# 8

# Environmental Impacts—Marine Ecosystems

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**Abstract**

This chapter presents a review of what is known about the impacts of climate change on the biota (plankton, benthos, fish, seabirds and marine mammals) of the North Sea. Examples show how the changing North Sea environment is affecting biological processes and organisation at all scales, including the physiology, reproduction, growth, survival, behaviour and transport of individuals; the distribution, dynamics and evolution of populations; and the trophic structure and coupling of ecosystems. These complex responses can be detected because there are detailed long-term biological and environmental records for the North Sea; written records go back 500 years and archaeological records many thousands of years. The information presented here shows that the composition and productivity of the North Sea marine ecosystem is clearly affected by climate change and that this will have consequences for sustainable levels of harvesting and other ecosystem services in the future. Multi-variate ocean climate indicators that can be used to monitor and warn of changes in composition and productivity are now being developed for the North Sea.

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## 8.1 Introduction

The North Sea is one of the most productive, intensively exploited and well-studied sea areas in the world. It lies just north of the boundary (~50°N) between the warm- and cool-temperate biogeographic regions (Dinter 2001), also referred to as Lusitanian and Boreal. Because of its size, topography, and physical and chemical diversity (described elsewhere), the North Sea encompasses a number of more or less coupled ecosystems with some shared properties. Deep areas of the northern North Sea and Norwegian trench are strongly influenced, both physically and in biota, by inflows from the Norwegian Sea, NW European shelf (Fig. 8.1 is an artist's impression of this ecosystem). The low salinity Baltic Sea outflow affects the Norwegian coastal area and the inflow from the English Channel and several major rivers affects the continental coastal areas of the southern North Sea. Shallower water depth, stronger tidal mixing and diminished ocean influence all contribute to greater seasonal variability in temperature in the southern North Sea, with summer temperature much higher than in the northern North Sea and winter temperatures much lower.

The North Sea has been exploited by humans since they resettled its shifting margins after the last ice age 10,000 years ago. It has also been the subject of conservation concern for many hundreds of years and the focus of many scientific studies of marine life, which show the inexorable decline of easily caught fish and shellfish species with vulnerable life histories, such as sturgeon *Acipenser sturio*, ling *Molva molva*, large elasmobranchs and oysters (see Chap. 12) (Le Masson du Parc 1727; Poulsen et al. 2007).

The long history of exploitation and study of the North Sea means that a great deal of long-term information on fish, shellfish and other biota exists or is currently being reconstructed from archives, archaeological material and museums (Fig. 8.2). Written records go back 500 years in some cases and archaeological records go back many thousands of years (Enghoff et al. 2007), covering a wide range of temperature conditions and providing a basis for establishing the response of the ecosystem to natural climate variability and long-term change, but confounded by the effects of increasing fishing pressure and other anthropogenic drivers. An introductory account of the ecosystems of the North Sea is included in Chap. 1.

Between 1983 and 2007 the sea surface temperature (SST) of the North Sea warmed at rates of up to 0.8 °C decade$^{-1}$ (see Chap. 2), which is an order of magnitude greater than the rate of global warming and among the highest in the world. The high rate of warming in the North Sea is partly due to anthropogenic factors but also to natural multi-decadal regional variability in the North Atlantic. Meyer et al. (2011) used sensitivity experiments to demonstrate that increasing air temperature is the main cause of the warming trend observed in the North Sea, accounting for about 75 % of observed (hindcast) changes in SST. From the record of Central England air temperature (CET, Fig. 8.3), which is the longest instrumented temperature time series in

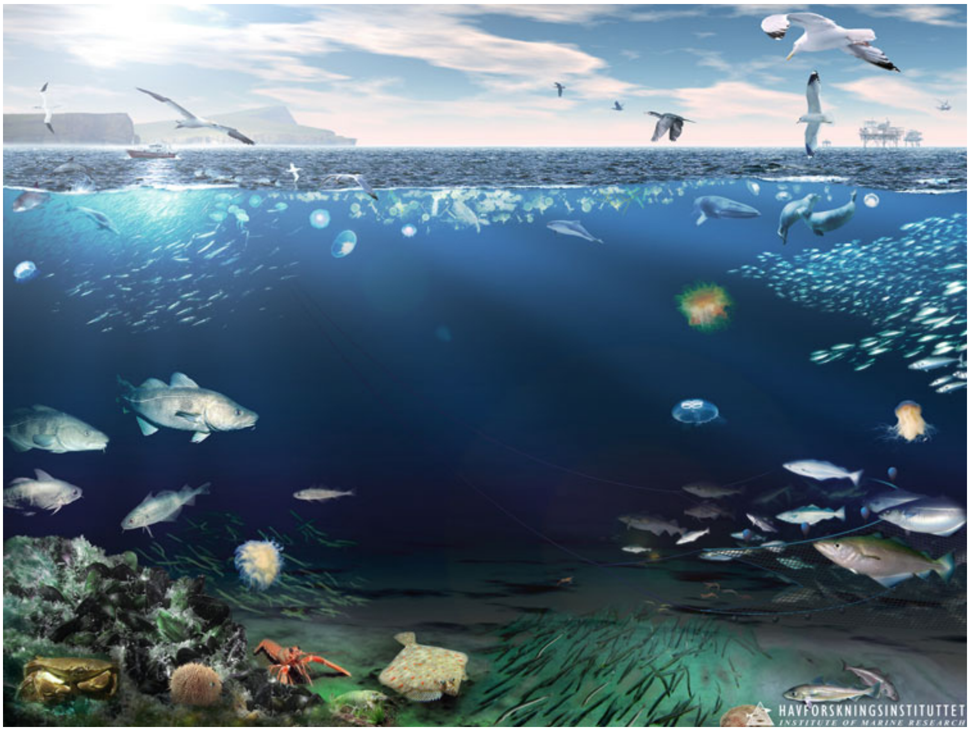

**Fig. 8.1** Artist's view of the ecosystem of the coastal northern North Sea. Artwork by Arild Sæther commissioned by the Institute of Marine Research, Norway

**Fig. 8.2** By the time Pieter Breughel the Elder created *Big Fish Eat Little Fish* in 1557, Europeans had been putting pressure on coastal and estuarine parts of the North Sea for centuries (Bolster 2008). Public domain work accessed through Wikimedia Commons

the world, it is known that recent CET is higher than at any time since observations began in 1659, except for a short period in the 1730s. Over the period 1975–2005 the variability in annual mean CET and sea-bed temperature (SBT) during the first quarter of the year match closely (Fig. 8.3).

The rate of warming that the North Sea experienced from 1983 to 2007 is too high to persist, and the component of the warming due to multi-decadal variability is expected to reverse. There are indeed indications in the data since 2008 that temperatures in the North Sea may be returning to lower levels.

The abrupt temperature increase that occurred in the late 1980s (Fig. 8.3) was particularly marked during the period January–March and can be related to a remarkable increase in south-westerly wind strength during the early part of the year (Siegismund and Schrum 2001), which is a useful reminder that in addition to the effects of rising temperature, there are probably several interrelated climatic factors, including wind-driven vertical mixing and changes in inflow to the North Sea, with resultant salinity and nutrient changes, that are also important.

Irrespective of the underlying causes of the changes in sea temperature and other oceanic and atmospheric variables since the early 1980s, it is evident that biota in the North Sea are responding to these strong signals. Changes in advection and mixing may also be driving changes in ocean chemistry that in turn affect biota. Abrupt changes in many components of the biota, sometimes called ‘regime shifts’, have been observed in the North Sea since the 1980s. Such changes probably have physical as well as biological causes, but the nature of the processes involved is by no means clear and it is notable that the term regime shift is not used in the chapters on physical processes. There is a wide-ranging debate on the extent to which low frequency biological variability reflects external forcing, internal ecological dynamics or a combination of the two (Doney and Sailley 2013). The North Sea is well placed to help resolve the causes and processes behind abrupt and continuous

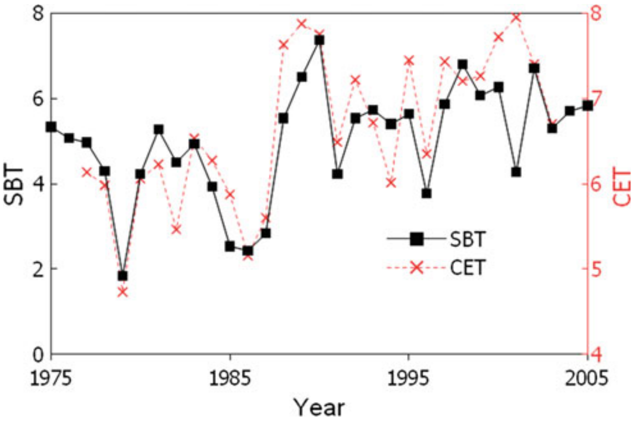

**Fig. 8.3** First quarter sea-bed temperature (SBT) and Central England air temperature (CET; R = 0.80; $p < 0.0001$). SBT data from Hiddink and ter Hofstede (2008). CET data from www.metoffice.gov.uk/hadobs/hadcet/cetml1659on.dat

**Table 8.1** Changes in North Sea biota in response to climate (from ICES 2008)

| | Zooplankton | Benthos | Fish | Seabirds |
|---|---|---|---|---|
| Total observations | 81 | 85 | 58 | 10 |
| No change | 8 | 13 | 1 | 0 |
| Change in expected direction | 68 | 47 | 43 | 6 |
| Change in opposite direction | 5 | 25 | 14 | 4 |

ecosystem responses to sub-annual-to-decadal physical variability, because spatially resolved, long-term records of physical and biological variables are both available and there have been marked changes in the two over recent decades (Schlüter et al. 2008; Kirby and Beaugrand 2009). The processes may also involve shifts in the biogeographic boundaries between cool- and warm-temperate ecosystems.

Climate change is a recent addition to the human pressures on marine ecosystems, but in this too the North Sea is relatively well studied and described. OSPAR, the intergovernmental body for protecting and conserving the Northeast Atlantic, commissioned a report in 2008 asking whether the impacts of climate change over past decades can be detected on North Sea and Northeast Atlantic biota (ICES 2008). The first step in addressing this question is to decide on the basis of theory and previous observations what the likely change in any feature (distribution, abundance, seasonal pattern) would be under the actual climate of the past decades. The vast majority of long-term data sets assembled for the North Sea (212 out of 234) showed changes in the distribution, abundance or seasonal patterns (maturation, breeding, other seasonal cycles) of zooplankton, benthos, fish and seabirds; 77 % of these changes were in the direction expected due to climate impacts (Table 8.1).

A global study of climate impacts on marine biota (Poloczanska et al. 2013) assembled over 1700 data series and showed a similar proportion (81–83 %) of time series responding consistently with the effects of climate change. The rate of distribution shift for leading edges (i.e. where the distribution is spreading into previously unoccupied areas for the species) is faster (~72 km decade$^{-1}$) than the rate of shift of trailing edges (~15 km decade$^{-1}$; where a previous occupied area is vacated). The overall global rates of distribution shift (~30 km decade$^{-1}$ for leading edges, centroids and trailing edges) matched the rates at which ocean surface isotherms had shifted over the same periods and locations (Burrows et al. 2011), but the rates of shift in spring phenology (seasonal timing) were not closely matched with changing seasonality of temperature. Rates of distribution shift varied among taxa and were fastest for phytoplankton and zooplankton. The rates at which both distribution and seasonal timing of marine biota had shifted were comparable to or greater than the rates observed for terrestrial biota. Almost half (45 %) of the data used in the global study of climate impacts on marine biota came from the Northeast Atlantic and a high proportion of these from the North Sea.

This chapter presents a review of what is known about the impacts of climate change on the biota of the North Sea. Plankton and benthos, which are habitat/life history categories, are each considered, as are the taxa fish, birds and marine mammals. Invertebrate taxa are addressed within the sections on plankton and benthos, but viruses, bacteria and the microbial loop are not covered. Other anthropogenic drivers of change such as fishing, habitat disturbance, eutrophication or pollution are dealt with in other chapters.

All North Sea biota are affected by a range of physical and chemical drivers, including inflowing water masses, currents within the North Sea, nutrients, atmospheric warming, winds and other mixing forces (buoyancy flux, tidal mixing) that influence the proximate physical, chemical and biological environment of the biota. Thus climate impacts are by no means limited to temperature effects; the major ocean climate variables are grouped by property type in Table 8.2. This changing environment affects biological processes and organisation at all scales. There are direct effects on the physiology, reproduction, growth, survival, behaviour and transport of individuals and on the distribution, dynamics and evolution of populations. Indirect effects include trophic interactions (predators, prey, competitors), the structure and coupling (e.g. benthic-pelagic coupling) of ecosystems and the effects of pathogens, symbionts and commensals. Life spans of very different length and feedbacks between levels of biological organisation (e.g. ecosystem effects on food supply) can result in cross-scale and lagged effects (Doney and Sailley 2013). Such linkages and ecosystem processes are considered in Sect. 8.7.

Because the North Sea is so well monitored and studied, the effects on marine biota of the very rapid rate of climate change in the region over the past 30 years are more likely to be detected and understood here than in other areas. The following sections review current knowledge of the effects of climate change on functional and taxonomic groups in the North Sea followed by a section on ecosystem effects and a final synthesis that draws together common features and conclusions.

**Table 8.2** Ocean climate variables grouped by property type

| Property type | Ocean climate variable |
|---|---|
| Atmospheric and sea surface | Wind |
| | Cloud cover |
| | Waves |
| | Sea level |
| Chemical and physical | Temperature |
| | Salinity |
| | pH |
| | Oxygen |
| | Nutrients |
| Dynamic | Currents |
| | Stratification |
| | Turbulence |
| | Upwelling |
| | Frontal processes |
| Seasonal | Storm events (for example) |

## 8.2 Plankton

Many studies have documented the strong influence of both climatic variability and global climate change on plankton ecosystems (Roemmich and McGowan 1995; Edwards and Richardson 2004; Richardson and Schoeman 2004; Mackas et al. 2007), indeed plankton often seem to amplify subtle climatic changes in areas such as the North Sea (Taylor et al. 2002). Some explanations have been proposed to explain the sensitivity of this group to climate (Taylor et al. 2002; Beaugrand et al. 2008), but the precise processes remain to be identified. One contributory factor may be that these organisms are ectotherms and that metabolic rates, growth, reproduction, activity and species interactions are all influenced by temperature (Atkinson 1994; Brown et al. 2004). A second factor could be that they react rapidly to climate change because of their short life cycle. A third that this group is not exploited directly, so that the main drivers are easier to identify. Phenological (Edwards and Richardson 2004) as well as biogeographic shifts (Beaugrand et al. 2009) have been observed in North Sea plankton. Abrupt community or ecosystem shifts (also called regime shifts or critical transitions) (Reid et al. 2001; Scheffer 2009) have been documented (Reid et al. 2001; Weijerman et al. 2005), including changes in phytoplankton and zooplankton (e.g. copepods, euphausiids, gelatinous species) and in holozooplankton (taxa whose whole lifecycle is planktonic) and merozooplankton (taxa with a partly planktonic life history) (Kirby et al. 2008).

### 8.2.1 Bottom-Up and Top-Down Control

Among environmental factors that may influence population dynamics and individual survival, temperature is probably the major factor. It is often highly correlated with observed changes in biological or ecological systems (Aebischer et al. 1990; Edwards and Richardson 2004; Weijerman et al. 2005; Hatun et al. 2009; Kirby and Beaugrand 2009; Buckley et al. 2012). Temperature modulates predator-prey interaction by influencing locomotion, functioning of sensory organs and activity. It might therefore be difficult to resolve the role of bottom-up (e.g. physics) and top-down (e.g. grazing/predation) effects. This probably also depends on the spatial scale of a study. At the scale of the spatial distribution of a species, the climate variability hypothesis states that the latitudinal range of species is primarily determined by their thermal tolerance (Stevens 1989). Temperature is indeed a key variable in the marine environment because it is affected by many hydro-climatic processes (Beaugrand et al. 2008) and because it exerts an effect on many fundamental biological and ecological processes (Sunday et al. 2012). At smaller scales however, this factor acts in synergy with others and the proportion of all factors acting on a species also varies spatially (i.e. throughout the distributional range of a species) and through time (i.e. seasonal and year-to-year scales) (Kirby and Beaugrand 2009). The level of turbulence in the water column (Rothschild and Osborn 1988), nutrient concentrations and their effect on phytoplankton concentration and composition (Behrenfeld et al. 2009), the amount of photosynthetically active radiation (Asrar et al. 1989) and the length of day (Fiksen 2000) in extratropical regions are key controlling factors. At small scale, the effect of top-down control may start to be detected. On the eastern Scotian Shelf, Frank et al. (2005) suggested a cascading effect of fishing from the top to the bottom level of the ecosystem, although this has been disputed, with changes in stratification being proposed as the driver (Pershing et al. 2015). Nevertheless, despite some evidence of top-down or wasp-waist control in certain marine ecosystems of the world (Cury et al. 2003), bottom-up control seems to be the most frequent type of control in pelagic ecosystems (Richardson and Schoeman 2004). However, data and studies are sparse and some statistical techniques can give ambiguous results. For example, it is statistically difficult to separate bottom-up control from a common response of organisms to climate change (Kirby and Beaugrand 2009). The persistent simplification of marine food webs by overexploitation (Pauly et al. 1998) may have diminished the importance of top-down control in marine ecosystems. Bottom-up control of plankton is likely to be more important than top-down control.

### 8.2.2 Climate and Changes in Phytoplankton Abundance and Phenology

A substantial literature describes long-term changes in North Sea phytoplankton communities (Reid et al. 1998; Edwards et al. 2009, 2012, 2014; Beaugrand et al. 2010). Total abundance of dinoflagellates has declined since 1960 whereas the total abundance of diatoms has remained virtually unchanged (Hinder et al. 2012). Among the dinoflagellate species, *Ceratium furca*, *Protoperidinium* spp. and to a lesser extent *Prorocentrum* spp., have shown a substantial reduction in summer since the beginning of the 2000s, but the phenology of dinoflagellates has not shifted towards spring, as shown in other studies (Edwards and Richardson 2004). The diatoms *Thalassiosira* spp., *Rhizosolenia imbricata shrubsolei* and *Pseudo-nitzschia seriata* have increased in abundance in spring. The diversity of dinoflagellates has increased in the Northeast Atlantic and in the North Sea (Beaugrand et al. 2010) as both temperature and seasonal stability in temperature have increased, whereas diatoms, which have higher diversity at intermediate and less seasonally stable temperatures, have shown less increase in diversity.

Analysis of daily (work days) sampling of phytoplankton, nutrients and temperature at Helgoland Roads (54° 11′ 3″N, 7° 54′E) from 1962 to 2008 showed that the phenology of three diatom species *Guinardia delicatula, Thalassionema nitzschioides* and *Odontella aurita* did not respond to climate warming in the same way and that overwintering population size, grazing, nutrient levels and water clarity affected their bloom timing (Schlüter et al. 2012). Such species-specific differences in sensitivity to forcing factors could lead to shifts in community structure with potentially far-reaching consequences for ecosystem dynamics. Not only does the marine food web depend on the quantity and timing of phytoplankton production, but also on qualitative features, such as the production of essential fatty acids (Røjbek et al. 2012).

The extratropical North Atlantic Ocean and its adjacent seas may be an important region for carbon export (Sarmiento et al. 2004). The biological pump may be less efficient in a warmer world because of changes in phytoplanktonic types (floristic shifts) but also because upward mixing of nutrients is likely to diminish, due to increased stratification of the oceans (Thomas et al. 2004; Bopp 2005). Deepening of the nutricline, as a result of increased stratification, would shift the phytoplankton community from diatoms (major exporters of carbon to depth) to coccolithophorids (Cermeño et al. 2008) and this latter group has increased in the North Sea (Beaugrand et al. 2013).

### 8.2.3 Climate Impacts on Biogeographic Boundaries and Biodiversity of Zooplankton

Major biogeographical shifts in zooplankton have been identified in the Northeast Atlantic in response to the warming observed in the region (Beaugrand and Ibañez 2002; Beaugrand et al. 2009) and based on the identification of nine calanoid copepod species assemblages using multivariate analyses (Beaugrand et al. 2002). There was a poleward increase in warm-water species and a reduction in the number of cold-water species in the same areas. All zooplankton assemblages exhibited coherent, long-term shifts but the speed of these biogeographic shifts was surprisingly rapid in comparison to rates of change in terrestrial systems (Parmesan and Yohe 2003). Warm-temperate, pseudo-oceanic species experienced a poleward shift of about 10° of latitude (52–62°N, 10°W) or 23 km $y^{-1}$ for the period 1958–2005 (Beaugrand et al. 2009). The magnitude of the species shifts was however similar to the northward movement of some isotherms (e.g. the 10 °C isotherm moved northwards by about 21.75 km $y^{-1}$) in the North Sea. The consequence of these shifts has been to increase the diversity of calanoid copepods in the Northeast Atlantic and its adjacent seas (such as the North Sea) (Beaugrand and Ibañez 2002; Beaugrand et al. 2010). Such increases in diversity have also been identified for other taxonomic groups such as dinoflagellates (Beaugrand et al. 2010) and fish (Hiddink and ter Hofstede 2008). The increase in copepod diversity has been paralleled by a concomitant reduction in their mean size (Beaugrand et al. 2010) due to both increased prevalence of species with smaller body size and decrease in body size within species due to increasing temperature. Size reduction may indicate an increase in the metabolism of plankton ecosystems and may have strong consequences for carbon export.

### 8.2.4 Regime Shift in the North Sea Plankton Community

Marine ecosystems are not all equally sensitive to global climate change and climatic variability (Beaugrand et al. 2008). There are critical thermal boundaries (CTB) where a small increase in temperature triggers abrupt ecosystem shifts (regime shift) and alters the abundance of primary producers, secondary producers and top predators. Such a boundary separates regions where abrupt ecosystem shifts have been reported in the North Atlantic and the North Sea. In these regions, termed vulnerability hotspots, temperature

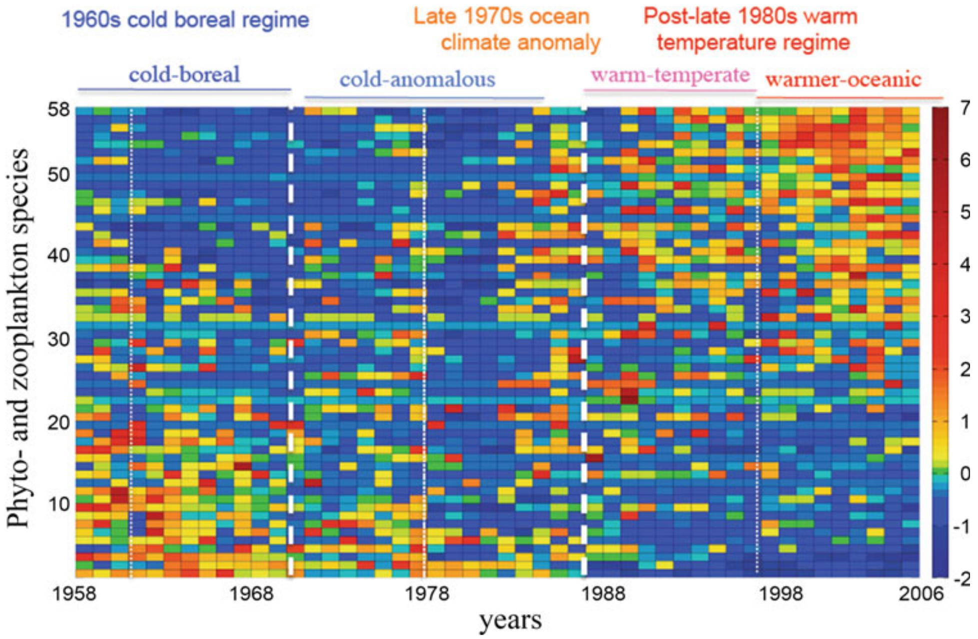

**Fig. 8.4** Change in North Sea plankton composition over the past 50 years. Standardised abundance of 83 phytoplankton and zooplankton taxa collected by the Continuous Plankton Recorder (CPR). The taxa are ordered according to the first principal component. Periods characterised by different hydro-climatic conditions are indicated. Adapted from Edwards et al. (2009)

increase has a substantial effect on the community and the ecosystem, modifying their biodiversity and carrying capacity (Beaugrand et al. 2008).

An abrupt ecosystem shift occurred in the North Sea during the mid-1980s (Fig. 8.4) (Reid et al. 2001). The North Sea is one of the most biologically productive ecosystems in the world. This system supports important fisheries leading to the catch of 5 % of the world's total fish and also contributes significantly to biogeochemical cycles (Thomas et al. 2004). The North Sea regime shift has involved an increase in phytoplankton biomass, and changes in plankton community structure, diversity and phenology (Reid et al. 1998; Beaugrand et al. 2003; Beaugrand 2004). The shift was detected in both pelagic and benthic realms (Kröncke et al. 1998; Reid and Edwards 2001; Warwick et al. 2002). Parallel changes occurred in large-scale and regional temperatures, in three trophic levels and in both holozooplanktonic and merozooplanktonic components (Kirby and Beaugrand 2009). The abrupt ecosystem shift that occurred during the 1980s in the North Sea had a detectable effect on about 40 % of species from all taxonomic groups collected by the Continuous Plankton Recorder (CPR) survey (Beaugrand et al. 2014).

The effect of warming on ecosystems is not a gradual process and species and communities are likely to experience a series of sudden and stepwise shifts alternating with periods of greater stability.

### 8.2.5 Long-Term Changes in Zooplankton

Long-term changes in the zooplankton community have been reviewed from time series at Arendal (northern Skagerrak; 58° 23′N, 8° 49′E), Helgoland Roads (54° 11′ 18″N, 7° 4′E) and Stonehaven (56° 57.80′N, 02° 06.20′W) together with other studies (Hay et al. 2011). Jellyfish abundance has increased (Lynam et al. 2005; Attrill 2007) and there have been reports of incursions of the oceanic scyphozoan *Pelagia noctiluca* into the North Sea, causing mortalities in farmed salmon (Licandro et al. 2010). The ctenophore *Mnemiopsis leidyi* was detected in the Skagerrak in 2006 (Oliveira 2007) and has since occurred in high densities at Arendal Station in late summer and autumn each year, when SSTs are above 20 °C. The Helgoland Roads time series showed abrupt shifts (earlier bloom timing) in the phenology of the ctenophores *Beroe gracilis* and *Pleurobrachia pileus* in 1987/88 (Schlüter et al. 2010) and an inverse relationship between SST anomalies and abundance of small copepods; lowest copepod abundance was observed in the 2000s when sea temperatures were warmest. A comparison of the Helgoland Roads and CPR data indicates a possible time-lagged synchrony (3–5 years) in copepod abundance (Hay et al. 2011): at Stonehaven, total copepod abundance was low in 1997 and 1998. The copepod *Eucalanus crassus*, included in the temperate pseudo-oceanic species assemblage that increased northwards along the European shelf-edge (Beaugrand et al. 2009), has been seen regularly in small numbers at Stonehaven in autumn since 2003.

Since 1958 the copepod *Calanus helgolandicus* has become roughly ten-fold more abundant than *C. finmarchicus* and is now among the most abundant species in the North Sea (Edwards et al. 2014; Fig. 8.5). The underlying climate-related processes have been investigated using life-stage structured models of the two species, combined with a high-resolution 3D circulation model to quantify

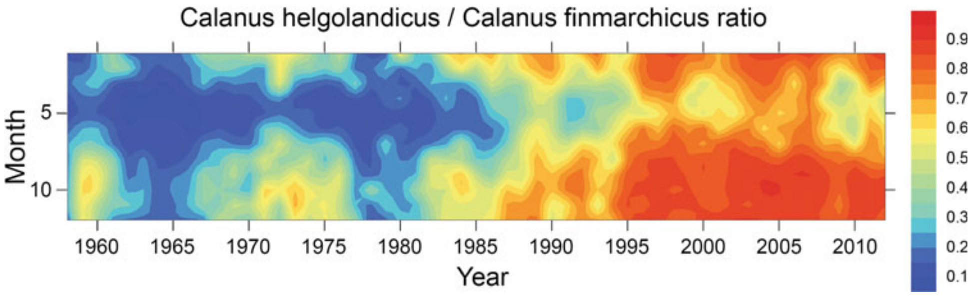

**Fig. 8.5** Ratio between the abundance of the temperate-water copepod species *Calanus helgolandicus* and the cold-water species *C. finmarchicus*. *Red* indicates a dominance of *C. helgolandicus* and *blue C. finmarchicus* (Edwards et al. 2014)

inflows into the North Sea and a regional ecosystem model to quantify biogeochemical and foodweb variables (Maar et al. 2013). Model results were tested against the long, spatially-resolved time series from the CPR and against detailed seasonal sampling of vertical distribution of life history stages. Increasing temperature is a major factor in observed changes in *Calanus* phenology, but changes in abundance are also influenced by advection of *C. finmarchicus* through the northern boundary of the North Sea, which is to some degree climate-related. The detailed observational time series available for the North Sea allow testing of quite complex process models on scales encompassing regional physical dynamics, water column processes and species life history. Observed changes in distribution and phenology are consistent with global patterns (Poloczanska et al. 2013), but there are important processes occurring at regional and local scales that modify the simple global pattern. It is probably too early to judge whether adaptive responses by marine zooplankton will keep pace with the current rapid changes in climate (Dam 2013).

The observational time series for North Sea plankton are longer and have better temporal and spatial coverage and resolution than any other in the world. Since many taxa have plankton life stages these time series can be used to analyse long-term change not only in holoplankton, but also in meroplankton, including benthic species and fish, and examples are given in later sections.

## 8.3 Benthos

This section does not attempt to provide a comprehensive review of all the known processes and mechanisms governing changes in the status of the North Sea benthic ecosystem, rather it attempts to highlight and describe some of the more important and well documented factors which appear to influence the benthos. For example, sediment composition, depth, food availability and water temperature are the main environmental factors governing the large-scale distribution of benthic species in the North Sea (e.g. Glémarec 1973; Duineveld et al. 1991). Small-scale temporal or spatial variability in the benthos, particularly in the shallower areas of the North Sea, may be attributed to temperature, tidal currents, riverine input including nutrient and sediment load, wind-induced swell and sediment resuspension (Rachor and Gerlach 1978; Kröncke et al. 2001) and more rarely to extremely cold winters or anoxia (Duineveld et al. 1991; Kröncke et al. 1998; Armonies et al. 2001).

Macrozoobenthos (relatively large bottom-dwelling animals) form a major component of the North Sea fauna. Most benthic species have pelagic life stages that are likely to be responsive to climate change. For example, the abundance of decapod larvae in the plankton is positively correlated with sea temperature and rising temperatures have resulted in recruitment of large numbers of swimming crabs of the sub-family Polybiinae in the southern North Sea (Luczak et al. 2012). However, once settled on the seabed most species have low mobility and a relatively long lifespan such that individuals reflect integrated effects of climate and other environmental changes over time at their location.

The role of bathymetry and prevailing environmental conditions in structuring the benthic community is examined and long-term temporal patterns are described. Examples of climate effects on macrofauna communities are given from two contrasting intertidal areas of the North Sea, the rocky shores of the British coast and the intertidal flats in the Wadden Sea. Benthic species play an important role in the food web, as a food source for higher trophic levels such as crabs, fishes and migrant birds.

### 8.3.1 Spatial Patterns

Early studies in Danish waters described the spatial patterns of the benthic fauna (Petersen 1914, 1918) and explained the importance of seabed sediment type as a major structuring force for macro-benthic communities. Later work examined the influence of hydrodynamic mixing and concluded that thermal stability of the water column (i.e. the occurrence and persistence of stratification) was also an important explanatory variable for benthic community structure (Glémarec 1973). Shallow mixed waters in the southern North Sea have benthic species assemblages that are distinct from those in the central North Sea between 50 and 100 m deep, and in the areas deeper than 100 m north of the Dogger Bank, where the water column is stratified for a significant proportion of the year. Benthic animals in the North Sea are generally categorised as northern, southern or cosmopolitan (Glémarec 1973; Rachor et al. 2007).

Wide-scale synoptic benthic surveys of the North Sea in 1986 (Heip et al. 1992; Künitzer et al. 1992) and repeated in 2000 (Rees et al. 2007a, b) showed a clear north-south gradient across a range of habitats in the species of molluscs, annelids, crustaceans and echinoderms present. There were gradients in diversity, abundance, biomass and average individual weight of the soft-bottom infauna. The macro-benthic infauna (animals living within the substratum), epifauna (animals living on or associated with the surface of the substratum) and fish assemblages had significantly correlated spatial patterns (Fig. 8.6).

The correlated distributions suggest that large-scale gradients in bathymetry, temperature and ocean currents were particularly important in structuring the benthos. Benthic community types, and the distribution of biomass and mean individual weights of species have been relatively stable over time (Kröncke and Reiss 2007).

The ability to detect changes in benthic communities in the North Sea is hampered by lack of regular, standardised time series, unlike the spatially and temporally extensive surveys of the North Sea plankton. Consistent long-time series for macrobenthos are limited to a few locations off the north-east coast of England (Frid et al. 2009a, b) and in the southern North Sea, off the Friesian coasts (Kröncke et al. 1998, 2001; Neumann et al. 2009). Thus, much of the understanding of trends in North Sea benthos is based on evidence from relatively few sites. However, because most benthic animals have planktonic life stages the recent advances in molecular analysis mean preserved plankton samples can be now be reanalysed (Kirby and Lindley 2005). North Sea plankton samples, collected monthly by CPR since 1948 from all parts of the North Sea, show increasing abundance of meroplankton (the planktonic life stages of benthic species) and a decline in the abundance of holoplankton (permanent planktonic species) since 1958 (Lindley and Batten 2002). In contrast to deeper water benthic species, rocky shore species are easier to survey due to their greater accessibility and because their community dynamics, biodiversity and ecology can be studied experimentally (Sagarin et al. 1999; Tomanek and Helmuth 2002).

Benthic community structure in the North Sea is affected by hydrographic variables; bottom water temperature has a particularly strong influence, but also bottom water salinity, and tidal stress (for the infauna). Chapter 1 discusses the dynamics of water masses in the North Sea and effects on hydrographic properties which affect the composition and productivity of pelagic (planktonic) communities (see Sect. 8.2) which, in turn, affect the benthic communities. The North Atlantic Oscillation (NAO) drives some of the observed changes in benthic-pelagic coupling and has been shown to affect benthic communities off north-eastern Germany (Kröncke et al. 1998, 2001) and in the Skagerrak off western Sweden (Tunberg and Nelson 1998), by causing variability in nutrient supply, changes in planktonic biomass and so

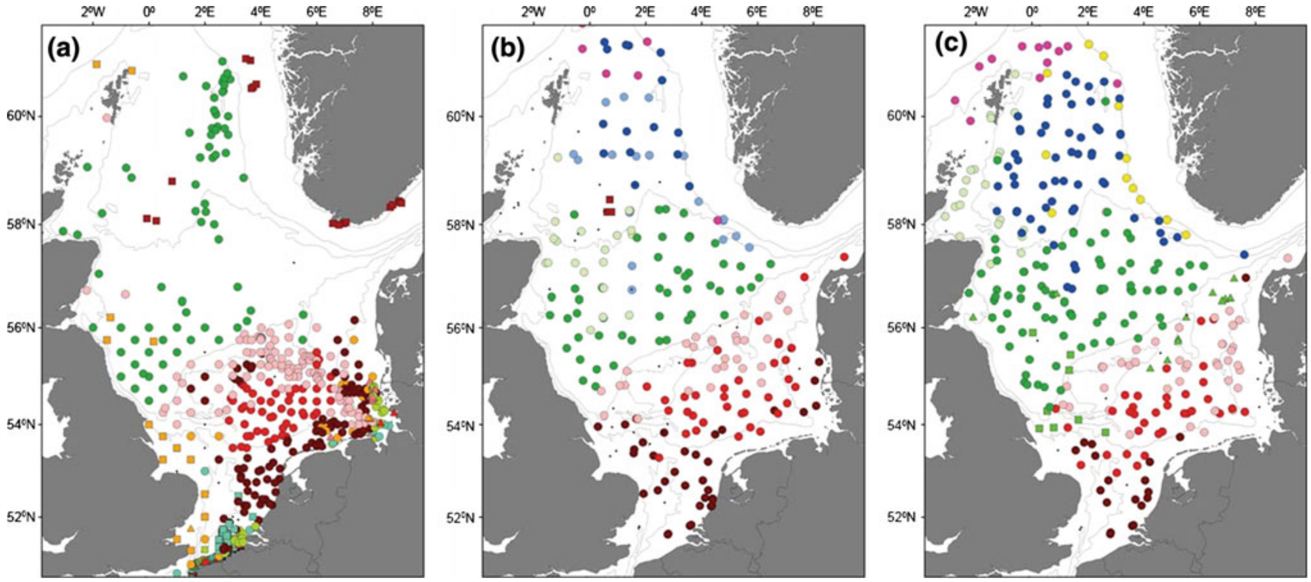

**Fig. 8.6** Distribution of **a** infauna, **b** epifauna, and **c** fish assemblages in the North Sea. *Colours* depict different assemblages. The underlying cluster analyses and taxa associated with each assemblage are given in Reiss et al. (2010)

changes in benthos through sedimentation (e.g. Tunberg and Nelson 1998; Reid and Edwards 2001; Kirby et al. 2007).

The occurrence and densities of a wide range of species show distributional depth limits, but also a close association with habitat type, on which biogeographical influences may be superimposed (Künitzer et al. 1992; Zühlke 2001). Water depth, prevalence of fine soft-sediments and community diversity all increase from south to north. Mean annual and maximum temperatures increase along a northwest to southeast gradient, while minimum temperature decreases (Hiddink et al. 2014) and is correlated with a decrease in biomass and individual weight of species (Eggleton et al. 2007; Willems et al. 2007). Coarser substrata in the south-western North Sea and eastern English Channel generally support species-rich communities and hence contrast with the trend for increasing diversity of the fauna of finer sediments to the north, highlighting the importance of sediment heterogeneity and stability in favouring a greater number of species present.

### 8.3.2 Climate-Driven Temporal Trends

The northern range edge of many benthic invertebrate species in the North Sea has expanded with increased temperature (Hiddink et al. 2014). For example, a southern trochid gastropod that was surveyed in British waters in the 1950s, 1980s and in 2002–2004 showed a range extension of up to 55 km between the 1980s and 2000s (Mieszkowska et al. 2007). Populations sampled over a latitudinal extent of 4° from northern limits towards the centre of the range showed synchronous increases in abundance throughout the years sampled, suggesting that a large-scale factor such as climate was driving the observed changes (Mieszkowska et al. 2007).

The abrupt rise in temperature (Fig. 8.3) and spring wind strength (Chap. 1) during the late 1980s that resulted in major changes (regime shift) in the plankton ecosystem (Fig. 8.4) was not observed to affect the macrobenthos until 1995/96 (Neumann et al. 2009; Luczak et al. 2012). Site-specific species richness increased off the northeast coast of England between the 1970s/1980s and 1990s/2000s (Frid et al. 2009a).

The annual abundance of planktonic larvae of three benthic phyla, Echinodermata, Arthropoda, and Mollusca, respond positively and immediately to changes in SST. The planktonic larvae of echinoderms and decapod crustaceans increased in abundance from 1958 to 2005, especially after the mid-1980s, as North Sea SST increased, but abundance of bivalve mollusc larvae declined. Changes in meroplankton abundance, coincident with increased phytoplankton and declining holoplankton, are probably due to the direct effects of rising SST on the pelagic community and indirect effects of warming on the reproduction and recruitment of many benthic marine invertebrates. The long-term decline in bivalve mollusc larvae may reflect increased predation on the settled larvae and adults by benthic decapods (Kirby et al. 2008). These alterations in the zooplankton may therefore reflect an ecosystem-wide restructuring of North Sea trophic interactions (Kirby et al. 2008).

Mean abundances of macrobenthos at depths of 40 to 120 m at two locations inside Gullmarsfjorden, on the Swedish west coast, and three locations outside the fjord, are negatively correlated with temperature at 600 m in the Skagerrak. This may be due to an NAO-influenced increase in the upwelling of nutrient-rich deep water resulting in increased primary production and food supply to the benthos (Hagberg and Tunberg 2000). Indeed, the impacts of climate change on benthic invertebrates seem to arise from changes in temperature, nutrients and hydrodynamics affecting food supply and hence reproduction (e.g. Kröncke et al. 1998, 2001; Armonies et al. 2001; Clark and Frid 2001).

### 8.3.3 Climate Impacts on Intertidal Species on Rocky Shores

It has long been known that many intertidal rocky shore species reach their biogeographic limits around the British Isles (Forbes 1858; Hawkins et al. 2009) and changes in the distribution of intertidal species on rocky shores have been related to climate variability and change for decades. For example, the relative abundance of two barnacle species during the early twentieth century—*Balanus balanoides*, a Boreal-Arctic species that reaches its southern limit in the SW British Isles and *Chthamalus stellatus*, a Lusitanian-Tropical species that reaches its northern limit in Scotland—was shown to be related to warm and cold periods (Southward and Crisp 1954). Recent surveys have updated these historic records and show that a number of warm-temperate rocky shore species have extended (or re-extended) their northern limits since the abrupt warming of the late 1980s (Southward et al. 1995; Mieszkowska et al. 2006). It seems that more southern, warm-water species have been recorded advancing polewards than northern, cold-water species retreating (Hawkins et al. 2009).

Responses seem to be species- and habitat-specific, with the likelihood of range extensions determined by a combination of life history traits including reproductive mode, fecundity, larval behaviour and larval duration, all of which have the potential to influence dispersal capability. In contrast to plankton in open pelagic systems, it is unlikely that whole assemblages of intertidal rocky shore species will shift simultaneously (Hawkins et al. 2009) owing to their specific requirements in terms of degree of exposure, vertical zonation and substrate attachment.

The balance between grazers/suspension feeders and fucoids is likely to alter as climate changes. Grazing on algae is likely to increase, and there will be stronger interactions between environmentally-induced stress and increased grazing pressure on early life stages of many species (Coleman et al. 2006; Hawkins et al. 2009).

### 8.3.4 Changes in Wadden Sea Intertidal Macrofauna Communities and Climate

In recent decades the fauna and flora on intertidal flats in the Wadden Sea have been affected by increasing temperature, accelerated sea-level rise, epidemic diseases, invasion of non-native species, and human pressures from fisheries, habitat alteration (seawall building, harbour construction, dredging), eutrophication and/or pollution (Oost et al. 2009).

A long-term survey (1930–2009) of changes in macrofauna communities in Jade Bay, a shallow sedimentary tidal bay in the German Wadden Sea shows increasing species richness from 65 taxa in the 1930s, to 83 taxa in the 1970s and 114 taxa in 2009 (Schückel and Kröncke 2013). The most striking difference between 1930 and 2009 was the increase in numbers of non-native species, which was attributed to species introduced by shipping. Since many of these species originated from warmer coasts, it is likely that their ability to settle, survive and reproduce in the North Sea is due to increasing temperature (Van der Graaf et al. 2009). Trophic structure in Jade Bay was dominated by surface deposit feeders in the 1930s, but this feeding mode had decreased by the 1970s. Suspension feeders, mainly bivalves, became dominant. Subsurface deposit feeders had increased by 2009 together with deposit and interface feeders, while suspension feeders had again declined (Schückel and Kröncke 2013).

Drivers behind the observed temporal patterns may be the decreasing nutrient levels in Jade Bay and the whole Wadden Sea between 1981 and 2003 (see also Chap. 3), but the decline of bivalve species biomass by 2009 may be due to frequent recruitment failure, related to temperature increase.

One consequence of the increase in winter temperatures of about 1.5 °C since the 1980s is greater body weight loss during winter, with subsequent production of fewer and smaller eggs (Beukema et al. 2002; Beukema and Dekker 2005). An alternative explanation for recruitment failure, also related to changes in sea temperature, might be enhanced shrimp predation of settled bivalve recruits. Juvenile grey (or common) shrimp *Crangon crangon* were more abundant after mild winters than after cold winters caused by earlier arrival of shrimps from the open, colder North Sea (Beukema and Dekker 2005). Grey shrimp abundance in Jade Bay was an order of magnitude higher in spring in the 2000s compared to the 1970s (Schückel and Kröncke 2013). More generally, increasing temperature is expected to favour crustaceans and especially the grey shrimp. The reason may be that increased temperatures are unfavourable for cod, an important predator, thus reducing the predation mortality of epibenthic species including the grey shrimp (Freitas et al. 2007). Predation by grey shrimp on bivalve spat (bottom-settled larvae) may have a knock-on effect on the productivity of the mussel beds as foraging areas for breeding shorebirds and refuelling areas for long-distance migratory birds. Young mussels are also foraged by the common starfish *Asterias rubens*, with little impact during average winter conditions, however this impact may rise with increasing temperature. An increase of 2 °C could double the rate of foraging by common starfish (Agüera et al. 2012). Thus, climate-induced changes on one trophic level can have important consequences for food-web structure and functioning; a change in species composition in favour of some key species may have cascading effects through the food web associated with intertidal areas. On the Dutch tidal flats the effects of increasing temperature have so far been small compared with human impacts, such as mechanical cockle fisheries. However, since dredging for cockles is currently banned, the effects of rising temperature may become more important in the future.

## 8.4 Fish

Over 200 species of fish have been recorded from the North Sea, including three species of Agnatha (lampreys and hagfish), about 40 species of Chondrichthyes (cartilaginous fishes) and the rest Osteichthyes (bony fishes). The fish fauna includes deepwater species along the northern shelf edge and in the deep Norwegian Trench and Skagerrak, many shelf sea species and also species that occur in shallow water and estuaries. Cold-water species such as Atlantic cod *Gadus morhua* and Atlantic herring *Clupea harengus* occur in the North Sea close to the warm end of their range and southern, warm-water species such as common sole *Solea solea* and sardine *Sardina pilchardus* close to the cold end of their range.

Abundances of each species range from rare to common, but with considerable variability in relative numbers over time, as the North Sea has undergone warmer and cooler periods since the last ice age (Enghoff et al. 2007). The post-glacial inundation of the area south of 55°N occurred about 8000 BP, so much of the North Sea has been invaded by fish fairly recently. Currently about 20 species, most targeted by commercial fisheries, account for 95 % of the total fish biomass.

### 8.4.1 Long-Term Change in Fish Fauna

The Atlantic Holocene warm period lasted from 7000 to 4000 BP, with temperatures on average 2–2.5 °C above recent annual means. Fish identified from archaeological remains of Mesolithic settlements in Denmark include at least 49 species, most of which are common today, but also several that occur mainly in warm-temperate water, including smoothhound *Mustelus* sp., common stingray *Dasyatis pastinaca*, European anchovy *Engraulis encrasicolus*, European seabass *Dicentrarchus labrax*, black sea bream *Spondyliosoma cantharus* and swordfish *Xiphias gladius* (Enghoff et al. 2007). These warmer water species have all reappeared or increased in abundance over the past thirty years.

Declining catches since the fourteenth century from accessible nearshore areas of the North Sea led to the development of ever more distant fisheries at Iceland, in the NW Atlantic and in the Barents Sea, to feed the growing human population.

### 8.4.2 Recent Effects of Climate Change on Fish

The increased abundance of warm-temperate fish species has had a remarkable effect on species richness in the North Sea. The ICES-coordinated International Bottom Trawl Survey (IBTS) Programme, samples more than 300 stations throughout the North Sea in the first quarter of each year (January–March). Over the period 1985 to 2006, species richness increased from around 60 species to almost 90 and the increase is positively related to the increase in sea-bottom temperature (SBT) during that quarter, which rose by an average of 0.7 °C decade$^{-1}$ (Fig. 8.7). The increase in species richness is consistent with both the earlier observation that rate of advance of leading edges of distributions is more rapid than the retreat of trailing edges and with the generally higher species richness of warmer areas. The apparent persistence of cool-temperate species during the Mesolithic warm period suggests that the effect is not just a transient one.

Climate (particularly temperature) can affect fish and other biota due to direct and indirect effects. Direct effects include physiological effects on growth and maturation, behavioural effects that alter migration and distribution, and displacement effects brought about by alteration of circulation patterns that transport and disperse eggs and larvae. Indirect effects include changes in the seasonal production of planktonic crustaceans, especially copepods, which form the larval diet of most fish species, and other complex food-web effects that result from changes in prey and predator communities and that can act at all life history stages. Examples of all these types of effect can be found in the North Sea, but because the variety and complexity of the processes (and their interactions) defy a concise, balanced review, the examples presented in the following sections are inevitably selective and partial.

### 8.4.3 Growth, Phenology and Behaviour

Atlantic cod *Gadus morhua*, being widely distributed, common and harvested both in the wild and in aquaculture is probably the most intensively studied marine fish species. Growth of cod has been shown to depend, among other factors, on food supply and temperature (Bjornsson et al. 2001). When food is not limited, the temperature producing the highest growth rate varies from >12 °C for juvenile fish (body mass <100 g) to <7 °C for adult fish (body mass <5000 g) (Brander 2010). This pattern of change in optimal temperature for growth with body size is due to changing metabolic constraints and means that the same change in temperature can cause both a reduction in growth rate of one life history stage and an increase in another. When food is limited, optimal growth occurs at lower temperatures.

Changes in phenology and growth are linked. Seasonal variations in otolith zone formation have been used to show how changes in temperature in the southern North Sea from 1985 to 2004 affected both phenology and growth of cod. Translucent otolith zones occur up to 22 days earlier in warm than in cold years and appear to be indicative of the onset of metabolic stress that results in slower growth

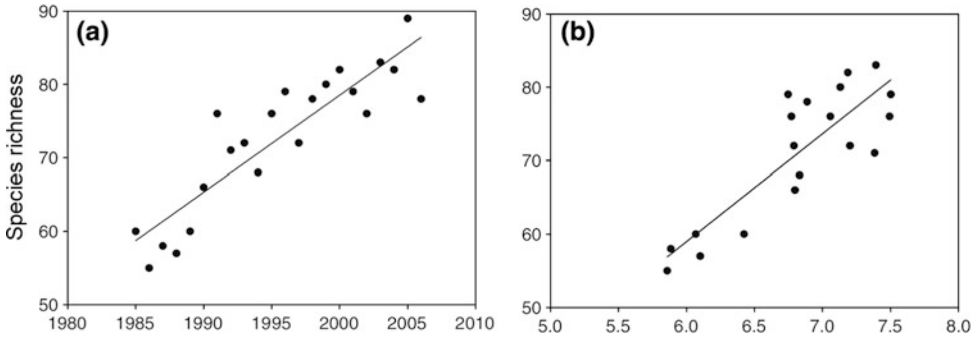

**Fig. 8.7** Change in North Sea fish species richness. **a** Total number of species increases with time. **b** Total number of species increases with temperature (Hiddink and ter Hofstede 2008)

(Millner et al. 2011). Although changes in available food (possibly due to seasonal mismatch in production timing) have been suggested as a possible cause of the change in translucent zone formation, experimental evidence indicates that direct temperature effects are more likely (Neat et al. 2008).

The effect of changing temperature on growth of more than 100,000 juvenile cod was investigated using a standardised annual fishing survey in the Skagerrak from 1919 to 2010 (Rogers et al. 2011). Warm springs (SST >4 °C) since 1987 led to increased growth of juvenile cod, but warm summers (SST >16 °C) resulted in reduced growth. Density-dependent effects were detected, but not at the lower population levels of recent years. Fine-scale mapping of fish densities and of local growth dynamics was required to resolve temperature and density effects.

Apart from demonstrating the value of long, detailed, standardised time series, this growth study suggests other important lessons for understanding and predicting the effects of climate. Effects of temperature on growth can be positive at one time of the year and negative at another, particularly where seasonal variability in temperature is high. In the Skagerrak the negative summer effects on cod growth may eventually outweigh the positive spring effects, as temperature rises, but the speed of this will depend on whether the juvenile fish can change their location, particularly their vertical distribution, in order to remain in cooler (deeper) water.

Information collected using data storage tags from eight regions of the North Atlantic shows that cod can tolerate a wide thermal range (typically 12 °C within a stock range) and have sophisticated behavioural thermoregulation. Cod from north of 57° 30′N in the North Sea experienced a range of temperature between 5.5 and 14.5 °C but south of this latitude the range experienced was much wider spanning from 2.3 to 19.5 °C. The temperature range in the southern North Sea is much wider than in the northern North Sea, with lower winter temperatures (Righton et al. 2010). The data storage tags showed that cod in the southern North Sea remained in water above their optimal temperature for growth during the summer, even when there was cooler water nearby, which some fish moved into (Neat and Righton 2007).

The growth rates of co-occurring juveniles of two flatfish species, common sole *Solea solea* (a warm-temperate species) and plaice *Pleuronectes platessa* (a cool-temperate species) responded differently to the effect of rising temperature in the southeast North Sea between 1970 and 2004 (Teal et al. 2008). Warmer winter temperatures significantly lengthened the growing period of juvenile sole but not of plaice and warmer summer temperatures increased the growth rate of sole and, to a lesser extent, plaice. From July to September there was evidence of food-limited growth; thus a reduction in food production in the nursery areas (whether due to increased temperature or other factors such as oxygen limitation) could result in further reduction of growth rates.

Four out of seven sole stocks around the British Isles, including those in the east-central and southern North Sea, showed a significant trend towards earlier spawning over the 40-year period 1970 to 2010, with peak timing of spawning advancing by 1.35 ± 0.19 weeks for every 1 °C rise in winter temperature (Fincham et al. 2013). This shift in phenology is at roughly the same rate as the change observed in cod zone formation.

Growth of haddock *Melanogrammus aeglefinus* in the North Sea seems to have responded to increasing temperature during the period 1970 to 2006, with faster growth rate, a smaller asymptotic size and earlier maturation (Baudron et al. 2011). This may affect the productivity and reproduction of the stock. An extension of this analysis to include seven other North Sea fish species also showed an overall decline in asymptotic size (Baudron et al. 2014), but half of the decline in asymptotic size took place prior to 1988, during a period when temperature declined, suggesting that other factors are at work such as food limitation (as previously mentioned for plaice and sole).

### 8.4.4 Distribution

Changes in distribution are often thought of as movements of a population brought about by migration, as ecological conditions become less favourable. In the extreme the original stocks or species occupying an area may be imagined moving out and another set moving in. This process clearly does not apply in the case of rooted plants or sessile organisms, which cannot move, and migration probably makes only a limited contribution to observed distribution shifts in fish. For example, genetic and meristic information shows that the European anchovy population expansion in the North Sea since the mid-1990s is due to increasing abundance of a relict North Sea population and not to a northward shift of southern conspecifics from the western English Channel and Bay of Biscay (Petitgas et al. 2012). Changing ecological conditions that affect growth, maturation, survival and reproductive output result in distribution shifts over time, due to population increase or decline within a given area. Nevertheless, there are also many examples of species being detected where they had never occurred before and these obviously require invasion either by passive transport during planktonic stages or by migration of juvenile and adult fish (Quero et al. 1998; Brander et al. 2003). Since most of the North Sea has existed for less than 10,000 years all fish species are relatively recent immigrants.

Forty-five years of annual international standardised scientific trawl surveys provide detailed information on the distribution of fish throughout the whole North Sea.[1] Other national scientific data sources go back to the early 20th century, as do detailed statistics of commercial catch and effort, thus including periods of cooling as well as warming. Most fish species have exhibited northerly shifts in mean latitude and/or movements into deeper water over the past thirty years. Boundary shifts occurred in half of the species with northerly or southerly range margins in the North Sea and all but one shifted northward. Species with northward-shifting distributions had faster life cycles and smaller body sizes than non-shifting species (Perry et al. 2005). The shifts in latitude or into deeper water were correlated with variations in temperature estimated from measurements carried out during the same surveys and implied that shifting species remained within a constant temperature range (Beare et al. 2004; Heath et al. 2012). The landings distributions of cod, saithe *Pollachius virens*, haddock, European hake *Merluccius merluccius*, and European seabass all showed northward shifts of 25–50 km decade$^{-1}$ between the 1970s and 1990s however these are the result of several interacting factors in addition to climate.

A detailed study of the changing distributions of plaice and sole since 1923 using a combination of research survey and commercial catch data shows contrasting patterns. The sole distribution shifted north from the 1920s to 1960 and then south, whereas plaice shifted north from 1947 onwards. Depth distributions also changed in opposite directions (see Fig. 8.8).

The distribution shift in plaice was attributed to climate change rather than fishing, but the sole distribution was influenced by both climate and fishing. However other factors including eutrophication, prey availability and habitat modification probably also need to be considered. There has been a remarkable westward jump in the plaice distribution since the late 1980s, apparently reflecting a collapse of the population in the east-central North Sea and increased abundance off Scotland (Engelhard et al. 2011). A similar analysis of changes in North Sea cod since 1912 (Engelhard et al. 2014) shows that their distribution shifted northward, but only since the late 1990s, and can be related to temperature. A major west to east shift in cod distribution from the early 1980s to 2000 can be related to fisheries-induced reduction in stock biomass rather than climate.

Red mullet *Mullus surmuletus* was not caught in research trawl surveys prior to the late 1980s but has become common in the north-eastern North Sea and also the Skagerrak (Fig. 8.9). This distribution pattern probably indicates that it has migrated into the North Sea from the north. There is some evidence that it migrates northward in winter to avoid the colder water in the southern North Sea (Beare et al. 2005).

The effects of climate and fishing interact to change the structure of fish communities. The scale of industrial (forage fish) fisheries in the North Sea has resulted in a fish community with fewer predatory fish compared to areas such as the Celtic Sea. Fish production in the North Sea is more strongly coupled to zooplankton production than is the case in the Celtic Sea and so it is likely that the effects of climate on North Sea fish are primarily via trophic links to the lower end of the food chain (Heath 2005). In this context the effects of climate change on lesser sandeel *Ammodytes marinus* may be particularly critical, since it is a non-migratory species that is very dependent on the availability of coarse sandy substrate (Heath et al. 2012).

### 8.4.5 Recruitment

Climate is one of the factors regulating recruitment of fish in the North Sea. It has been shown to influence many species, including cod, sole, plaice and herring. Temperature generally has a positive effect on recruitment of cod stocks at the cold end of their latitudinal range and a negative effect on warm-water stocks, including the North Sea stock (Planque and Fredou 1999). The relation has been shown using different statistical stock-recruitment models (Olsen et al. 2011; Ottersen et al. 2013) and is thought to be responsible for the series of high recruitment during the cold period of the 1960s and early 1970s (O'Brien et al. 2000; Brander and Mohn 2004), contributing also to the 'gadoid outburst' of the late 1960s to mid-1980s, when productivity of cod and other demersal stocks was extraordinarily high (Cushing 1984; Rijnsdorp et al. 2010). Cod recruitment has been low during recent warm years and the stock biomass may remain low unless cooler conditions return (Olsen et al. 2011).

Direct physiological effects of temperature on cod (particularly growth) have already been described. The temperature effect on recruitment is mediated through survival during the planktonic and early life stages and is probably due to a combination of direct and indirect effects. Production of a sufficient supply of the right sizes and quality of zooplankton prey, in particular the cool-temperate copepod *Calanus finmarchicus*, at the right time of year affects cod survival and recruitment (Beaugrand et al. 2003; Mieszkowska et al. 2009). Climate-related changes in spring SST and copepod abundance have consequences for the spatial patterns of recruitment in the North Sea (Nicolas et al. 2014) and probably for adult distribution as well.

Herring in the North Sea have experienced two periods of weak recruitment during recent decades. Poor recruitment during the period 1971–1979 has been ascribed to low

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[1] http://ices.dk/marine-data/data-portals/Pages/DATRAS.aspx.

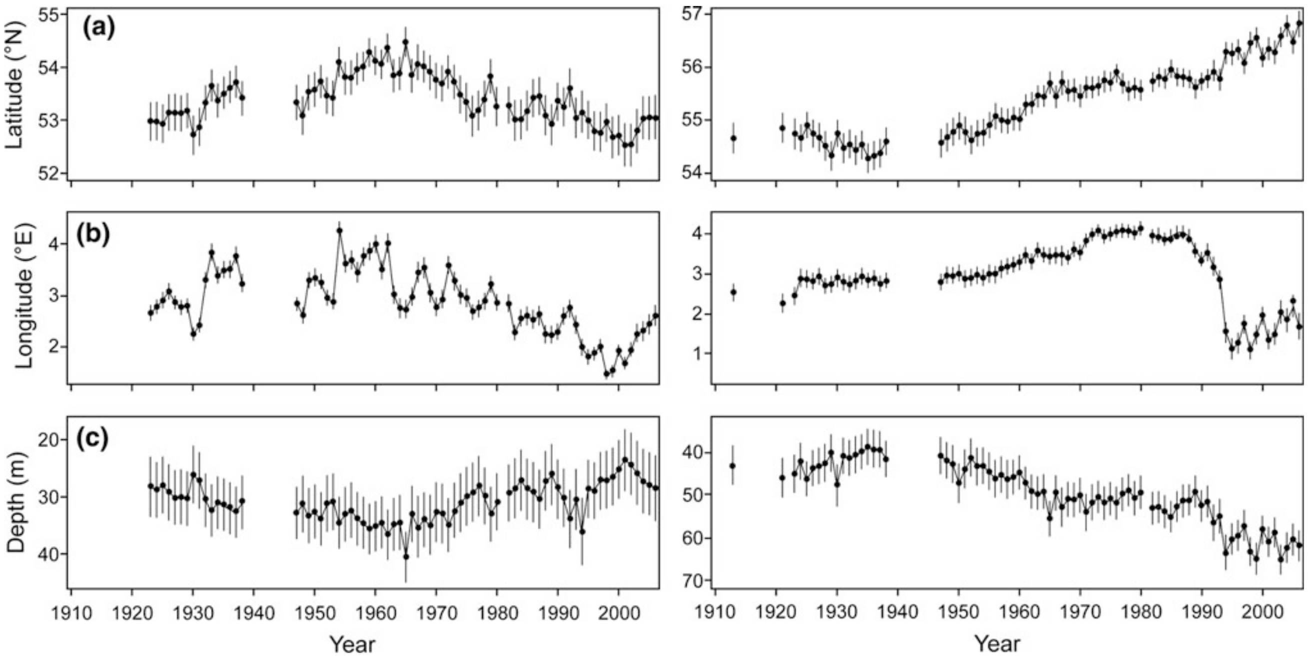

**Fig. 8.8** Long-term changes in **a** latitude **b** longitude and **c** depth of North Sea sole (*left panels*) and plaice (*right panels*) using weighted mean catch-per-unit-effort (vertical bars are standard error of means) (Engelhard et al. 2011)

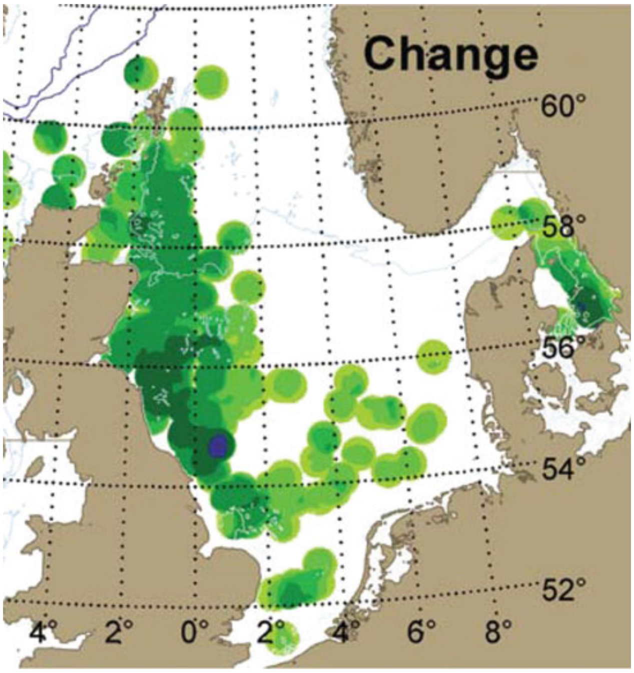

**Fig. 8.9** Change in abundance of red mullet in first-quarter research surveys. The *darker the colour*, the greater the increase in abundance in the period 2000–2005 relative to 1977–1989 within each ½° latitude ×1° longitude rectangle (ICES 2008)

spawning biomass and insufficient egg production, however, recruitment to the central and northern populations may also have been affected by reduced Atlantic inflow into the north-western North Sea, resulting in unfavourable environmental conditions (Corten 2013). A second, continuing period of weak recruitment began in 2002, when the adult population was large and exploitation low. This is ascribed to the warming of the North Sea and substantial changes in the zooplankton community described earlier in this chapter (Payne et al. 2009, 2013) which resulted in lower growth rates of larvae and hence probably lower survival. The North Sea herring population consists of several spawning components and recruitment is the sum of the survivors of many spawning events, with different spawning grounds and timing, experiencing different environmental conditions (Hjøllo et al. 2009; Rijnsdorp et al. 2009). It is therefore naïve to search for single environmental drivers; spatial and temporal differences must be taken into account, as must the influence of parental factors (Dickey-Collas et al. 2010).

It is paradoxical that recruitment of both sole and plaice is higher following cold spring conditions (Ottersen et al. 2013), since plaice is close to the warm end of its range in the North Sea and sole is close to the cold end of its range. Cold temperatures in March delay spawning in sole, but it is not known whether recruitment is determined during the pelagic egg and larval stages, or during the early demersal stage (van der Land 1991; Kjesbu et al. 1998; Rijnsdorp and Witthames 2005).

For plaice the higher survival during colder winters is probably related to mortality of their predators during both the pelagic and early demersal stages (Van der Veer et al.

2009). Temperature may also affect the transport of the pelagic egg and larval stages, thus influencing the proportion of larvae reaching coastal nursery grounds (Van der Veer et al. 1998; Bolle et al. 2009). Available habitat for plaice in the North Sea may be reduced with climate change (Petitgas et al. 2013).

### 8.4.6 Prediction

The North Sea is one of the few areas where it is possible to compare several models of the effects of climate change on fish distribution and to test them against detailed long time series of actual distribution change. Three 'climate envelope' models (AquaMaps, Maxent, and the Sea Around Us project model) were used to project distributions of 14 North Sea fish species, based on data on existing distributions in relation to a range of environmental parameters, with some 'expert guidance' to exclude areas where the species were known not to exist (Jones et al. 2012). The three approaches produced predictions of relative habitat suitability which were reasonable given the occurrence data of each species. However, this analysis does not indicate whether there are differences in the capabilities of each model to expose specific features of the distribution, such as the pattern of relative habitat suitability (Jones et al. 2012).

Uncertainties arise from differences in data-types used, parameterisation and model structure. A multi-model ensemble approach is essential to project distribution ranges. It is evident that there can be an almost limitless number of factors and interactions influencing distribution ranges that are not included in the list of environmental variables in the box (e.g. substrate type, parasites, essential trophic links, oxygen). In the North Sea the dynamics and hydrographic characteristics of inflows from the English Channel, western European Shelf, Norwegian Sea and Baltic Sea have a huge bearing on the potential for species to invade and survive.

The experience of trying to determine the causes of observed changes in fish distributions in the North Sea is valuable because it shows how difficult this can be. The availability of good long-term data tends to show that simple hypotheses (e.g. fish move north when it gets warmer) are incorrect or incomplete. The effects of fish behaviour, genetic adaptation, habitat dependency and the impacts of fishing, result in complex responses that are not explained by simple climate envelope predictions. This point is well illustrated by a recent study that analysed research survey data from 33 years of summer (69 1° × 1° rectangles) and winter (84 1° × 1° rectangles) trawl surveys for the ten most abundant demersal species in the commercial fisheries (Rutterford et al. 2015). General additive models (GAMs) trained on ten-year time periods early in the series can reliably predict later periods for most species using seasonal temperatures, depth and salinity, with co-varying habitat variables also important. The result of coupling these GAMs with projections of North Sea ocean climate for the next 50 years suggests that future distributions of most of the ten current major demersal species will be constrained by the availability of habitat of suitable depth, leading to pronounced changes in community structure, species interactions and fisheries potential for these species. Rutterford et al. (2015) advised caution when applying process-based model projections of distributional shifts, and proposed that interpretations should be informed by data-driven modelling approaches, especially when using predictions for policy and management planning.

Ocean acidification will undoubtedly affect fish in the North Sea, however the nature and time-scale of these effects is difficult to predict. The early life stages of fish are probably more sensitive and vulnerable to acidification, but the main impacts may be indirect, through changes in other more sensitive taxa and in the productivity and structure of the lower trophic levels. Calcifying planktonic organisms are likely to be affected by the end of the 21st century but the direct effect on fish sensory systems may also cause subtle behavioural changes with possible population-level implications (Wittmann and Pörtner 2013).

### 8.4.7 Climate and Fish Fauna in the Dutch Wadden Sea

The previous sections mainly relate to the open North Sea, and the impacts of climate change on fish may be different in the shallow southern parts such as the Wadden Sea, a nursery area for many fish species, including several commercially fished stocks. The relatively warm water, rich food supply and possibilities to hide from predators provide a safe haven for young fish of species such as plaice, sole, whiting *Merlangius merlangus*, herring, and sprat *Sprattus sprattus*. The adults often spawn further offshore in the North Sea and the eggs and/or larvae drift with the currents towards the coast and into the Wadden Sea (Bolle et al. 2009; Dickey-Collas et al. 2009). Here they can grow rapidly, feeding on invertebrates or plankton. During the first years of life they show seasonal migrations: spending the growing season inside the Wadden Sea and moving to the deeper waters in the North Sea in winter. Besides its role as a nursery area, the Wadden Sea is also home to resident fish species and provides feeding habitat and passage to migrants and seasonal visitors.

Pronounced changes have taken place in the biomass of demersal fish in the Dutch Wadden Sea since monitoring started in 1960–1970. In particular, the marine juvenile guild shows a dome-shaped pattern in abundance, with an increase from the start of the time series, peaking in the 1980s and decreasing towards the present. The role of the Dutch Wadden Sea as a nursery area seems to have changed considerably, a pattern which is most prominent in plaice but also apparent in some other flatfish species. The densities of 0-year old plaice have strongly reduced since the mid-1980s to a stable and low level that has not changed since 2000. The period in which they use the area has also changed: instead of staying from early spring until October, they now tend to disappear in July/August. The 1- and 2-year olds have disappeared completely since the end of the 20th century.

Although several mechanisms may be operating, climate change is a likely cause of these alterations. Using dynamic energy budgets, Teal et al. (2012) showed that the most likely explanation for the recent loss of the nursery function, especially for plaice, is that increased temperatures make coastal areas unsuitable for growth. Growth rate data for 0-year old plaice showed that recent higher summer temperatures result in metabolic activity raised to levels at which food becomes limiting (Teal et al. 2008).

In contrast to the decline observed in overall biomass, dominated by marine juveniles, the resident species show an increase followed by a stable period in the coastal area. However, understanding of the mechanisms acting on the different resident species is still very limited. One exception is the discovery that the decline observed in eelpout *Zoarces vivparus* in the Wadden Sea since 1985 is due to an increase in temperature above the thermal maximum of the species, causing thermally limited oxygen delivery (Pörtner and Knust 2007).

Thus, the mechanisms underlying the large changes observed in the fish fauna of the Wadden Sea are still largely unknown. They are certainly partly climate related, but the impacts of changes in food, predators and abiotic factors acting on the different life stages are still poorly understood (Rijnsdorp et al. 2009).

## 8.5 Seabirds

Predicting the effects of climate variability on and through the different trophic levels is a major challenge, and one that increases in complexity at successively higher levels of the food web (Myksvoll et al. 2013). Seabirds are typically at the top of the marine food web and are the most numerous and visible of marine top predators. Furthermore, they are considered important indicators of the state of the marine ecosystem (Piatt and Sydeman 2007; Wanless et al. 2007). Worldwide, seabirds have declined faster than terrestrial bird groups with comparable numbers of species (Croxall et al. 2012), with most trends consistent with climate change (Poloczanska et al. 2013).

Seabirds can be affected by changing climate both directly, for example, if extreme weather becomes more frequent, or indirectly, through changes in their food supply. There is a substantial body of evidence suggesting that in most cases indirect effects are the more important of the two, with fluctuations in seabird demography and population dynamics caused in part by climate fluctuations acting through the availability and distribution of food. Effects of climate on life history traits have been documented across many species and populations (Sandvik and Erikstad 2008; Satterthwaite et al. 2012) including black-legged kittiwakes *Rissa tridactyla* (Aebischer et al. 1990; Furness and Tasker 2000) and (northern) fulmars *Fulmarus glacialis* (Thompson and Ollason 2001) in the North Sea.

### 8.5.1 Trends in Number of Breeding Birds

Seabird populations in the North Sea have shown strong changes in most species over recent decades. While populations may have been at a historic low in the early decades of the 20th century, most species strongly increased in the latter half of the 20th century (e.g. Mitchell et al. 2004; Mendel et al. 2008). The relaxation of persecution, egg collection and exploitation are probably the most important factors underlying these increases at least initially (Camphuysen and Garthe 2000). Commercial fisheries, especially through the vast amounts of discards and offal (Garthe et al. 1996), and overfishing of predatory fish (Furness 2002) are also likely to have been major drivers. Seabird population trends have developed differently since the end of the 20th century and many populations are now in decline, while others are relatively stable and some show increasing abundance (Fig. 8.10). The reasons for these trends are difficult to quantify, but ongoing changes in fisheries practice and climate-related changes are likely to be involved.

### 8.5.2 Case Studies Highlighting Climate Impacts on North Sea Seabirds

*Case Study 1: The role of changes in oceanography and industrial fisheries in the decline of black-legged kittiwakes*. In the North Sea, climate is known to affect several seabird populations through their main prey species, lesser sandeel, also called sandlance. Although Arnott and Ruxton (2002) and van Deurs et al. (2009) found this species to be sensitive to changes in sea temperature, this important forage fish is very difficult to study, and little is known about how it is affected by rising sea temperatures.

Studies indicate that in recent warmer years, birds have been struggling to find sufficient food for their chicks, because sandeels have been too few, too small, too lean, or have not been available at the right time. Several species of seabird breed later and less successfully, and survival of adult birds is also lower in warmer years (Daunt and Mitchell 2013).

Breeding success of black-legged kittiwakes in the UK, particularly at colonies along the North Sea coast, has been advocated as a reliable and sensitive indicator of the state of the marine ecosystem for those predators that are reliant on sandeel (Furness and Tasker 2000; Wanless et al. 2007). Breeding success at a given colony of black-legged kittiwakes in the UK is therefore considered to reflect some measure of sandeel availability during the period that birds are associated with the colony, and this assumption is supported by a clear regional clustering of kittiwake breeding success corresponding to the known spatial structuring in sandeel populations (Frederiksen et al. 2005).

Black-legged kittiwake populations have declined by more than 50 % since 1990, a period during which a lesser sandeel fishery was active and profound oceanographic changes occurred. Frederiksen et al. (2004b) studied the role of fisheries and oceanography in kittiwake declines on the Isle of May, southeast Scotland, where sandeels are the main prey. Breeding success and adult survival were low when the sandeel fishery was active (1991–1998) and were also negatively correlated with winter sea temperature, with a 1-year lag for breeding success. An observed improvement in breeding success from 2000 onwards has not been enough to halt the population decline. To stabilise the population, breeding success must increase to unprecedented levels or survival needs to increase substantially. Stochastic modelling indicated that the population was unlikely to increase if the fishery was active or sea temperature increased, and that the population was almost certain to decrease if both occurred. Sandeel recruitment is reduced in warm winters, and Frederiksen et al. (2004a) proposed that this explains the temperature effects on kittiwake survival and breeding success. The sandeel fishery also had a strong effect on kittiwake demographic performance, although the exact mechanism is unclear as kittiwakes and fishermen target different sandeel age groups.

*Case Study 2: Breeding success of North Sea seabirds related to copepod abundance and distribution*. The copepod *Calanus finmarchicus* is a key species for the trophodynamics of boreal ecosystems of the North Atlantic Ocean (Planque and Batten 2000). The species is a very important prey item for the small fish favoured by seabirds (Beaugrand et al. 2003). In particular, the recruitment of lesser sandeel in the North Sea is strongly positively correlated with *C. finmarchicus* abundance (van Deurs et al. 2009).

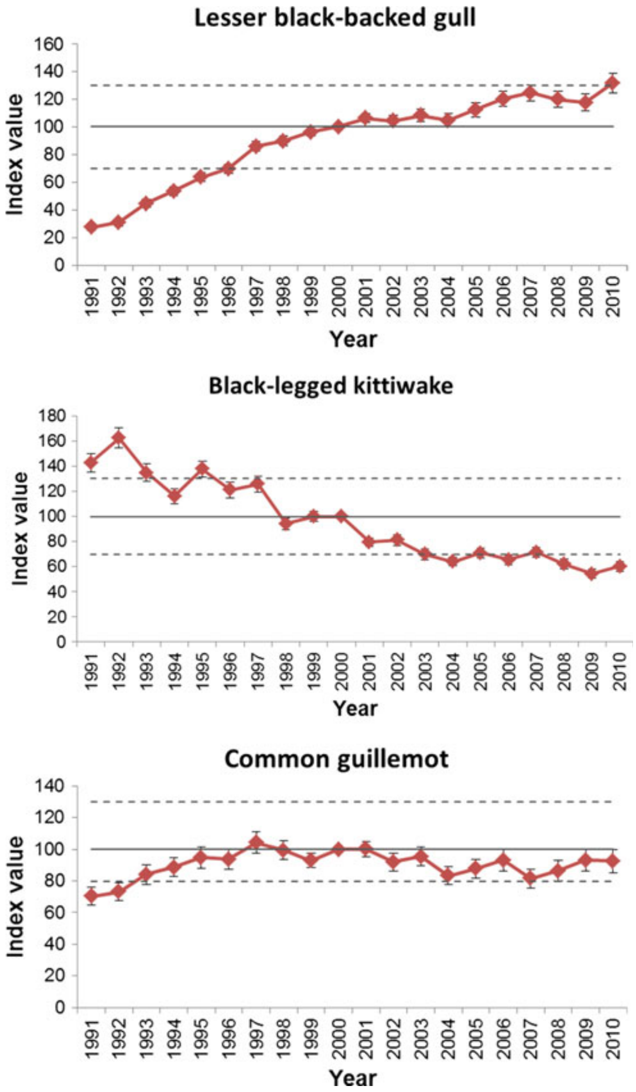

**Fig. 8.10** Contrasting population trends for three seabird species breeding in the Greater North Sea from 1991–2010 (OSPAR Region II). Year 2000 was chosen as the baseline with the index value set to 100. *Vertical lines* show standard errors. ICES (2011)

It is generally accepted that the distribution of *C. finmarchicus* in the North Atlantic reflects its thermal niche, along with advection from deep-water overwintering areas onto continental shelves such as the North Sea (Speirs et al. 2006; Helaouet and Beaugrand 2007). In accordance with recent warming, large declines in abundance of *C. finmarchicus* have occurred in the North Sea (Beaugrand et al. 2002) and low reproductive success of several forage-fish-dependent seabird species has been linked to these declines (Frederiksen et al. 2006).

If *C. finmarchicus* is not replaced by other zooplankton suitable as prey for small fish, seabird populations are likely to experience reduced breeding success, leading to further declines in population size (Frederiksen et al. 2013). Indeed, a close relative of *C. finmarchicus*, the warm-temperate *C. helgolandicus* has increased in abundance in the North Sea over recent decades as *C. finmarchicus* abundance has declined (Beaugrand et al. 2002). Nevertheless, *C.*

*helgolandicus* does not appear to be a full replacement for *C. finmarchicus* in terms of ecosystem functioning, particularly the ability to sustain large stocks of schooling, planktivorous fish (Bonnet et al. 2005). There are several reasons for this: *C. helgolandicus* are smaller, have a lower lipid content, and tend to occur at low densities early in spring when most fish larvae need access to abundant copepod prey (Beaugrand et al. 2003). Frederiksen et al. (2013) anticipated that because of these shifts in the zooplankton community resulting in declines in abundance of fish such as sandeel and the lack of obvious replacements for these as seabird prey, it is likely that breeding populations of piscivorous seabirds in the boreal Northeast Atlantic, including the North Sea will shift northwards. Consequently, the large seabird populations currently present in, for example, eastern Scotland could disappear (Frederiksen et al. 2013).

*Case Study 3: Climate impact on breeding phenology in three seabird species.* Breeding at the right time of year is essential to ensure that the energy demands of reproduction, particularly the nutritional requirements of growing young, coincide with peak food availability. Global climate change is likely to cause shifts in the timing of peak food availability, which the animals need to be able to adjust the time at which they initiate breeding. Frederiksen et al. (2004a) tested the hypothesis that regulation of breeding onset should reflect the scale at which organisms perceive their environment by comparing phenology of three seabird species at a North Sea colony. As expected, the phenology of two dispersive species, black-legged kittiwake and common guillemot *Uria aalge*, correlated with a large-scale environmental cue, the NAO, whereas a resident species, the European shag *Phalacrocorax aristotelis*, was more affected by local conditions (SST) around the colony. Annual mean breeding success was lower in years in which breeding took place later than normal for European shags, but not for the other two species. Since correlations among climate patterns at different scales are likely to change in the future, these findings have important implications for how migratory animals can respond to future climate change (Frederiksen et al. 2004a).

*Case Study 4: Climate effects on the North Sea marine food web may influence coastal ecology through seabirds.* Temperature is an important driver of the trophodynamics of the North Sea ecosystem. Recent warming, in combination with overfishing, has caused major changes in trophic interactions within the marine food web (Kirby and Beaugrand 2009). Luczak et al. (2012) studied the relation between lesser black-backed gulls *Larus fuscus graelsii* and swimming crabs (of the Polybiinae sub-family), important food species for the gulls during their breeding season. Luczak and co-workers found a related increase in sea temperature, the abundance of swimming crabs and that of lesser black-backed gulls in 21 major breeding colonies around the North Sea. Interestingly, their cross-correlation analyses suggest the propagation of a climate signal from SST through decapod larvae, adult crabs and lesser black-backed gulls with lags that match the biology of each trophic group. This is indicative of climate-induced changes in the marine fauna extending to the avian fauna, and thus to the terrestrial food web around the seabird colonies (Luczak et al. 2012).

*Case Study 5: Vulnerability of the seabird community in the western North Sea to climate change and other anthropogenic impacts*. Most seabird studies have tended to consider the impacts of single stressors on single species at specific times of the year, and so may be unrepresentative of the combined effects of pressures experienced by top predator communities over an annual cycle (Burthe et al. 2014). For marine top predators, there is evidence to suggest that interactions between climate and other threats may be additive (Frederiksen et al. 2004b; Burthe et al. 2014). Burthe et al. (2014) studied the cumulative effects of multiple stressors on a community of seabirds in the North Sea. More precisely, they examined vulnerability to climate change and other anthropogenic threats in a seabird community (45 species; 11 families) that used the Forth and Tay region (eastern Scotland) of the North Sea for breeding, overwintering or migration between 1980 and 2011. They found only 13 % of the seabird community in the Forth and Tay region to fall within the categories of low or very low population concern to future warming, whereas in considering multiple anthropogenic threats 73 % of the species in this bird community were considered to be of high or very high population concern for the future (Burthe et al. 2014).

*Case Study 6: Effects of extreme climatic events on coastal birds breeding in low-lying saltmarshes* (for a more extensive review see Chap. 9). Van de Pol et al. (2010) investigated whether the frequency, magnitude and timing of rare but catastrophic flooding events have changed over time in Europe's largest estuary, the Wadden Sea. They subsequently quantified how this had affected the flooding risk of six saltmarsh nesting bird species (both seabird species and coastal species). Maximum high tide has increased twice as fast as mean high tide over the past four decades, resulting in more frequent and more catastrophic flooding of nests, especially around the time when most eggs have just hatched. By using data on species' nest elevations, on the timing of egg-laying and on the length of time that the eggs and chicks are at risk from flooding, van de Pol et al. (2010) showed that flood risk increased for all six species (even after accounting for compensatory land accretion) and that this could worsen in the near future if the species do not adapt. This study provides the first evidence that increasing flooding risks have reduced the reproductive output below stable population levels in at least one species, the Eurasian oystercatcher *Haematopus ostralegus*. Sensitivity analyses show that birds would benefit most from adapting their nest-site selection to higher areas. However, historically the lower saltmarsh has been favoured for its proximity to the feeding grounds and for its low vegetation, aiding predator detection. Van de Pol et al. (2010) concluded that it is more difficult for birds to infer that habitat quality has decreased from changes in the frequency of rare and unpredictable extreme events than from trends in climatic means. The result is, at present, that the lower parts of the saltmarsh may function as an ecological trap.

### 8.5.3 Concluding Comments

The Case Studies clearly indicate that climate change influences North Sea seabirds. While this may be true for population developments in some species, it is more obvious for demographic parameters such as the number of chicks hatched and/or fledged and survival rates of adults and young birds. The breeding phenology of several seabird species is also affected (e.g. Frederiksen et al. 2004a). For migrating landbirds air temperature is often the main climate factor (e.g. Cotton 2003). In contrast, temperature changes usually act indirectly on seabirds via changes in the ecosystem, mainly through food supply (Wanless et al. 2007; Frederiksen et al. 2013). However, there may also be direct effects of temperature on seabirds as air and water temperatures may influence energetic costs for birds in maintaining body temperature (e.g. Fort et al. 2009). With generally increasing temperatures this may lead to northward trends for breeding and wintering in some species (Huntley et al. 2007). Northward shifts, probably out of the North Sea, may also result from changes in zooplankton community structure acting through main prey species like sandeel (Frederiksen et al. 2013).

Analyses of possible relationships between climate factors and seabirds are often impeded by difficulties in differentiating between natural variability and anthropogenic factors, thus complicating analyses on direct and indirect effects (Burthe et al. 2014). This is especially true for changes in fisheries practice that include overfishing of predatory fish, production of discards and offal, and direct mortality through fishing gear (reviewed by Tasker et al. 2000).

Some of the many ways in which seabirds respond to climate change were summarised by the International Council for the Exploration of the Sea (ICES 2008) as follows (see also Table 8.3):

- a warming trend may advance the timing of breeding in some species and delay it in others
- seabirds exhibit some flexibility in the timing of breeding, but are ultimately constrained by the often long reproductive period (up to five months from egg-laying to chick-fledging)
- seabirds are long-lived and so often able to ‘buffer’ short-term (<10 years) environmental variability, especially at the population level
- seabirds are vulnerable to both spatial and temporal mismatches in prey availability, especially when breeding at fixed colony sites with restricted foraging capacities (e.g. foraging distance, diving capacity).

## 8.6 Marine Mammals

### 8.6.1 Climate Change Impacts on Marine Mammals

All organisms display tolerance limits that, when exceeded, lead to negative impacts on metabolism, growth, and reproduction, or even death. Endothermic (i.e. ‘warm-blooded’) organisms such as marine mammals must maintain a relatively constant body temperature, and changes in the ambient temperature outside their preferred range therefore require additional expenditures of energy. If ambient temperatures become too high or too low to maintain body temperature within tolerable limits, adverse effects are likely (Howard et al. 2013). Thus, increasing severity of extreme weather events or changes in average winter or summer temperatures can have negative impacts on endothermic marine species, and repeated mortality events resulting from thermal stress can lead to population decreases (Howard et al. 2013).

In addition to the direct physiological temperature effect, climate change is also expected to affect marine mammals indirectly. This may be through changes in temperature, turbulence and surface salinity inducing productivity shifts at different trophic levels, shifts that can flow up the food web and affect prey availability for top predators. Marine mammals typically exploit patchy prey species that they require in dense concentrations and so their distributions tend to reflect those oceanographic features, both static (e.g. depth and slope) and more mobile (e.g. fronts and upwelling zones), where productivity is high.

Other important indirect pathways by which climate change may affect marine mammals include changes in critical habitats (due to warming) and in nesting and rearing beaches (due to sea-level rise) and increases in diseases and biotoxins (due to rising temperatures and shifts in coastal currents) (Simmonds and Isaac 2007; Howard et al. 2013). Populations may become more vulnerable to climate change owing to interaction with non-climate stressors resulting from human activities, such as pollution and fishing (Howard et al. 2013).

**Table 8.3** Examples of links between climate variables and seabird behaviour (including distribution and condition) in the North Sea

| Seabird parameter | Species | Region | Climate variable | Sign of correlation with warming |
|---|---|---|---|---|
| Breeding range | Lesser black-backed gull | UK | Sea temperature | Positive |
| | Northern gannet | UK | Sea temperature | Positive |
| Non-breeding range | Lesser black-backed gull | UK | Sea temperature | Positive |
| Reproductive success | Northern fulmar | Orkney | NAO index | Negative (hatching), positive (fledging) |
| | Black-legged kittiwake | Isle of May | Sea temperature | Negative |
| | Black-legged kittiwake | Orkney, Shetland | Sea temperature | Negative |
| Annual survival | Northern fulmar | Orkney | NAO index | Negative |
| | Black-legged kittiwake | Isle of May | Sea temperature | Negative |
| | Atlantic puffin | North Sea | Sea temperature | Negative |
| Population change | Black-legged kittiwake | Isle of May | Sea temperature | Negative |
| Nesting date | Black-legged kittiwake | Isle of May | NAO index | Positive |
| | Common guillemot | Isle of May | NAO index | Positive |
| | Common guillemot | Isle of May | Sea temperature | Negative |
| | Razorbill | Isle of May | Sea temperature | Negative |
| | European shag | Isle of May | Wind | Negative |
| Foraging cost | Common guillemot | Isle of May | Stormy weather | Positive |
| | Northern fulmar | Shetland | Wind speed | Negative |

ICES (2008)

Macleod (2009) predicted that certain characteristics put some marine mammal species at greater risk from climate-induced changes than others. These include a distribution range that is restricted to non-tropical waters (including temperate species) and a preference for shelf waters (like the North Sea). Conversely, the more mobile (or otherwise flexible) marine mammal species may, to some extent, be able to adapt to climate change (Simmonds and Isaac 2007).

### 8.6.2 Distributional Shifts in Harbour Porpoise

The harbour porpoise *Phocoena phocoena* inhabits coastal or shelf waters of the northern hemisphere. It is the most abundant cetacean species in the North Sea region (Hammond et al. 2008) and its abundance on the European Atlantic continental shelf was estimated to be around 375,000 in 2005 (Hammond et al. 2013). In the shallow southern North Sea the number of harbour porpoises appears to have increased since the early 1990s (Hammond et al. 2002; Camphuysen 2004; Camphuysen and Peet 2006; SCANS II 2008), however, although still common, numbers in the northern North Sea have declined (SCANS II 2008; Øien 2010; Evans and Bjørge 2014). The reasons for this are not known, but a major distributional shift appears to have taken place from the north-western North Sea in 1994 to the south-western part in 2005 (Hammond et al. 2002, 2013; Fig. 8.11).

The harbour porpoise is a species with high energetic demand, especially as mature females are pregnant and lactating at the same time during most of the year. It is very likely that food availability is a major criterion for habitat selection (Gilles 2009). The shift in distribution shown in Fig. 8.11 may be due to an increase in herring abundance in the southern North Sea (Hammond et al. 2013) but the increase in herring abundance cannot simply be related to higher temperatures, since herring in the southern North Sea are already at the warm boundary of their distribution.

There may, however, be other ways that increasing temperature may affect harbour porpoises. MacLeod et al. (2007) reported that in the Scottish part of the North Sea this species consumed a significantly smaller proportion of sandeels in spring 2002 and 2003 in comparison with their baseline period (1993–2001). Furthermore, in the baseline period only 5 % of the stranded porpoises examined had died of starvation, whereas starvation was the cause of death of 33 % from 2002 and 2003. MacLeod et al. (2007) showed that a lower proportion of sandeels in the diet of porpoises in spring increases the likelihood of starvation. The reduced proportion of sandeels in the porpoise diet is likely to have been because sandeel spawning stock biomass (SSB) and recruitment in the North Sea were substantially lower in 2002 and 2003 than during the baseline period. Fishing is probably the main cause of the decline in sandeel but high winter sea temperatures also tend to reduce their recruitment (Arnott and Ruxton 2002). It follows that climate-induced warming may be the ultimate cause of poor body condition

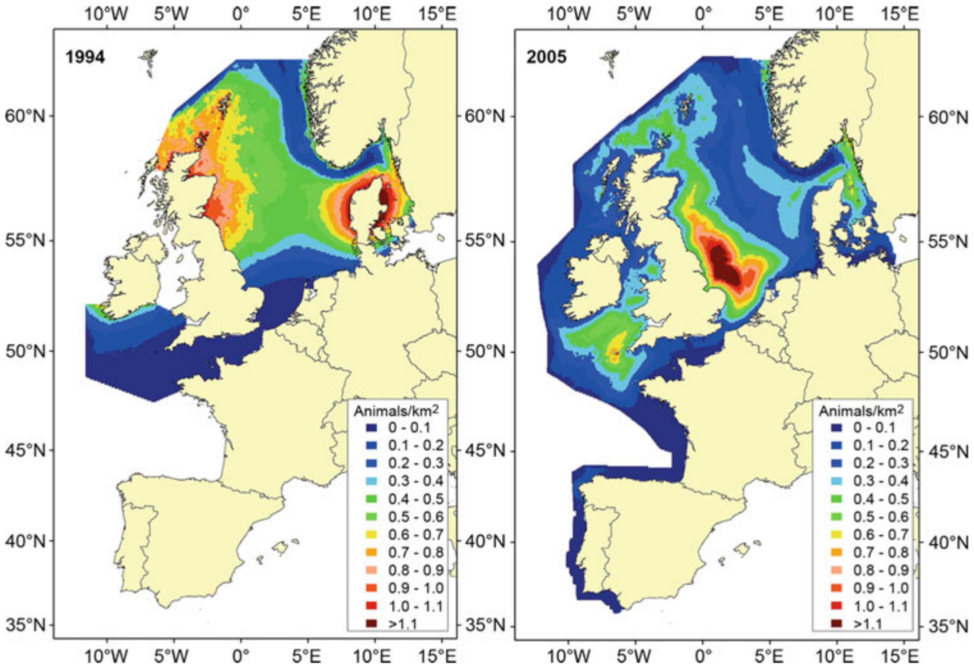

**Fig. 8.11** Predicted density surface for harbour porpoises in 1994 and 2005 (SCANS and SCANS II surveys; Hammond et al. 2013)

of harbour porpoises in Scottish North Sea waters, resulting in an increased likelihood of starvation (MacLeod et al. 2007).

### 8.6.3 Rising Temperatures Favour Warm-Water Dolphins

There is evidence of recent changes in range expansion for several dolphin species in the North Sea region. One such case is the (common) bottlenose dolphin *Tursiops truncatus*, off the northeast coast of Scotland. Here they are at the northern limit of their distribution. The causes behind this increase in distribution are still unknown, but may be related to changes in abundance and/or distribution of prey (Wilson et al. 2004; Learmonth et al. 2006), which may also be linked to climate change.

Another species reported to have exhibited recent range shifts is the white-beaked dolphin *Lagenorhynchus albirostris*; Fig. 8.12). This is a species distributed mainly in cold temperate to Arctic waters. In the North Atlantic they are limited to high latitudes (Evans et al. 2003; MacLeod et al. 2005; Baines et al. 2006; Evans and Smeenk 2008). They are among the most abundant delphinid species in the North Sea in summer; sightings are much rarer during winter. Stranding records have shown a significant increase of the species in the southern North Sea since the 1960s. During recent decades they have regularly been detected in the Southern Bight (Bakker and Smeenk 1987; Kinze et al. 1997; Camphuysen and Peet 2006). However, these changes need not be directly related to changes in sea temperature, but may simply reflect natural or human-induced alterations in particular fish stocks that are favoured prey of the species.

Recent changes in the cetacean community around the British Isles, including the northern North Sea, have been related to increasing local water temperature. (Short-beaked) common dolphin *Delphinus delphis* is a warm-temperate species, commonly found in tropical waters and only sporadically in the North Sea. Over recent years common dolphins have been quite regularly seen in the North Sea even in winter (Sea Watch Foundation, unpubl. data; Evans and Bjørge 2014). This may reflect the expanding range of typically warmer water fish species like anchovy and sardine (ICES 2008; Evans and Bjørge 2014).

However, this northward expansion of common dolphin habitat into the northern North Sea is not necessarily due to global climate change. There were both strandings and sightings in that region during the 1980s and a peak in the number of strandings on the North Sea shores of the UK was reported as far back as the 1930s (Fraser 1946) and along the Dutch coast in the 1940s (Bakker and Smeenk 1987; Camphuysen and Peet 2006). These changes in common dolphin distribution may reflect climatic fluctuations on interdecadal scales, such as caused by the Atlantic Multidecadal Oscillation.

White-beaked and common dolphins have similar habitat and diet preferences. It has been suggested that the two species might partition their otherwise shared niche according to temperature to reduce the potential for competition at this time of year (Macleod et al. 2008). As temperature seems to be important in determining the relative distribution of these species, the range of the white-beaked

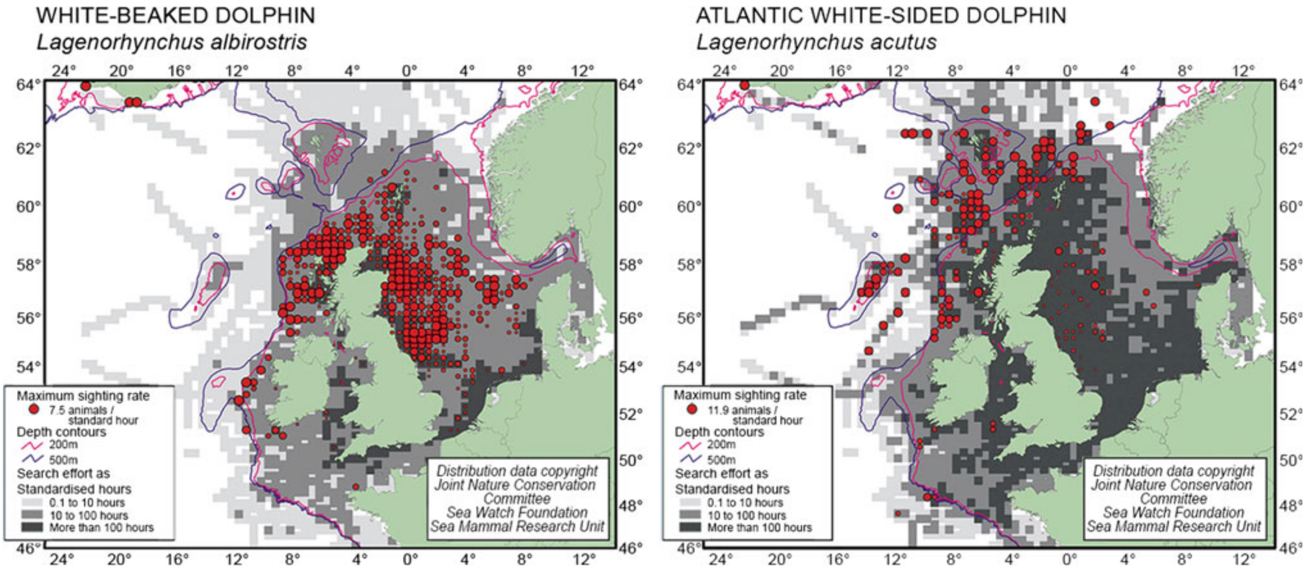

**Fig. 8.12** Distribution, relative abundance and associated effort for white-beaked dolphin and Atlantic white-sided dolphin (Reid et al. 2003)

dolphin might be expected to contract in response to rising sea temperature, while that of the common dolphin may expand (Macleod et al. 2008).

Off north-west Scotland (Macleod et al. 2005) the relative occurrence and abundance of white-beaked dolphins has declined and that of common dolphins increased in comparison to previous studies, suggesting a decrease in range of the former and increase of the latter. This may be due to competitive exclusion, as suggested in the previous paragraph, or direct effects of changes in temperature. Independent of the mechanisms, if temperature increase continues some formerly abundant cold-water species, such as white-beaked dolphins and Atlantic white-sided dolphins (*Lagenorhynchus acutus*; Fig. 8.12) may be displaced, in particular from the northern North Sea, by species like the short-beaked common and striped dolphin *Stenella coeruleoalba* (MacLeod et al. 2005; Learmonth et al. 2006; Evans and Bjørge 2014). The white-beaked dolphin, which favours shelf habitats, may be placed under increased pressure if it loses the north-west European continental shelf from within its range (Evans and Bjørge 2014).

### 8.6.4 Exotic Visitors to the North Sea

A number of warm-water species have in recent decades been recorded for the first time in UK waters, including the North Sea. This includes Blainville's beaked whale *Mesoplodon densirostris* (1993), Fraser's dolphin *Lagenodelphis hosei* (1996), and dwarf sperm whale *Kogia sima* (2011), while ten of eleven strandings of pygmy sperm whale *Kogia breviceps* in Britain and Ireland have occurred since 1980 (Evans et al. 2003; Deaville and Jepson 2011). Between January and April 2008 there were 18 strandings in Wales, Scotland, and Ireland of another typically warm-water species, the Cuvier's beaked whale *Ziphius cavirostris* (Dolman et al. 2010). Although these strandings may not be directly related to climate change, they occurred much further north than would be expected for these species, and generally at times of the year when sea temperatures are at their highest. However, care should be taken in drawing conclusions from such a limited number of records of vagrants (Evans and Bjørke 2014).

If the warming continues, more visits of warm-water vagrants to north-west Europe are to be expected. Likely species include Bryde's whale *Balaenoptera edeni*, pygmy sperm whale, dwarf sperm whale, rough-toothed dolphin *Steno bredanensis*, and Atlantic spotted dolphin *Stenella frontalis*. Baleen whales, like humpbacks *Megaptera novaeangliae* and fin whales *Balaenoptera physalus*, that normally move southwards in winter to warmer waters to breed, may increasingly do so within the waters around the UK, some even in the North Sea (Evans and Bjørge 2014).

### 8.6.5 Effect of Climate Change on Seals in the North Sea

The harbour seal *Phoca vitulina* and grey seal *Halichoerus grypus* are the most common seal species in the North Sea. Grey seals occur in temperate and subarctic waters on both sides of the North Atlantic Ocean in three distinct populations. The Eastern Atlantic population is found mostly around the coasts of Great Britain and Ireland, as well as on the coasts of the Faroe Islands, Iceland, Norway and north-western Russia as far east as the White Sea. With an estimated number of 415,000 to 475,000 individuals, the species is not threatened as a whole and grey seal numbers are currently increasing at most locations (Thompson and Harkönen 2008). The harbour seal is found throughout the coastal waters of the northern hemisphere. A global population of 350,000 to 500,000 is estimated. Haul-out sites are important for the species, as they are used for resting, moulting, pupping and lactation (Adelung et al. 2004; Reijnders et al. 2005).

There is yet little or no evidence for direct effects of climate change on either of the North Sea seal species, however changes to their physical habitat, through sea-level rise for example may cause haul-out locations in caves or on low-lying coasts to be modified or even lost. More frequent storms and associated storm surges may also have unfavourable effects (Evans and Bjørke 2014).

Harbour seals and grey seals are both opportunistic feeders, but the majority of their diet comprises only a few species, depending on the area. In European waters they are primarily demersal or benthic feeders. Important prey species here include sandeel, Atlantic cod, saithe, herring and some flatfishes (Hall 2002; Santos and Pierce 2003; Hammond and Grellier 2006). Thus, it seems likely that climate may affect seals indirectly, through changes in abundance or distribution of one or more of their most important prey species.

## 8.7 Ecosystem Effects

Previous sections have presented evidence of substantial changes in plankton, benthos, fish, seabirds and marine mammals in the North Sea over the past century and have related these to climate change. Planktonic and benthic ecosystems are coupled in several ways; many benthic species have planktonic stages and the settled, adult benthic stages are often dependent on planktonic food sources. It is therefore not surprising to find some common patterns of response to climate change, and that the response of plankton generally precedes the benthic response. This section considers whether common patterns, which are found to varying degrees in fish, seabirds and marine mammals, can be described as changes (or regime shifts) in the North Sea ecosystem as a whole. Common features examined include external drivers, timing of changes (both phenological and interannual), common processes (growth, recruitment, survival) and ecosystem characteristics (distribution, diversity, trophic structure).

### 8.7.1 An Integrated Ecosystem Assessment

An integrated analysis of available North Sea time series data was conducted by Kenny et al. (2009). The analysis was based on 114 variables with long (unbroken) records and broad spatial coverage making them suitable for assessing the North Sea as a whole. The data comprised abiotic environmental variables (including surface and bottom water temperature and nutrient concentrations, and wind speed and direction), plankton, seabirds, fish and fishing pressure. The initial study covered the period 1983 to 2003, but the analysis has since been extended to include data to 2007 (ICES 2009). The later analysis indicates that the North Sea ecosystem as a whole has undergone a series of shifts in state and that the rate of change in the ecosystem has varied over time, with some groups of years having greater similarity than others (Fig. 8.13). The pattern of change reveals three (possibly four) distinct groups of years with a shift in the system occurring between 1990 and 1991 characterised by declines in the dominance of cod SSB, average demersal fish length and *C. finmarchicus* abundance. In contrast, a second shift occurred between 2001/2002 and 2003/2004 which was initially dominated by an increase in average pelagic fish length, sea bottom temperature and *C. helgolandicus* abundance, but was then dominated by an increase or return in state of average demersal fish length and cod SSB.

A number of ‘key’ signals of environmental change in the North Sea ecosystem, such as bottom temperature, zooplankton and pelagic fish length, demonstrate strong trends over time (Fig. 8.14). It is clear that the period 1989 to 1991 represented a time of rapid change in all three components, with the apparent 1-year lag between them suggesting that the ecosystem shift at this time was driven by a step-change in temperature.

Integrated ecosystem assessments are an essential part of an ecosystem approach to the management of marine resources, that is, “An integrated approach to management that considers the entire ecosystem, including humans, with the goal to maintain an ecosystem in a healthy, productive, and resilient condition so that it can provide the services we want and need” (McLeod et al. 2005). This assessment and the information presented in previous sections of this chapter shows that the composition and productivity of North Sea marine ecosystems are affected by climate change and that this has consequences for sustainable levels of harvesting and for other ecosystem services. It is clearly valuable to have indicators that can be used to monitor and forewarn of changes in composition and productivity and multi-variate ocean climate indicators of this type are now being developed for the North Sea and other well-studied areas such as the California Current (Sydeman et al. 2014).

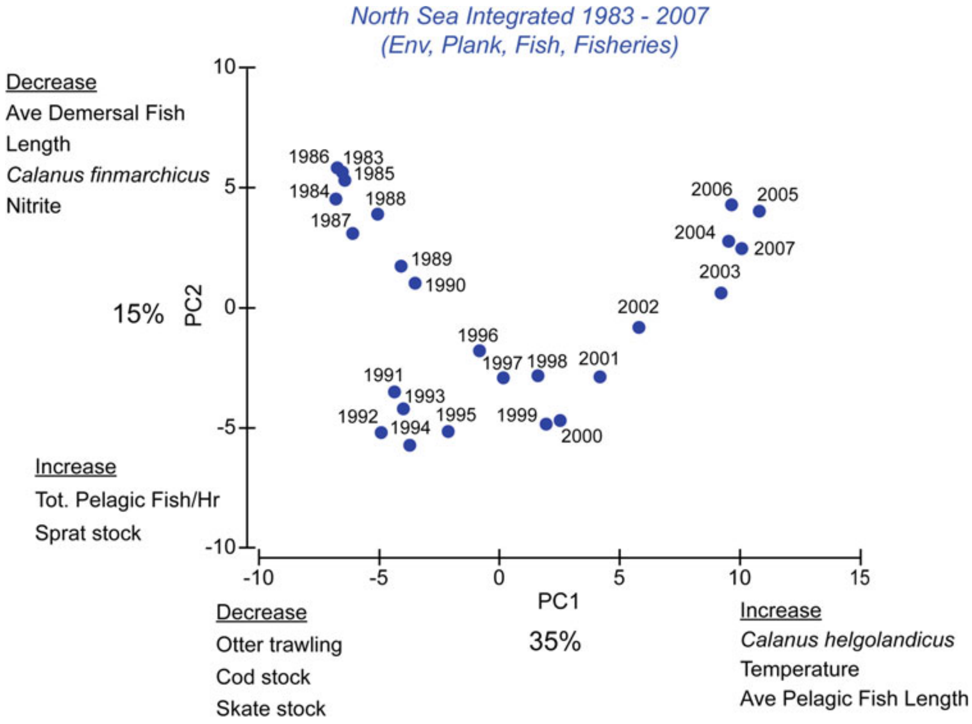

**Fig. 8.13** Principal component analysis performed on an integrated data set comprising 106 separate state and pressure variables representing several components of the North Sea ecosystem between 1983 and 2007

## 8.7.2 Examples of Climate Impacts Across Trophic Levels

*Case Study 1: Climate affects cod through zooplankton prey*. Survival of North Sea cod larvae is linked to their degree of temporal overlap with zooplankton prey. This is referred to as the 'match–mismatch hypothesis' (Cushing 1990; Durant et al. 2007). Indeed, changes in plankton phenology linked to climate (Sect. 8.2) are seen as a factor contributing to the decline in the North Sea cod stock, although overfishing also plays an important role (Nicolas et al. 2014). Copepod biomass, euphausiid abundance, and prey size have also been shown to influence survival of North Sea cod through early life stages (Beaugrand et al. 2003).

The decline in the quality and quantity of planktonic prey from the 'gadoid outburst' of the 1960s to the periods of low recruitment (after the mid-1980s) was related to an increase in SST. Consequently, high sea temperatures may have had a double negative impact on larval cod survival in the North Sea. Temperature increases metabolic rate and so increases energy demand while at the same time it decreases the quality and quantity of prey available for larvae (the energy supply). The temperature rise may therefore have resulted in an energy imbalance for larval cod, causing increased larval mortality (Beaugrand et al. 2003). The increased rate of development probably resulted in a mismatch with prey (Daewel et al. 2011). On the other hand, high temperatures should also shorten the time from spawning through hatching to metamorphose, which should be favourable for the survival of the cod progeny (Ottersen et al. 2010).

*Case Study 2: Climate effects from phytoplankton to seabirds*. Many seabirds are at the top of the food chain (see also Sect. 8.5) and it is important to understand which pathways climate signals follow through the food web to influence the different seabird life-history traits (Sandvik et al. 2012; Myksvoll et al. 2013). Aebischer et al. (1990) reported clear similarities between trends in long-term data

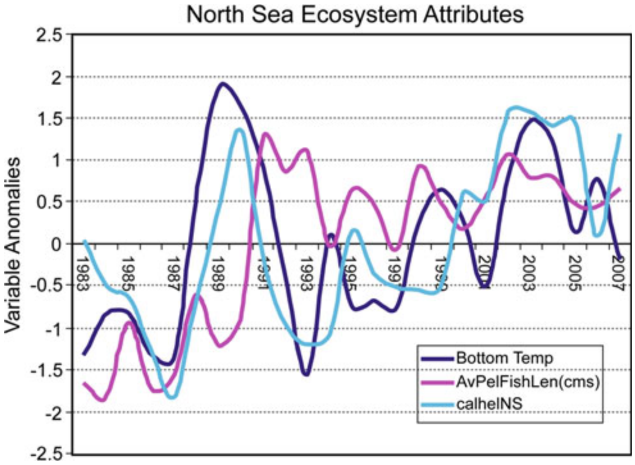

**Fig. 8.14** Trends in state of three 'key' components of the North Sea ecosystem; bottom temperature, *Calanus helgolandicus* abundance and average pelagic fish length between 1983 and 2007 (ICES 2009)

series of westerly weather and at four trophic levels in the North Sea: phytoplankton, zooplankton, herring, and black-legged kittiwakes, but the mechanisms behind the similarity were unclear. Frederiksen et al. (2006) also demonstrated consistent trends across four trophic levels, from plankton to seabirds, in the North Sea but again the causal links were undefined. Thompson and Ollason (2001) showed how ocean climate variation had lagged effects on a Scottish pelagic seabird species through cohort differences in recruitment related to temperature changes in summer. Burthe et al. (2012) compared phenological trends for species from four levels of a North Sea food web over the period 1983–2006 when SST increased significantly. The results suggest trophic mismatch between five seabird species breeding in the North Sea and their sandeel prey, but no evidence of an impact on the seabird breeding success or population dynamics (Burthe et al. 2012). Also, the significant increase in the number of lesser black-backed gulls from 1996 onwards has been linked to the earlier mentioned temperature-driven increase in recruitment of swimming crabs in wide areas of the southern North Sea. These crabs are a key prey item for the seagulls (Luczak et al. 2012).

## 8.8 Brief Synthesis and Reflection on Future Development

This chapter has presented examples of how the changing environment affects biological processes and organisation at all scales, including the physiology, reproduction, growth, survival, behaviour and transport of individuals; the distribution, dynamics and evolution of populations; and the trophic structure and coupling (e.g. benthic-pelagic coupling) of ecosystems. There have been particularly rapid changes in temperature and other climate-related variables since the early 1980s, with many well described effects on North Sea ecosystems. However the examples presented in this chapter also show that biological responses in terms of growth, survival, phenology and population shifts are often more complex than might be expected from thermal response models or bioclimate envelope models (Cheung et al. 2011; Baudron et al. 2014). For example, the growth response of juvenile cod to increasing temperature in the Skagerrak was positive during spring but negative in summer, with a detectable density effect, but only at stock levels that have not been observed for many decades. Distributions of fish species (cod, plaice, sole) have not simply shifted northwards over time in response to temperature; other factors including fishing, eutrophication, prey availability and habitat alteration must also be considered and for some species there are major east-west shifts (see also the change in harbour porpoise distribution shown in Fig. 8.11). The dynamics of the water mass exchanges between the North Sea and the North Atlantic, the English Channel and the Baltic Sea have a major influence on temperature, salinity and nutrient fields within the North Sea and also on invasion routes for biota.

These examples of complex responses can be detected because there are detailed long-term biological and environmental records for the North Sea. The Skagerrak cod records go back to 1929; distributions of commercially important fish species can be inferred from spatially resolved fisheries data going back to the 1920s and before; scientific fishing surveys provide detailed distribution and population structure data on all fish since the early 1970s; the CPR provides spatially resolved monthly records of zooplankton (including larvae of fish and benthic species) and some phytoplankton data back to 1948. In addition to these well maintained observational time-series data are accumulating from historic reconstructions (e.g. Poulsen et al. 2007), archaeology (Enghoff et al. 2007) and other sources. The wealth of sampling and scientific analysis that exists for the North Sea shows the need to look deeper than simple, direct effects and linear responses to one or two variables and to be wary of general conclusions from incomplete models (Heath et al. 2012). It is salutary to find that even in a very well-studied species such as cod in the North Sea, the causes of changes in distribution, abundance and population structure over the past century are still not fully understood, but are undoubtedly complex.

Uncertainty over the causes of observed changes in cod over the past century, despite detailed time series on the physical and chemical environment and on other drivers of change, in particular fishing, must temper our confidence in projections of future changes in cod. The quality and credibility of such biological projections depend on the quality of projections of future changes in environmental variables and on the correct identification and representation of all important processes. A systematic approach that applies basic, mechanistic ecological principles to new situations and that emphasises the testing of hypotheses in experimental frameworks may be useful in identifying and constructing appropriate process models (Kordas et al. 2011). There may also be unknown factors and interactions as the system changes beyond previous limits, including those concerning pH and oxygen.

The changes in biota described in this chapter and in particular the ‘regime shift’ of the late 1980s might be regarded as evidence of the sensitivity of the North Sea ecosystem to changes in the environment, particularly temperature (Philippart et al. 2011). However given that the environmental changes were very large and rapid and that although the biotic response was evident, it did not include loss of characteristic North Sea species or a complete change in the character of the ecosystems, it could be argued that this demonstrated that the ecosystem response showed great resilience. Increases in species richness seem to have been due to the addition of warm-temperate species without the loss of cool-temperate species. The warm period since the late 1980s is still too short to determine whether the present ecosystem state is transitional and whether the cool-temperate species will gradually disappear, but evidence from archaeological material laid down during the Mesolithic warm period (4000–7500 y BP) indicates that cool-temperate species may remain (Enghoff et al. 2007) at least until temperatures rise by considerably more. The time taken for this to happen depends on the rate of global warming but also on decadal regional variability, which could maintain a cooler state over the next few decades.

Substantial biological changes in the Northeast Atlantic including the North Sea have been associated with shifts in the sub-polar gyre and warming over recent decades (Hatun et al. 2009). This includes large-scale modification of the phenology and distribution of plankton assemblages (Beaugrand et al. 2002; Edwards and Richardson 2004; Richardson and Schoeman 2004), changes in the availability of food resources and species, reproduction of benthic animals, composition of fish assemblages (Attrill and Power 2002; Simpson et al. 2011), and recruitment to the North Sea cod stock (Clark et al. 2003; Olsen et al. 2011).

The diversity of the North Sea ecosystem may lead to contrasting responses to future climate change. For instance, the increase in temperature, light (through improved transparency), and wind in the south-eastern North Sea have probably contributed to the increase in algal biomass in this region during the period 1948–2004 (Llope et al. 2009). While their data suggest that phytoplankton biomass may have reached a maximum in the southernmost parts of the North Sea, Llope et al. (2009) concluded that phytoplankton biomass in the northern North Sea would continue to respond positively to a warmer, brighter, and windier future if current trends are maintained.

Projections of the phenological responses of individual species under climate change have not yet been made, but the empirical evidence suggests that phenological changes will continue as climate warming continues. It is currently uncertain whether genetic adaptations within species populations will be able to cope with these changes, at least partly, or whether the pace of climate change is too fast for genetic adaptations to take place. This uncertainty is further compounded by the difference in phenological responses between species and functional groups. If current patterns and rates of phenological change are indicative of future trends, climate warming may exacerbate trophic mismatching and result in disruption of the functioning, persistence and resilience of North Sea ecosystems.

It is not clear whether general species attributes (e.g. trophic level) are sufficient to predict future outcomes or whether careful study of the individual species is required, however the differences in phenological responses between different diatom species indicates the latter (Schlüter et al. 2012).

## References

Adelung D, Liebsch N, Wilson RP (2004) Telemetrische Untersuchungen zur räumlichen und zeitlichen Nutzung des schleswig-holsteinischen Wattenmeeres und des angrenzenden Seegebietes durch Seehunde (*Phoca vitulina vitulina*) in Hinblick auf die Errichtung von Offshore-Windparks. – Teilprojekt 6 im Endbericht zum Verbundvorhaben "Marine Warmblüter in Nord- und Ostsee: Grundlagen zur Bewertung von Windkraftanlagen im Offshore-Bereich". FKZ 0327520

Aebischer NJ, Coulson JC, Colebrookl JM (1990) Parallel long-term trends across four marine trophic levels and weather. Nature 347:753–755

Agüera A, Trommelen M, Burrows F, Jansen JM, Schellekens T, Smaal A (2012) Winter feeding activity of the common starfish (*Asterias rubens* L.): The role of temperature and shading. J Sea Res 72:106–112

Armonies W, Herre E, Sturm M (2001) Effects of the severe winter 1995/96 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the island of Sylt. Helgoland Mar Res 55:170–175

Arnott SA, Ruxton GD (2002) Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. Mar-Ecol Prog Ser 238:199–210

Asrar G, Myneni R, Kanemasu ET (1989) Estimation of plant canopy attributes from spectral reflectance measurements. In: Asrar G (ed) Theory and Application of Optical Remote Sensing. Wiley

Atkinson D (1994) Temperature and organism size - a biological law for ectotherms. Advances in Ecological Research, vol 25

Attrill MJ (2007) Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. Limnol Oceanogr 52:480–485

Attrill MJ, Power M (2002) Climatic influence on a marine fish assemblage. Nature 417:275–278

Baines ME, Reichelt M, Anderwald P, Evans PGH (2006) Monitoring a changing world - searching the past for long-term trends in the occurrence of cetaceans around the UK. In: Abstracts, 20th Annual Conference of the European Cetacean Society, Gdynia, Poland, 2-7 April 2006

Bakker J, Smeenk C (1987) Time-series analysis of *Tursiops truncatus*, *Delphinus delphis*, and *Lagenorhynchus albirostris* strandings on the Dutch coast. ECS Newslet 1:14–19

Baudron AR, Needle CL, Marshall CT (2011) Implications of a warming North Sea for the growth of haddock *Melanogrammus aeglefinus*. J Fish Biol 78:1874–89

Baudron AR, Needle CL, Rijnsdorp AD, Marshall CT (2014) Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. Global Change Biol 20:1023–1031

Beare DJ, Burns F, Greig A, Jones EG, Peach K, Kienzle M, McKenzie E, Reid DG (2004) Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. Mar-Ecol Prog Ser 284:269–278

Beare DJ, Burns F, Jones E, Peach K, Reid DG (2005) Red mullet migration into the northern North Sea during late winter. J Sea Res 53:205–212

Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog Oceanogr 60:245–262

Beaugrand G, Ibañez F (2002) Spatial dependence of calanoid copepod diversity in the North Atlantic Ocean. Mar-Ecol Prog Ser 232:197–211

Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296:1692–1694

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–664

Beaugrand G, Edwards M, Brander K, Luczak C, Ibanez F (2008) Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. Ecol Lett 11:1157–1168

Beaugrand G, Luczak C, Edwards M (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. Global Change Biol 15:1790–1803

Beaugrand G, Edwards M, Legendre L (2010) Marine biodiversity, ecosystem functioning, and carbon cycles. P Natl Acad Sci USA 107:10120–10124

Beaugrand G, McQuatters-Gollop A, Edwards M, Goberville E (2013) Long-term responses of North Atlantic calcifying plankton to climate change. Nature Clim Change 3:263–267

Beaugrand G, Harlay X, Edwards M (2014) Detecting plankton shifts in the North Sea: a new abrupt ecosystem shift between 1996 and 2003. Mar Ecol Progr Ser 502:85–104

Behrenfeld MJ, Siegel DA, O'Malley RT, Maritorena S (2009) Global ocean phytoplankton. In: State of the Climate in 2008, pp. 568–573. Peterson TC, Baringer MO (Eds)

Beukema JJ, Dekker R (2005) Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Mar-Ecol Prog Ser 287:149–167

Beukema JJ, Cadée GC, Dekker R (2002) Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. J Sea Res 48:111–125

Bjornsson B, Steinarsson A, Oddgeirsson M (2001) Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). ICES J Mar Sci 58:29–38

Bolle LJ, Dickey-Collas M, van Beek JKL, Erftemeijer PLA, Witte JIJ, van der Veer HW, Rijinsdorp AD (2009) Variability in transport of fish eggs and larvae. III. Effects of hydrodynamics and larval behaviour on recruitment in plaice. Mar-Ecol Prog Ser 390:195–211

Bolster WJ (2008) Putting the ocean in Atlantic history: Maritime communities and marine ecology in the northwest Atlantic, 1500–1800. Am Hist Rev 113:19–47

Bonnet D, Richardson A, Harris R, Hirst A, Beaugrand G, Edwards M, Ceballos S, Diekman R, Lopez-Urrutia A, Valdes L, Carlotti F, Molinero JC, Weikert H, Greve W, Lucic D, Albaina A, Yahia ND, Umani SF, Miranda A, dos Santos A, Cook K, Robinson S, de Puelles MLF (2005) An overview of *Calanus helgolandicus* ecology in European waters. Progr Oceanogr 65:1–53

Bopp L (2005) Response of diatoms distribution to global warming and potential implications: A global model study. Geophys Res Lett 32: L19606. doi:10.1029/2005GL023653

Brander K (2010) Impacts of climate change on fisheries. J Marine Syst 79:389–402

Brander K, Mohn R (2004) Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 61:1558–1564

Brander KM, Blom G, Borges MF, Erzini K, Henderson G, MacKenzie BR, Mendes H, Ribeiro J, Santos AMP, Toresen R (2003) Changes in fish distribution in the eastern North Atlantic: are we seeing a coherent response to changing temperature? ICES Mar Sc 219:261–270

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Towards a metabolic theory of ecology. Ecology 85:1771–1789

Buckley LB, Hurlbert AH, Jetz W (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. Glob Ecol Biogeogr 21:873–885

Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, Brown C, Bruno JF, Duarte CM, Halpern BS, Holding J, Kappel CV, Kiessling W, O'Connor MI, Pandolfi JM, Parmesan C, Schwing FB, Sydeman WJ, Richardson AJ (2011) The pace of shifting climate in marine and terrestrial ecosystems. Science 334:652–655

Burthe S, Daunt F, Butler A, Elston DA, Frederiksen M, Johns D, Newell M, Thackeray SJ, Wanless S (2012) Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. Mar-Ecol Prog Ser 454:119–133

Burthe SJ, Wanless S, Newell MA, Butler A, Daunt F (2014) Assessing the vulnerability of the marine bird community in the western North Sea to climate change and other anthropogenic impacts. Mar-Ecol Prog Ser 507:277–295

Camphuysen CJ (2004) The return of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters. Lutra 47:113–122

Camphuysen CJ, Garthe S (2000) Seabirds and commercial fisheries: population trends of piscivorous seabirds explained? In: Kaiser MJ, de Groot SJ (eds) The effects of fishing on non-target species and habitats: Biological, conservation and socio-economic issues. Blackwell

Camphuysen CJ, Peet G (2006) Whales and Dolphins of the North Sea. Fontaine Uitgewers. pp 420

Cermeño P, Dutkiewicz S, Harris RP, Follows M, Schofield O, Falkowski PG (2008) The role of nutricline depth in regulating the ocean carbon cycle. P Natl Acad Sci USA 105:20344–20349

Cheung WWL, Dunne J, Sarmiento JL, Pauly D (2011) Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. ICES J Mar Sci 68:1008–1018

Clark RA, Frid CLJ (2001) Long-term changes in the North Sea ecosystem. Environ Rev 9:131–187

Clark RA, Fox CJ, Viner D, Livermore M (2003) North Sea cod and climate change – modelling the effects of temperature on population dynamics. Global Change Biol 9:1669–1680

Coleman RA, Underwood AJ, Benedetti-Cecchi L, Aberg P, Arenas F, Arrontes J, Castro J, Hartnoll RG, Jenkins SR, Paula J, Della Santina P, Hawkins SJ (2006) A continental scale evaluation of the role of limpet grazing on rocky shores. Oecologia 147:556–564

Corten A (2013) Recruitment depressions in North Sea herring. ICES J Mar Sci 70:1–15

Cotton PA (2003) Avian migration phenology and global climate change. P Natl Acad Sci USA 100:12219–12222

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv Int 22:1–34

Cury P, Shannon L, Shin YJ (2003) The functioning of marine ecosystems: a fisheries perspective. In: Sinclair M, Valdimarsson G (eds) Responsible fisheries in the marine ecosystem. FAO and CAB international, Rome

Cushing DH (1984) The gadoid outburst in the North Sea. J Cons Int Explor Mer 41:159–166

Cushing DH (1990) Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Adv Mar Biol 26:249–294

Daewel U, Peck MA, Schrum C (2011) Life history strategy and impacts of environmental variability on early life stages of two marine fishes in the North Sea: an individual-based modelling approach. Can J Fish Aquat Sci 68:426–443

Dam HG (2013) Evolutionary adaptation of marine zooplankton to global change. Ann Rev Mar Sci 5:349–370

Daunt F, Mitchell I (2013) Impacts of climate change on seabirds. MCCIP Science Review 2013:125–133

Deaville R, Jepson PD (2011) UK Cetacean Strandings Investigation Programme. Final Report to Defra for the period 1 January 2005 – 31 December 2010. Institute of Zoology, London

Dickey-Collas M, Bolle L, van Beek J, Erftemeijer P (2009) Variability in transport of fish eggs and larvae. II. Effects of hydrodynamics on the transport of Downs herring larvae. Mar-Ecol Prog Ser 390:183–194

Dickey-Collas M, Nash RDM, Brunel T, van Damme CJG, Marshall CT, Payne MR, Corten A, Geffen AJ, Peck MA, Hatfield EMC, Hintzen NT, Enberg K, Kell LT, Simmonds EJ (2010) Lessons learned from stock collapse and recovery of North Sea herring: a review. ICES J Mar Sci 67:1875–1886

Dinter WP (2001) Biogeography of the OSPAR Maritime Area. German Federal Agency for Nature Conservation, Bonn, Germany

Dolman SJ, Pinn E, Reid RJ, Barley JP, Deaville R, Jepson PD, O'Connell M, Berrow S, Penrose RS, Stevick PT, Calderan S, Robinson KP, Brownell Jr RL, Simmonds MP (2010) A note on the unprecedented stranding of 56 deep-diving odontocetes along the UK and Irish coast. Mar Biodiv Rec 3:1–8

Doney SC, Sailley SF (2013) When an ecological regime shift is really just stochastic noise. P Natl Acad Sci USA 110:2438–2439

Duineveld GCA, Kuenitzer A, Niermann U, De Wilde PAJ, Gray JS (1991) The macrobenthos of the North Sea. Neth J Sea Res 28:53–56

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271–283

Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884

Edwards M, Beaugrand G, John AWG, Johns DG, Licandro P, McQuatters-Gollop, Reid PC (2009) Ecological Status Report: results from the CPR survey 2007/2008. SAHFOS Tech Rep 6:1–12

Edwards M, Helaouet P, Johns DG, Batten S, Beaugrand G, Chiba S, Head EJH, Richardson AJ, Verheye HM, Wootton M, Flavell M, Hosie G, Takahashi K, Ward P (2012) Global Marine Ecological Status Report: results from the global CPR survey 2010/2011. SAHFOS Tech Rep 9:1–40

Edwards M, Helaouet P, Johns DG, Batten S, Beaugrand G, Chiba S, Hall J, Head E, Hosie G, Kitchener J, Koubbi P, Kreiner A, Melrose C, Pinkerton M, Richardson AJ, Robinson K, Takahashi K, Verheye HM, Ward P, Wootton M (2014) Global Marine Ecological Status Report: results from the global CPR survey 2012/2013. SAHFOS Tech Rep 10:1–37

Eggleton JD, Smith R, Reiss H, Rachor E, Vanden Berghe E, Rees HL (2007) Species distributions and changes (1986–2000). In: Rees HL, Eggleton JD, Vanden Berghe E (eds) Structure and Dynamics of the North Sea Benthos. ICES Coop Res Rep 288:91–108

Engelhard GH, Pinnegar JK, Kell LT, Rijnsdorp AD (2011) Nine decades of North Sea sole and plaice distribution. ICES J Mar Sci 68:1090–1104

Engelhard GH, Righton DA, Pinnegar JK (2014) Climate change and fishing: a century of shifting distribution in North Sea cod. Global Change Biol 20:2473–2483

Enghoff IB, MacKenzie BR, Nielsen EE (2007) The Danish fish fauna during the warm Atlantic period (ca. 7000–3900 BC): Forerunner of future changes? Fish Res 87:167–180

Evans PGH, Bjørge A (2014) Impacts of climate change on marine mammals. MCCIP Sci Rev 2013:134–148

Evans PGH, Smeenk C (2008) White-beaked dolphin *Lagenorhynchus albirostris*. In: Harris S, Yalden DW (eds) Mammals of the British Isles. Mammal Society, Southampton

Evans PGH, Anderwald P, Baines ME (2003) Status Review of UK Cetaceans. Report to English Nature and Countryside Council for Wales

Fiksen O (2000) The adaptive timing of diapause – a search for evolutionarily robust strategies in *Calanus finmarchicus*. ICES J Mar Sci 57:1825–1833

Fincham JI, Rijnsdorp AD, Engelhard GH (2013) Shifts in the timing of spawning in sole linked to warming sea temperatures. J Sea Res 75:69–76

Forbes E (1858) The distribution of marine life, illustrated chiefly by fishes and molluscs and radiata. In: Johnston AK (ed) AK Johnston's Physical Atlas. Johnston, Edinburgh

Fort J, Porter WP, Gremillet D (2009) Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. J Exp Biol 212:2483–2490

Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. Science 308:1621–1623

Fraser FC (1946) Report on Cetacea stranded on the British Coasts from 1933 to 1937. The British Museum (Natural History), London

Frederiksen M, Harris MP, Daunt F, Rothery P, Wanless S (2004a) Scale-dependent climate signals drive breeding phenology of three seabird species. Global Change Biol 10:1214–1221

Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson LJ (2004b) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. J Appl Ecol 41:1129–1139

Frederiksen M, Wright PJ, Harris MP, Mavor RA, Heubeck M, Wanless S (2005) Regional patterns of kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. Mar-Ecol Prog Ser 300:201–211

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J Anim Ecol 75:1259–1268

Frederiksen M, Anker-Nilssen T, Beaugrand G, Wanless S (2013) Climate, copepods and seabirds in the boreal Northeast Atlantic – current state and future outlook. Global Change Biol 19:364–372

Freitas V, Campos J, Fonds M, Van der Veer HW (2007) Potential impact of temperature change on epibenthic predator-bivalve prey interactions in temperate estuaries. J Therm Biol 32:328–340

Frid CLJ, Garwood PR, Robinson LA (2009a) Observing change in a North Sea benthic system: A 33 year time series. J Marine Syst 77:227–236

Frid CLJ, Garwood PR, Robinson LA (2009b) The North Sea benthic system: a 36 year time-series. J Mar Biol Assoc UK 89:1–10

Furness RW (2002) Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. ICES J Mar Sci 59:261–269

Furness RW, Tasker ML (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. Mar-Ecol Prog Ser 202:253–264

Garthe S, Camphuysen CJ, Furness RW (1996) Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Mar-Ecol Prog Ser 136:1–11

Gilles A (2009) Characterisation of harbour porpoise (*Phocoena phocoena*) habitat in German waters. PhD thesis, University of Kiel, Germany

Glémarec M (1973) The benthic communities of the European North Atlantic shelf. Oceanogr Mar Biol 11:263–289

Hagberg J, Tunberg BG (2000) Studies on the covariation between physical factors and the long-term variation of the marine soft bottom macrofauna in Western Sweden. Estuar Coast Shelf S 50:373–385

Hall A (2002) Gray seal *Halichoerus grypus*. In: Perrin WF, Wursig B, Thewissen GM (eds) Encyclopedia of Marine Mammals. Academic Press

Hammond PS, Grellier K (2006) Grey seal diet composition and prey consumption in the North Sea. Final report to Department for Environment Food and Rural Affairs on project MF0319

Hammond PS, Berggren P, Benke H, Borchers DL, Collet A, Heide-Jørgensen MP, Heimlich S, Hiby AR, Leopold MF, Oien N (2002) Abundance of harbour porpoises and other cetaceans in the North Sea and adjacent waters. J Appl Ecol 39:361–376

Hammond PS, Bearzi G, Bjørge A, Forney K, Karczmarski L, Kasuya T, Perrin WF, Scott M, Wang J, Wells R, Wilson B (2008) *Phocoena phocoena*. In: 2008 IUCN Red List of Threatened Species. International Union for Conservation of Nature (IUCN), Gland, Switzerland

Hammond PS, Macleod K, Berggren P, Borchers DL, Burt L, Cañadas A, Desportes G, Donovan GP, Gilles A, Gillespie D, Jonathan Gordon J, Hiby L, Kuklik I, Leaper R, Lehnert K, Leopold M, Lovell P, Øien N, Paxton CGM, Ridoux V, Rogan E, Samarra F, Scheidat M, Sequeira M, Siebert U, Skov H, Swift R, Tasker ML, Teilmann J, Canneyt OV, Vázquez JA (2013) Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. Biol Cons 167:107–122

Hatun H, Payne MR, Beaugrand G, Reid PC, Sando AB, Drange H, Hansen B, Jacobsen JA, Bloch D (2009) Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales. Prog Oceanogr 80:149–162

Hawkins SJ, Sugden HE, Mieszkowska N, Moore PJ, Poloczanska E, Leaper R, Herbert RJH, Genner MJ, Moschella PS, Thompson RC, Jenkins SR, Southward AJ, Burrows MT (2009) Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. Mar-Ecol Prog Ser 396:245–259

Hay S, Falkenhaug T, Omli L, Boersma M, Renz J, Halsband-Lenk C, Smyth T et al (2011) Zooplankton of the North Sea and English Channel. In: O'Brien T, Wiebe PH, Hay S (eds) ICES Coop Res Rep: ICES Zooplankton Stat Rep 2008/2009.

Heath MR (2005) Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. ICES J Mar Sci 62:847-868

Heath MR, Neat FC, Pinnegar JK, Reid DG, Sims DW, Wright PJ (2012) Review of climate change impacts on marine fish and shellfish around the UK and Ireland. Aquat Conserv Freshw Ecosyst 22:337–367

Heip C, Basford D, Craeymeersch JA, Dewarumez JM, Dorjes J, Dewilde P, Duineveld G, Eleftheriou A, Herman PMJ, Niermann U, Kingston P, Kunitzer A, Rachor E, Rumohr H, Soetaert K, Soltwedel T (1992) Trends in biomass, density and diversity of North-Sea macrofauna. ICES J Mar Sci 49:13–22

Helaouet P, Beaugrand G (2007) Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. Mar-Ecol Prog Ser 345:147–165

Hiddink JG, ter Hofstede R (2008) Climate induced increases in species richness of marine fishes. Global Change Biol 14:453–460

Hiddink JG, Burrows MT, García Molinos J (2014) Temperature tracking by North Sea benthic invertebrates in response to climate change. Global Change Biol 21:doi:10.1111/gcb.12726

Hinder SL, Hays GC, Edwards M, Roberts EC, Walne AW, Gravenor MB (2012) Changes in marine dinoflagellate and diatom abundance under climate change. Nature Clim Change 2:271–275

Hjøllo SS, Skogen MD, Svendsen E (2009) Exploring currents and heat within the North Sea using a numerical model. J Marine Syst 78:180–192

Howard J, Babij E, Griffis R, Helmuth B, Himes-Cornell A, Niemier P et al (2013) Oceans and marine resources in a changing climate. Oceanography and Marine Biology: An Annual Review 51

Huntley B, Green R, Collingham Y, Willis SG (2007) A climatic atlas of European breeding birds. Lynx Edicions, Barcelona

ICES (2008) The effect of climate change on the distribution and abundance of marine species in the OSPAR Maritime Area. ICES Coop Res Rep 293:45. International Council for the Exploration of the Sea (ICES), Copenhagen

ICES (2009) Report of the Working Group on Holistic Assessments of Regional Marine Ecosystems (WGHAME). ICES CM 2009/RMC:13. International Council for the Exploration of the Sea (ICES), Copenhagen

ICES (2011) Report of the Working Group on Seabird Ecology (WGSE). ICES Doc. CM 2011/SSGEF:07. International Council for the Exploration of the Sea (ICES), Copenhagen

Jones MC, Dye SR, Pinnegar JK, Warren R, Cheung WWL (2012) Modelling commercial fish distributions: Prediction and assessment using different approaches. Ecol Model 225:133–145

Kenny AJ, Skjoldal HR, Engelhard GH, Kershaw PJ, Reid JB (2009) An integrated approach for assessing the relative significance of human pressures and environmental forcing on the status of Large Marine Ecosystems. Prog Oceanogr 81:132–148

Kinze CC, Addink M, Smeenk C, García Hartmann M, Richards HW, Sonntag RP, Benke H (1997) The white-beaked dolphin (*Lagenorhynchus albirostris*) and the white-sided dolphin (*Lagenorhynchus acutus*) in the North and Baltic Seas, review of available information. Rep Intern Whaling Commis 47:675–681

Kirby RR, Beaugrand G (2009) Trophic amplification of climate warming. Proc R Soc B 276:4095–4103

Kirby RR, Lindley JA (2005) Molecular analysis of Continuous Plankton Recorder samples, an examination of echinoderm larvae in the North Sea. J Mar Biol Assoc UK 85:451–459

Kirby RR, Beaugrand G, Lindley JA, Richardson AJ, Edwards M, Reid PC (2007) Climate effects and benthic-pelagic coupling in the North Sea. Mar-Ecol Prog Ser 330:31–38

Kirby RR, Beaugrand G, Lindley JA (2008) Climate-induced effects on the meroplankton and the benthic-pelagic ecology of the North Sea. Limnol Oceanogr 53:1805–1815

Kjesbu OS, Witthames PR, Solemdal P, Walker MG (1998) Temporal variations in the fecundity of Arcto-Norwegial cod (*Gadus morhua*) in response to natural changes in food and temperature. J Sea Res 40:303–321

Kordas RL, Harley CDG, O'Connor MI (2011) Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. J Exp Mar Biol Ecol 400:218–226

Kröncke I, Reiss H (2007) Changes in community structure (1986–2000) and causal influences. In: Rees HL, Eggleton JD et al (eds) Structure and dynamics of the North Sea benthos. ICES Coop Res Rep 288

Kröncke I, Dippner JW, Heyen H, Zeiss B (1998) Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. Mar-Ecol Prog Ser 167:25–36

Kröncke I, Zeiss B, Rensing C (2001) Long-term variability in macrofauna species composition off the island of Norderney (East Frisia, Germany) in relation to changes in climatic and environmental conditions. Senck marit 31:65–82

Künitzer A, Basford D, Craeymeersch JA, Dewarumez JM, Dorjes J, Duineveld GC, Eleftheriou A, Heip C, Herman P, Kingston P, Niermann U, Rachor E, Rumohr H, de Wilde PAJ (1992) The benthic infauna of the North Sea: Species distribution and assemblages. ICES J Mar Sci 49:127–143

Le Masson du Parc (1727) Peches et pecheurs du domaine maritime aquitain au XVIII siecle. Proces Verbaux des visites faites par ordre du Roy concernant la peche en mer. Les Editions de l'Entre-deux-Mers

Learmonth JA, MacLeod CD, Santos MB, Pierce GJ, Crick HQP, Robinson RA (2006) Potential effects of climate change on marine mammals. Oceanography and Marine Biology: An Annual Review 44: 431–464

Licandro P, Conway DVP, Daly Yahia MN, Fernandez de Puelles ML, Gasparini S, Hecq JH, Tranter P, Kirby RR (2010) A blooming jellyfish in the northeast Atlantic and Mediterranean. Biol Lett 6:688–691

Lindley JA, Batten SD (2002) Long-term variability in the diversity of North Sea zooplankton. J Mar Biol Assoc UK 82:31–40

Llope M, Chan KS, Ciannelli L, Reid PC, Stige LC, Stenseth NC (2009) Effects of environmental conditions on the seasonal distribution of phytoplankton biomass in the North Sea. Limnol Oceanogr 54:512–524

Luczak C, Beaugrand G, Lindley JA, Dewarumez JM, Dubois PJ, Kirby RR (2012) North Sea ecosystem change from swimming crabs to seagulls. Biol Lett 8:821–824

Lynam CP, Hay SJ, Brierley AS (2005) Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. J Mar Biol Assoc UK 85:435–450

Maar M, Møller EF, Gürkan Z, Jónasdóttir SH, Nielsen TG (2013) Sensitivity of *Calanus* spp. copepods to environmental changes in the North Sea using life-stage structured models. Prog Oceanogr 111:24–37

Mackas DL, Batten S, Trudel M (2007) Effects on zooplankton of a warmer ocean: Recent evidence from the Northeast Pacific. Prog Oceanogr 75:223–252

MacLeod CD (2009) Global climate change, range changes and potential implications for the conservation of marine cetaceans, a review and synthesis. Endang Spec Res 7:125–136

Macleod CD, Bannon SM, Pierce GJ, Schweder C, Learmouth JA, Herman JS, Reid RJ (2005) Climate change and the cetacean community of north-west Scotland. Biol Conserv 124:477–483

MacLeod CD, Begona Santos M, Reid RJ, Scott BE, Pierce GJ (2007) Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises? Biol Lett 3:185–188

MacLeod CD, Weir CR, Santos MB, Dunn TE (2008) Temperature-based summer habitat partitioning between white-beaked and common dolphins around the United Kingdom and Republic of Ireland. J Mar Biol Assoc UK 88:1193–1198

McLeod KJ, Lubchenco J, Palumbi SR, Rosenberg AA (2005) Scientific consensus statement on marine ecosystem-based management. Signed by 219 academic scientists and policy experts with relevant expertise and published by the Communication Partnership for Science and the Sea (COMPASS) at http://compassonline.org/sites/all/files/document_files/EBM_Consensus_Statement_v12.pdf

Mendel B, Sonntag N, Wahl J, Schwemmer P, Dries H, Guse N, Müller S, Garthe S (2008) Profiles of seabirds and waterbirds of the German North and Baltic Seas. Distribution, ecology and sensitivities to human activities within the marine enviroment. Naturschutz und Biologische Vielfalt 61

Meyer EMI, Pohlmann T, Weisse R (2011) Thermodynamic variability and change in the North Sea (1948–2007) derived from a multidecadal hindcast. J Marine Syst 86:35–44

Mieszkowska N, Kendall MA, Hawkins SJ, Leaper R, Williamson P (2006) Changes in the range of some common rocky shore species in Britain – a response to climate change? Mar Biodiv 183:241–251

Mieszkowska N, Hawkins SJ, Burrows MT, Kendall MA (2007) Long-term changes in the geographic distribution and population structures of *Osilinus lineatus* (Gastropoda : Trochidae) in Britain and Ireland. J Mar Biol Assoc UK 87:537–545

Mieszkowska N, Genner MJ, Hawkins SJ, Sims DW (2009) Effects of climate change and commercial fishing on Atlantic cod *Gadus morhua*. Adv Mar Biol 56:213–273

Millner RS, Pilling GM, Mccully SR (2011) Changes in the timing of otolith zone formation in North Sea cod from otolith records : an early indicator of climate-induced temperature stress? Mar Biol 158:21–30

Mitchell PI, Ratcliffe N, Newton SF, Dunn TE (2004) Seabird populations of Britain and Ireland. Results of the Seabirds 2000 census. Poyser, London

Myksvoll MS, Erikstad KE, Barrett RT, Sandvik H, Vikebo F (2013) Climate-driven Ichthyoplankton drift model predicts growth of top predator young. PLOS One. 8:e79225. doi:10.1371/journal.pone.0079225

Neat F, Righton D (2007) Warm water occupancy by North Sea cod. Proc Biol Sci 274:789–798

Neat FC, Wright PJ, Fryer RJ (2008) Temperature effects on otolith pattern formation in Atlantic cod *Gadus morhua*. J Fish Biol 73:2527–2541

Neumann H, Reiss H, Rakers S, Ehrich S, Kroncke I (2009) Temporal variability in southern North Sea epifauna communities after the cold winter of 1995/1996. ICES J Mar Sci 66:2233–2243

Nicolas D, Rochette S, Llope M, Licandro P (2014) Spatio-temporal variability of the North Sea cod recruitment in relation to temperature and zooplankton. PLOS One 9:e88447. doi:10.1371/journal.pone.0088447

O'Brien CM, Fox C, Planque B, Casey J (2000) Climate variability and North Sea cod. Nature 404:142

Øien N (2010) Report of the Norwegian 2009 survey for minke whales within the Small Management Area EN – the North Sea. IWC SC/62/RMP7

Oliveira OMP (2007) The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic seas. Aquat Invas 2:185–189

Olsen EM, Ottersen G, Llope M, Chan K, Beaugrand G, Stenseth C, Stenseth NC (2011) Spawning stock and recruitment in North Sea cod shaped by food and climate. Proc R Soc B 278:504–510

Oost AP, Labat P, Wiersma A, Hofstede J (2009) Climate. Thematic Report no. 4.1. In: Marencic H, De Vlas J (eds) Quality Status Report 2009. Wadden Sea Ecosystem 25. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group

Ottersen G, Kim S, Huse G, Polovina JJ, Stenseth NC (2010) Major pathways by which climate may force marine fish populations. J Marine Syst 79:343–360

Ottersen G, Stige LC, Durant JM, Chan K-C, Rouyer TA, Drinkwater KF, Stenseth NC (2013) Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. Mar-Ecol Prog Ser 480:205–225

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. Science 279:860–863

Payne MR, Hatfield EMC, Dickey-Collas M, Falkenhaug T, Gallego A, Groger J, Licandro P, Llope M, Munk P, Rockmann C, Schmidt JO, Nash RDM (2009) Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. ICES J Mar Sci 66:272–277

Payne M, Stine D, Worsøe Clausen L, Munk P, Mosegaard H, Nash R (2013) Recruitment decline in North Sea herring is accompanied by reduced larval growth rates. Mar-Ecol Prog Ser 489:197–211

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915

Pershing AJ, Mills KE, Record NR, Stamieszkin K, Wurtzell KV, Byron CJ, Fitzpatrick D, Golet WJ, Koob E (2015) Evaluating trophic cascades as drivers of regime shifts in different ocean ecosystems. Phil Trans R B 370:20130265

Petersen CGJ (1914) Valuation of the sea II. The animal communities of the sea bottom and their importance for marine zoogeography. Rep Dan Biol Sta 21:1–44

Petersen CGJ (1918) The sea bottom and its production of fishfood. Rep Dan Biol Sta 25:1–62

Petitgas P, Alheit J, Peck MA, Raab K, Irigoien X, Huret M, van der Kooij J, Pohlmann T, Wagner C, Zarraonaindia I, Dickey-Collas M (2012) Anchovy population expansion in the North Sea. Mar-Ecol Prog Ser 444:1–13

Petitgas P, Rijnsdorp AD, Dickey-Collas M, Engelhard GH, Peck MA, Pinnegar JK, Drinkwater K, Huret M, Nash RDM (2013) Impacts of climate change on the complex life cycles of fish. Fish Oceanogr 22:121–139

Philippart CJM, Anadon R, Danovaro R, Dippner JW, Drinkwater KF, Hawkins SJ, Reid PC (2011) Impacts of climate change on European marine ecosystems: Observations, expectations and indicators. J Exp Mar Biol Ecol 400:52–69

Piatt J, Sydeman WJ (2007) Seabirds as indicators of marine ecosystems. Theme Section. Mar-Ecol Prog Ser 352:199–309

Planque B, Batten SD (2000) *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. ICES J Mar Sci 57:1528–1535

Planque B, Fredou T (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 56:2069–2077

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel C V, O'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ (2013) Global imprint of climate change on marine life. Nature Clim Change 3:919–925

Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315: 95–97

Poulsen B, Holm P, MacKenzie BR (2007) A long-term (1667–1860) perspective on impacts of fishing and environmental variability on fisheries for herring, eel, and whitefish in the Limfjord, Denmark. Fish Res 87:181–195

Quero JC, Du Bui MH, Vayne JJ (1998) Les observations de poissons tropicaux et le rechauffement des eaux dans l'Atlantique europeen. Oceanol Acta 21:345–351

Rachor E, Gerlach SA (1978) Changes of macrobenthos in a sublittoral sand area of the German Bight, 1967 to 1975. Rap Proces 172:418–431

Rachor E, Reiss H, Degraer S, Duineveld GCA, Van Hoey G, Lavaleye M, Willems W, Rees HL (2007) Structure, distribution and characterizing species of North Sea macrozoobenthos communities in 2000. In: Rees HL, Eggleton JD et al (eds) Structure and dynamics of the North Sea benthos. ICES Coop Res Rep 288

Rees HL, Eggleton JD, Rachor E, Vanden Berghe E (2007a) Structure and dynamics of the North Sea benthos. ICES Coop Res Rep 288

Rees HL, Eggleton JD, Rachor E, Vanden Berghe E, Aldridge JN, Bergman MJN, Bolam T, Cochrane SJ, Craeymeersch JA, Degraer S, Desroy N, Dewarumez J-M, Duineveld GCA, Essink K, Hillewaert H, Irion G, Kershaw PJ, Kröncke I, Lavaleye MSS, Mason C, Nehring S, Newell R, Oug E, Pohlmann T, Reiss H, Robertson M, Rumohr H, Schratzberger M, Smith R, van Dalfsen J, Van Hoey G, Vincx M, Willems W (2007b) The ICES North Sea Benthos Project 2000: aims, outcomes and recommendations. ICES CM 2007, A:21

Reid PC, Edwards M (2001) Long-term changes in the pelagos, benthos and fisheries of the North Sea. Senck marit 31:107–115

Reid PC, Edwards M, Hunt HG, Warner JA (1998) Phytoplankton change in the North Atlantic. Nature 391:546

Reid PC, de Fatima Borges M, Svendsen E (2001) A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. Fish Res 50:163–171

Reid JB, Evans PGH, Northridge SP (eds) (2003) Atlas of Cetacean Distribution in North-West European Waters. Joint Nature Conservation Committee. Peterborough

Reijnders PJH, Abt KF, Brasseur SMJM, Camphuysen K, Reineking B, Scheidat M, Siebert U, Stede M, Tougaard J, Tougaard S (2005) Marine Mammals. In: Essink K, Dettmann C, Farke H, Laursen K, Lüerßen G, Marencic H, Wiersinga W (eds) Wadden Sea Quality Status Report 2004. Wadden Sea Ecosystem No. 19. Trilateral Monitoring and Assessment Group, Common Wadeen Sea Secretariat, Wilhelmshaven

Reiss H, Degraer S, Duineveld GCA, Kroncke I, Aldridge J, Craeymeersch JA, Eggleton JD, Hillewaert H, Lavaleye MSS, Moll A, Pohlmann T, Rachor E, Robertson M, Vanden Berghe E, van Hoey G, Rees HL (2010) Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. ICES J Mar Sci 67:278–293

Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. Science 305:1609–1612

Righton D, Andersen K, Neat F, Thorsteinsson V, Steingrund P, Svedäng H, Michalsen K, Hinrichsen H, Bendall V, Neuenfeldt S, Wright P, Jonsson P, Huse G, van der Kooij J, Mosegaard H, Hüssy K, Metcalfe J (2010) Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. Mar-Ecol Prog Ser 420:1–13

Rijnsdorp AD, Witthames PR (2005) Ecology of reproduction In: Gibson RN (ed) Flatfish Biology and Exploitation. Academic Press

Rijnsdorp AD, Peck MA, Engelhard GH, Mollmann C, Pinnegar JK (2009) Resolving the effect of climate change on fish populations. ICES J Mar Sci 66:1570–1583

Rijnsdorp AD, Peck MA, Engelhard GE, Möllmann C, Pinnegar JK (2010) Resolving climate impacts on fish stocks. ICES Coop Res Rep 301:371

Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California current. Science 267:1324–1326

Rogers LA, Stige LC, Olsen EM, Knutsen H, Chan K-C, Stenseth NC (2011) Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. P Natl Acad Sci USA 108:1961–1966

Røjbek M, Jacobsen C, Tomkiewicz J, Støttrup J (2012) Linking lipid dynamics with the reproductive cycle in Baltic cod *Gadus morhua*. Mar-Ecol Prog Ser 471:215–234

Rothschild BJ, Osborn TR (1988) Small scale turbulence and plankton contact rates. J Plank Res 10:465–474

Rutterford LA, Simpson SD, Jennings S, Johnson MP, Blanchard JL, Schön PJ, Sims DW, Tinker J, Genner MJ (2015) Future fish distributions constrained by depth in warming seas. Nature Clim Change 5:569–573

Sagarin RD, Barry JP, Gilman SE, Baxter CH (1999) Climate-related change in an intertidal community over short and long time scales. Ecol Monogr 69:465–490

Sandvik H, Erikstad KE (2008) Seabird life histories and climatic fluctuations: a phylogenetic-comparative time series analysis of North Atlantic seabirds. Ecography 31:73–83

Sandvik H, Erikstad KE, Saether BE (2012) Climate affects seabird population dynamics both via reproduction and adult survival. Mar-Ecol Prog Ser 454:273–284

Santos MB, Pierce GJ (2003) The diet of harbour porpoise (*Phocoena phocoena*) in the eastern North Atlantic. Oceanogr Mar Biol Ann Rev 41:355–390

Sarmiento JL, Slater R, Barber R, Bopp L, Doney SC, Hirst AC, Kleypas J, Matear R, Mikolajewicz U, Monfray P, Soldatov V, Spall SA, Stouffer R (2004) Response of ocean ecosystems to climate warming. Global Biogeochem Cy 18: doi:10.1029/2003GB002134

Satterthwaite WH, Kitaysky AS, Mangel M (2012) Linking climate variability, productivity and stress to demography in a long-lived seabird. Mar-Ecol Prog Ser 454:221–235

SCANS II (2008) Small Cetaceans in the European Atlantic and North Sea. Final report to the European Commission under project LIFE04NAT/GB/000245. Available from SMRU, Gatty Marine Laboratory, University of St Andrews, Scotland

Scheffer M (2009) Critical Transitions in Nature and Society. Princeton University Press.

Schlüter MH, Merico A, Wiltshire KH, Greve W, von Storch H (2008) A statistical analysis of climate variability and ecosystem response in the German Bight. Ocean Dyn 58:169–186

Schlüter MH, Merico A, Reginatto M, Boersma M, Wiltshire KH, Greve W (2010) Phenological shifts of three interacting zooplankton groups in relation to climate change. Global Change Biol 16:3144–3153.

Schlüter MH, Kraberg A, Wiltshire KH (2012) Long-term changes in the seasonality of selected diatoms related to grazers and environmental conditions. J Sea Res 67:91–97

Schückel U, Kröncke I (2013) Temporal changes in intertidal macrofauna communities over eight decades: A result of eutrophication and climate change. Estuar Coast Shelf S 117:210–218

Siegismund F, Schrum C (2001) Decadal changes in the wind forcing over the North Sea. Clim Res 18:39–45

Simmonds MP, Isaac SJ (2007) The impacts of climate change on marine mammals: early signs of significant problems. Oryx 41:19–26

Simpson SD, Jennings S, Johnson MP, Blanchard JL, Scho P, Sims DW, Genner MJ (2011) Continental shelf-wide response of a fish assemblage to rapid warming of the sea. Curr Biol 21:1565–1570

Southward AJ, Crisp DJ (1954) Recent changes in the distribution of the intertidal barnacles *Chthamalus stellatus* Poli and *Balanus balanoides* L. in the British Isles. J Anim Ecol 23:163–177

Southward AJ, Hawkins SJ, Burrows MT (1995) 70 years observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. J Therm Biol 20:127–155

Speirs DC, Gurney WSC, Heath MR, Horbelt W, Wood SN, de Cuevas BA (2006) Ocean-scale modelling of the distribution, abundance, and seasonal dynamics of the copepod *Calanus finmarchicus*. Mar-Ecol Prog Ser 313:173–192

Stevens G (1989) The latitudinal gradient in geographic range – how so many species coexist in the tropics. Am Nat 133:240–256

Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of animals. Nature Clim Change 2:1–5

Sydeman WJ, Thompson SA, García-Reyes M, Kahru M, Peterson WT, Largier JL (2014) Multivariate ocean-climate indicators (MOCI) for the central California Current: Environmental change, 1990–2010. Prog Oceanogr 120:352–369

Tasker ML, Camphuysen CJ, Cooper J, Garthe S, Montevecchi WA, Blaber SJM (2000) The impacts of fishing on marine birds. ICES J Mar Sci 57:531–547

Taylor AH, Icarus Allen J, Clark PA (2002) Extraction of a weak climatic signal by an ecosystem. Nature 416:629–632

Teal LR, Leeuw JJ De, Veer HW Van Der, Rijnsdorp AD (2008) Effects of climate change on growth of 0-group sole and plaice. Mar-Ecol Prog Ser 358:219–230

Teal LR, van Hal R, van Kooten T, Ruardij P, Rijnsdorp AD (2012) Bio-energetics underpins the spatial response of North Sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) to climate change. Global Change Biol 18:3291–3305

Thomas H, Bozec Y, Elkalay K, de Baar HJW (2004) Enhanced open ocean storage of CO2 from shelf sea pumping. Science 304:1005–1008. doi:10.1126/science.1095491

Thompson D, Härkönen T (2008) *Halichoerus grypus*. In: IUCN 2009. IUCN Red List of Threatened Species. Version 2009.2. www.iucnredlist.org. Downloaded on 17 December 2009

Thompson PM, Ollason JC (2001) Lagged effects of ocean climate change on fulmar population dynamics. Nature 413:417–420

Tomanek L, Helmuth B (2002) Physiological ecology of rocky intertidal organisms: a synergy of concepts. Integr Comp Biol 42:771–775

Tunberg BG, Nelson WG (1998) Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic communities on the Swedish west coast? Mar-Ecol Prog Ser 170:85–94

Van de Pol M, Ens BJ, Heg D, Brouwer L, Krol J, Maier M, Exo K-M, Oosterbeek K, Lok T, Eising CM, Koffijberg K (2010) Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? J Appl Ecol 47:720–730

Van der Graaf AJ, Jonker S, Herlyn M, Kohlus J, Vinther HF, Reise K, De Jong D, Dolch T, Bruntse C, De Vlas J (2009) Seagrass. Thematic report no. 12. In: Marencic H, De Vlas J (eds) Quality Status report 2009. Wadden Sea Ecosystem No. 25. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group. Wilhelmshaven

Van der Land MA (1991) Distribution of flatfish eggs in the 1989 egg surveys in the southeastern North Sea, and mortality of plaice and sole eggs. Neth J Sea Res 27:277–286

Van der Veer HW, Ruardij P, Van den Berg AJ, Ridderinkhof H (1998) Impact of interannual variability in hydrodynamic circulation on egg and larval transport of plaice *Pleuronectes platessa* L. in the southern North Sea. J Sea Res 39:29–40

Van der Veer HW, Bolle LJ, Geffen AJ, Witte JIJ (2009) Variability in transport of fish eggs and larvae. IV. Interannual variability in larval stage duration of immigrating plaice in the Dutch Wadden Sea. Mar-Ecol Prog Ser 390:213–223

Van Deurs M, van Hal R, Tomczak MT, Jonasdottir SH, Dolmer P (2009) Recruitment of lesser sandeel *Ammodytes marinus* in relation to density dependence and zooplankton composition. Mar-Ecol Prog Ser 381:249–258

Wanless S, Frederiksen M, Daunt F, Scott BE, Harris MP (2007) Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. Prog Oceanogr 72:30–38

Warwick R, Ashman C, Brown A, Clarke K, Dowell B, Hart B, Lewis RE Shillabeer N, Somerfield P, Tapp JF (2002) Inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional environmental events. Mar-Ecol Prog Ser 234:1–13

Weijerman M, Lindeboom H, Zuur AF (2005) Regime shifts in marine ecosystems of the North Sea and Wadden Sea. Mar-Ecol Prog Ser 298:21–39

Willems W, Rees HL, Vincx M, Goethals P, Degraer S (2007) Relations and interactions between environmental factors and biotic properties. In: Rees HL, Eggleton JD et al (eds) Structure and dynamics of the North Sea benthos. ICES Coop Res Rep 288

Wilson B, Reid RJ, Grellier K, Thompson PM, Hammond PS (2004) Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins. Anim Conserv 7:331–338

Wittmann AC, Pörtner H (2013) Sensitivities of extant animal taxa to ocean acidification. Nature Clim Change 3:995–1001

Zühlke R (2001) Monitoring biodiversity of epibenthos and demersal fish in the North Sea and Skagerrak. EC Project 98/021. Monitoring Report 2001 to the Commission of the European Community