, disease transfer and genetic effects such as hybridisation with native congeners (Lovei 1997, Ruiz et al. 1997, D'Antonio et al. 2001). Unfortunately, predicting how an increase in the dominance of non-indigenous species and new invasions will influence community composition and the functioning of the north-eastern Atlantic is a major challenge. Concerted European and global action is urgently required to advance environmentally sound shipping and aquaculture practices to minimise the risk from new invasions.

Conclusions

This review has demonstrated that strong linkages exist between the North Atlantic Ocean, North Atlantic shelf seas and the Arctic and Nordic Seas. These are due to atmospheric, oceanic and human movements, which in turn affect the dispersal of nutrients, organisms and contaminants throughout the region. Studying the North Atlantic and the associated shelf seas as an integrated 'basin-scale' system is a key challenge for the early twenty-first century. Similarly, all the major components of the regional ecosystem food webs will need to be considered together. This concept underpins the 'end-to-end' approach which aims to couple models from physics all the way to the higher tropic levels (Travers et al. 2007). Future progress will depend on the extensive use of mathematical models but these need feeding with data from existing and new observation systems along with the relevant experimental studies needed to parameterise vital rates. Even with modern computing capabilities, it is impossible to represent all trophic levels to the same degree. One suggested approach is to concentrate the biological resolution at the level of the species (or trophic level) of interest and to decrease the resolution, both up and down the trophic levels, moving away from the target (deYoung et al. 2004). This is a pragmatic suggestion but implies that we will need to develop separate models for specific questions. Other researchers propose a 'tool-box' approach by which subsystem models can be coupled in different configurations. Despite these difficulties, significant progress is being made in constructing practical 'end-to-end' models (Steele et al. 2007, Travers et al. 2007, Cury et al. 2008). Along with the accompanying observations and process studies, such models provide tools for the improved, integrated understanding of marine ecosystems that will help to meet the increasing demands for ecosystem-based marine management (Cury et al. 2008).

This review has shown that the major linkages within the north-eastern Atlantic are due to the ocean currents. In turn these are affected by regional atmospheric forcing displaying dominant modes such as the AMO and NAO (Hurrell & van Loon 1997, Marshall et al. 2001, Hurrell & Dickson 2004). Atmospheric forcing also plays a critical role in local processes such as water column warming and stratification, particularly in the shelf-seas (Sharples et al. 2006). Although the broad mechanisms by which atmospheric forcing influences water exchange between the open ocean and the shelves are clear, the role of shelf-break mixing remains poorly understood. Better understanding of how these large-scale horizontal and vertical processes operate is needed.

This review has shown how physical forcing ultimately affects all trophic levels in the north-eastern Atlantic (Cushing 1982, Fasham et al. 2001, Mann & Lazier 2005, Frederiksen et al. 2006). Studies covered in this review have clearly demonstrated that basin-scale forcing affects both biogeography and ecosystem structure and function. There is clear evidence that regions within the north-eastern Atlantic are warming particularly rapidly. Studies reviewed have shown how species ranges are changing in response and how new alien species may become established. Such changes will affect ecosystem structure, trophic interactions, and potentially productivity. Clearly, climate change is now high on the scientific, political and societal agendas but our ability to predict how the north-eastern Atlantic ecosystem will respond is still limited. This review has also shown that the North Atlantic is a particularly important component of the global carbon cycle (Thomas et al. 2004a, Pätsch & Kühn 2008). However, it remains uncertain how the shelf seas biological pump will be affected by climate change and how such changes will feed back to the global climate. An integrated approach in the linked systems of the North Atlantic related to ecosystem structure is clearly called for, renewing and extending the approach taken in the early 1990s in the Joint Global Ocean Flux Study (JGOFS) programme (Ducklow & Harris 1993).

There is a clear challenge to develop better predictive ability for at least the dominant components of the North Atlantic pelagic ecosystem, the related biogeochemical processes and the feedbacks with the climate system. Society increasingly demands an ecosystem approach to management of marine resources (Jennings 2005) and this will require new collaborative research programmes. The variability and changes we are observing in the north-eastern Atlantic affect population dynamics, trophic functioning, and dispersal and migration patterns. An integrated approach will advance studies of ecosystems throughout the north-eastern Atlantic and lead to better understanding of the processes involved in population variability of key species and their interactions. In addition, the global scale of the climate, environmental and anthropogenic forcings considered in this review, combined with the strong linkages between the shelf and deep ocean ecosystems, suggest a need to focus on integrated basin-scale processes rather than on individual regional programmes. This will of necessity require better international cooperation as no single nation has all the resources needed for such studies.

Ultimately the aim must be to develop an integrated ecosystem approach to management of human activites in the north-eastern Atlantic. A predictive understanding of the mechanisms by which climate change, biodiversity, and habitat dynamics and exploitation interact to influence the dynamics of the associated ecosystems should be a goal. This approach should lead to improved scientific ecosystem-based approaches to conservation of natural resources, the maintenance of biodiversity, and a better understanding of the key role of this region in the global carbon cycle.

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