Part III

Impacts of Recent and Future Climate Change on Ecosystems

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

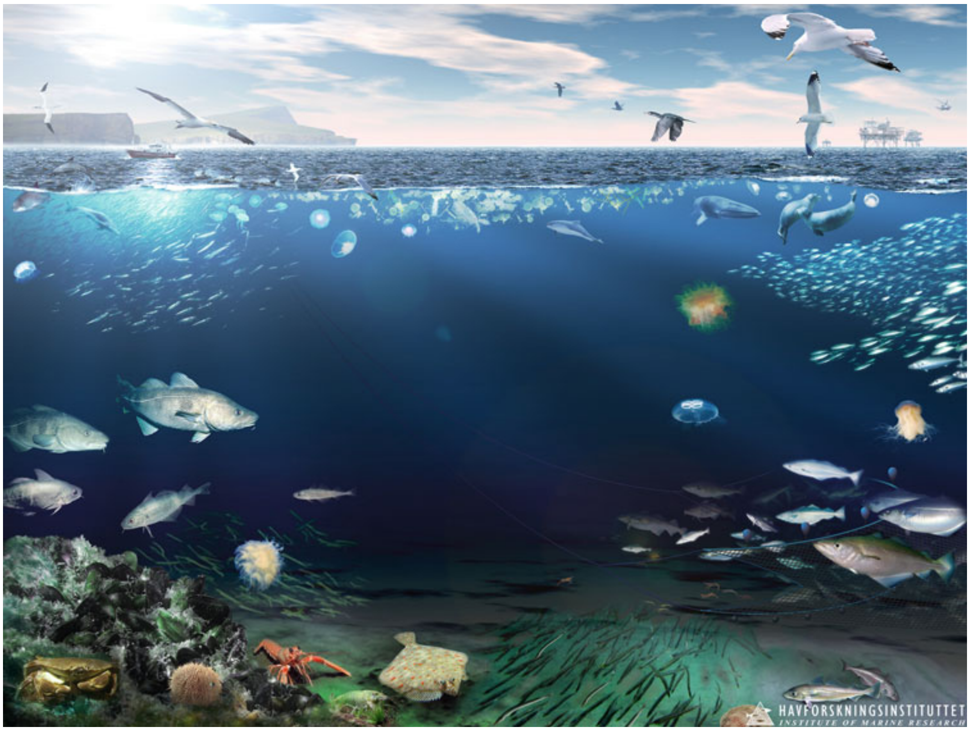

Fig. 8.1 Artist's view of the ecosystem of the coastal northern North Sea. Artwork by Arild Sæther commissioned by the Institute of Marine Research, Norway

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

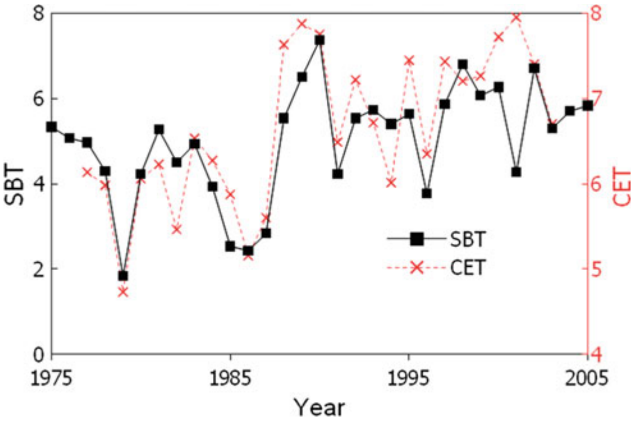

Fig. 8.3 First quarter sea-bed temperature (SBT) and Central England air temperature (CET; R = 0.80; $p < 0.0001$). SBT data from Hiddink and ter Hofstede (2008). CET data from www.metoffice.gov.uk/hadobs/hadcet/cetml1659on.dat

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 ($\sim$72 km decade^{-1}) than the rate of shift of trailing edges ($\sim$15 km decade^{-1}; where a previous occupied area is vacated). The overall global rates of distribution shift ($\sim$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

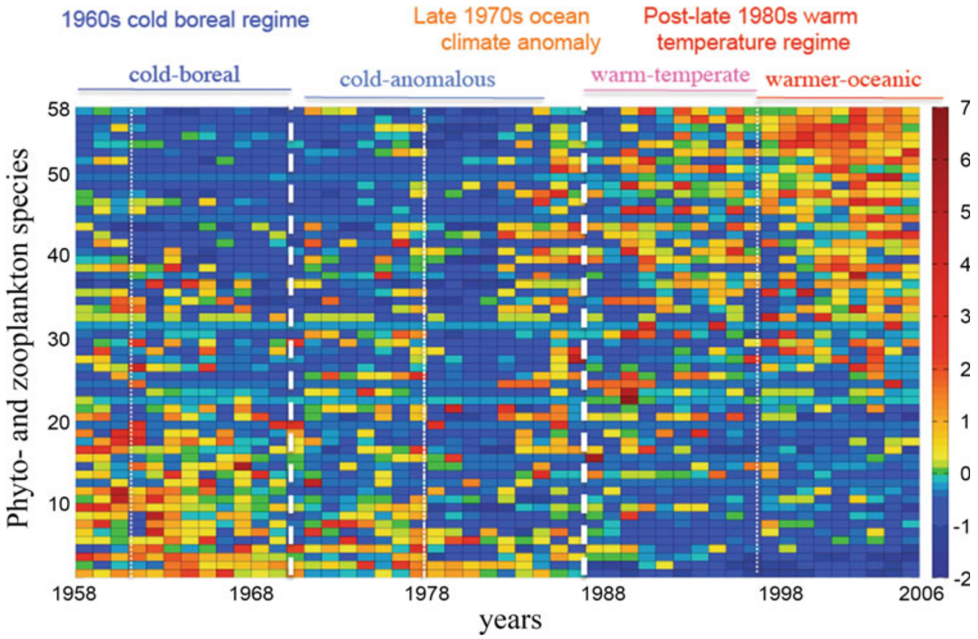

Fig. 8.4 Change in North Sea plankton composition over the past 50 years. Standardised abundance of 83 phytoplankton and zooplankton taxa collected by the Continuous Plankton Recorder (CPR). The taxa are ordered according to the first principal component. Periods characterised by different hydro-climatic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

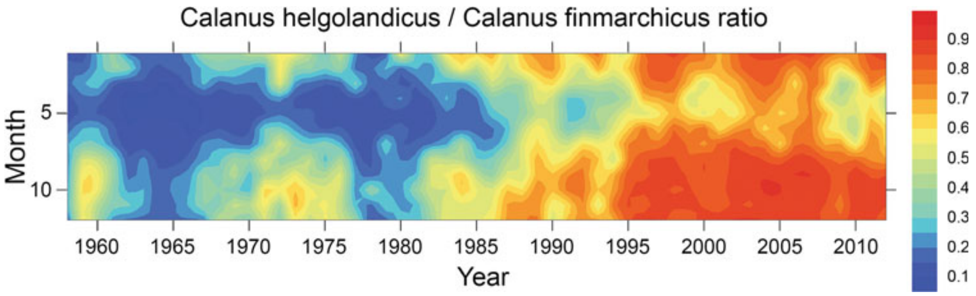

Fig. 8.5 Ratio between the abundance of the temperate-water copepod species *Calanus helgolandicus* and the cold-water species *C. finmarchicus*. *Red* indicates a dominance of *C. helgolandicus* and *blue C. finmarchicus* (Edwards et al. 2014)

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

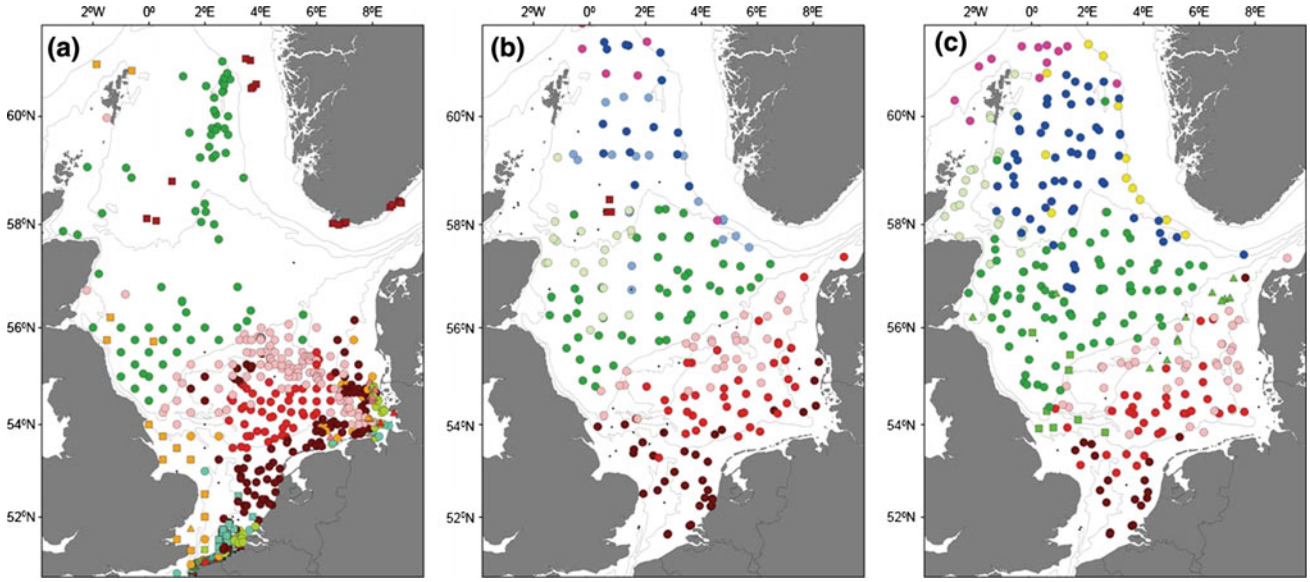

Fig. 8.6 Distribution of **a** infauna, **b** epifauna, and **c** fish assemblages in the North Sea. *Colours* depict different assemblages. The underlying cluster analyses and taxa associated with each assemblage are given in Reiss et al. (2010)

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

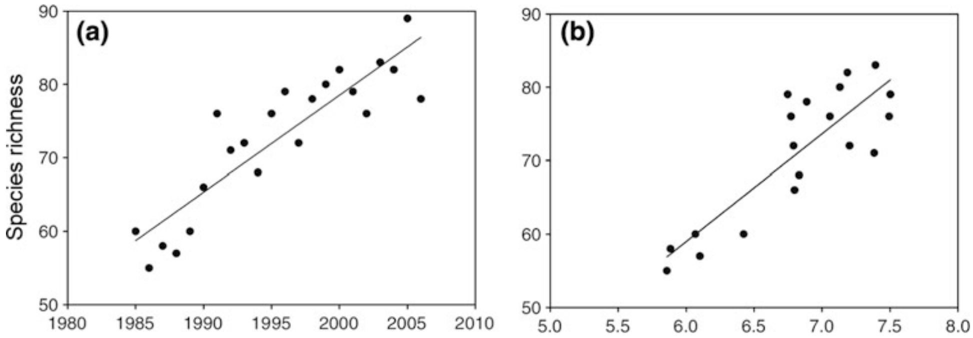

Fig. 8.7 Change in North Sea fish species richness. **a** Total number of species increases with time. **b** Total number of species increases with temperature (Hiddink and ter Hofstede 2008)

(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.

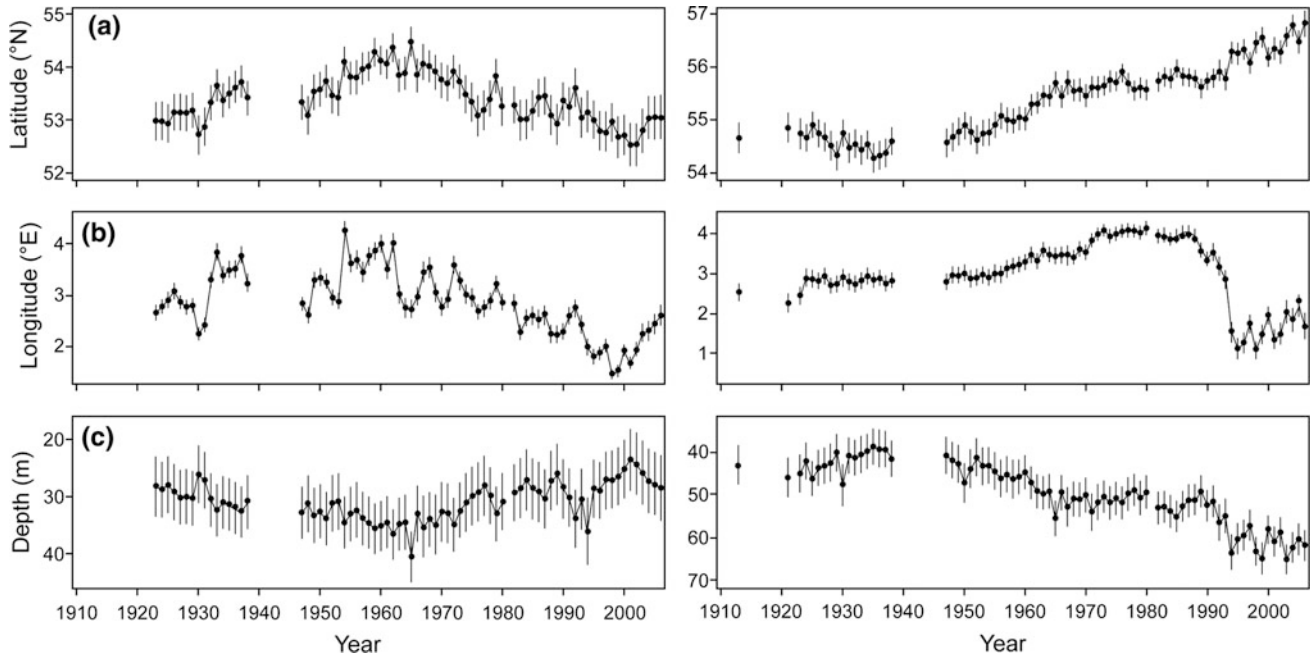


Fig. 8.8 Long-term changes in **a** latitude **b** longitude and **c** depth of North Sea sole (*left panels*) and plaice (*right panels*) using weighted mean catch-per-unit-effort (vertical bars are standard error of means) (Engelhard et al. 2011)

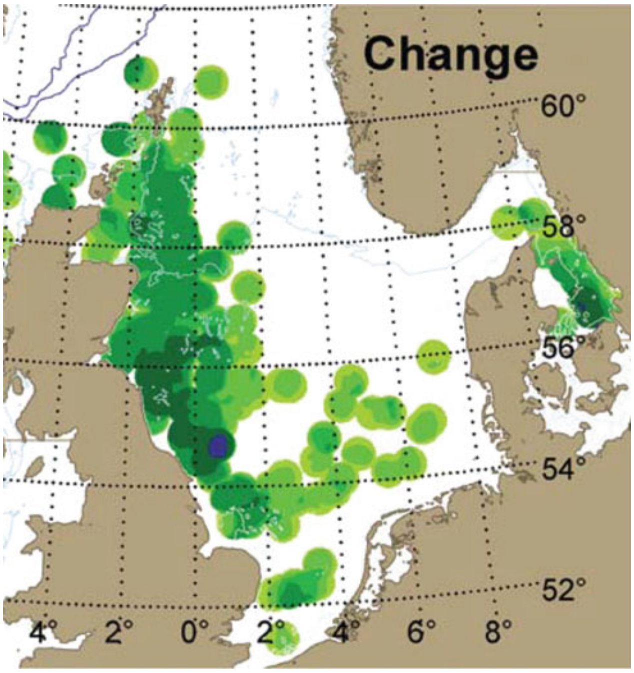


Fig. 8.9 Change in abundance of red mullet in first-quarter research surveys. The *darker the colour*, the greater the increase in abundance in the period 2000–2005 relative to 1977–1989 within each ½° latitude ×1° longitude rectangle (ICES 2008)

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

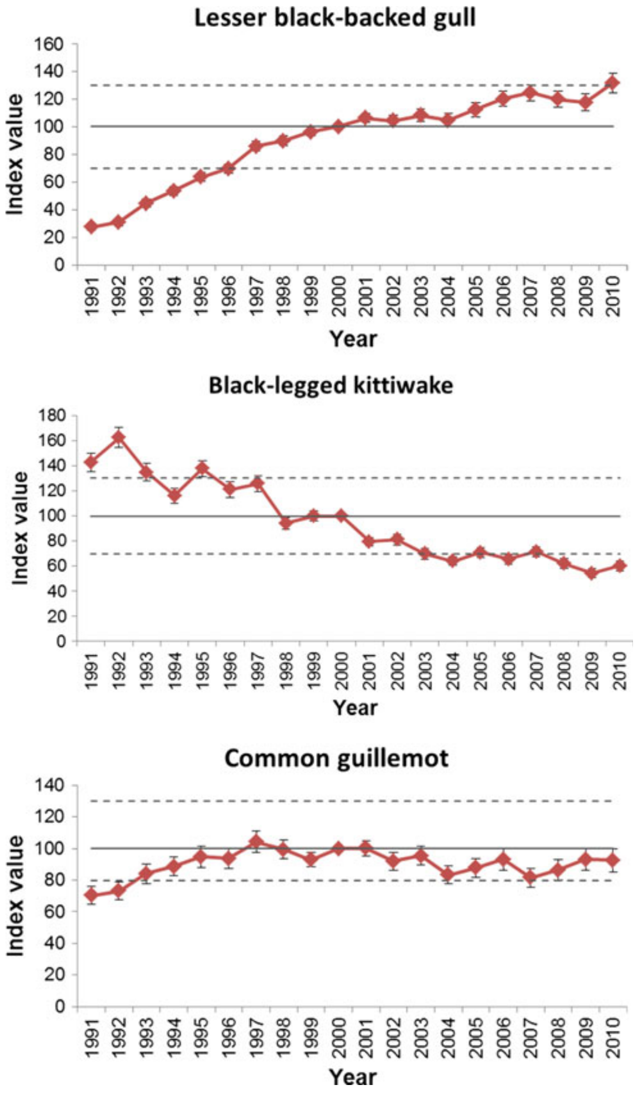
Case Study 1: The role of changes in oceanography and industrial fisheries in the decline of black-legged kittiwakes. In the North Sea, climate is known to affect several seabird populations through their main prey species, lesser sandeel, also called sandlance. Although Arnott and Ruxton (2002) and 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).


Lesser black-backed gull

Black-legged kittiwake

Common guillemot

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).

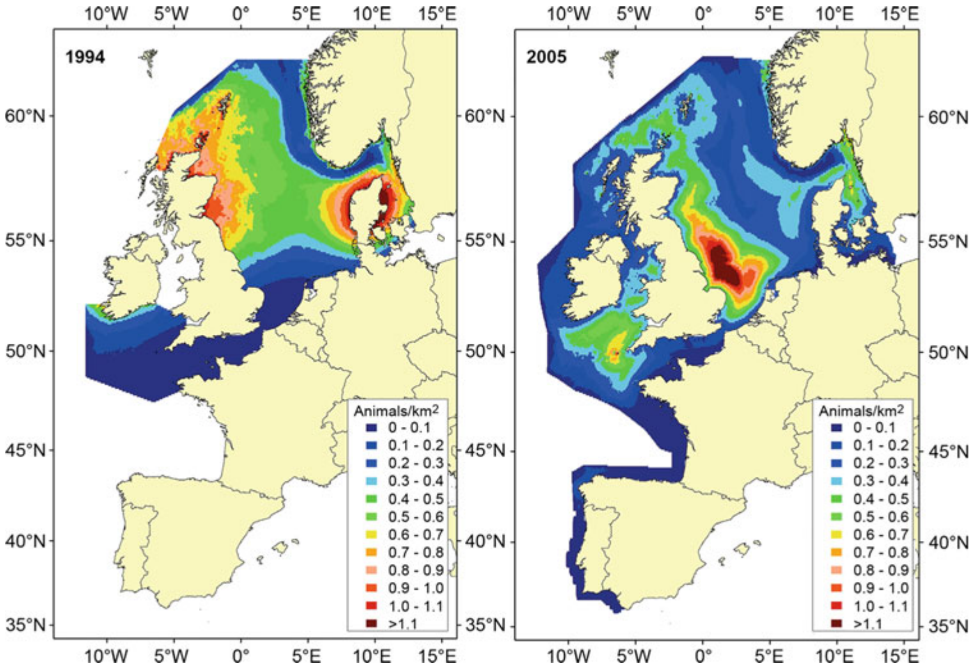
8.6.2 Distributional Shifts in Harbour Porpoise

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

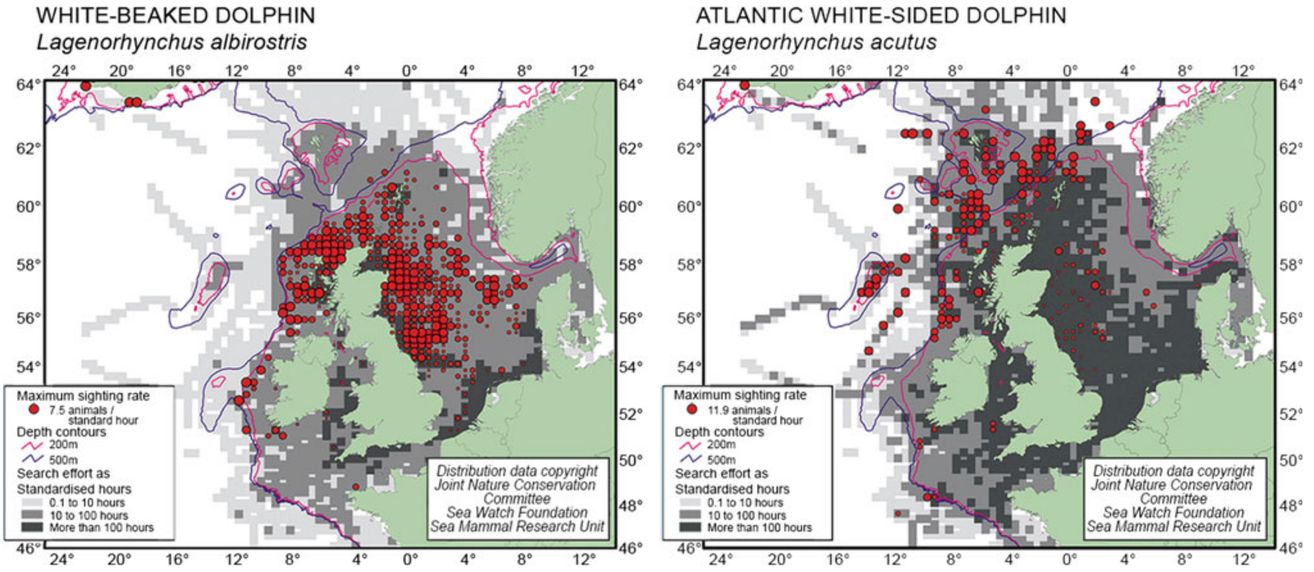
There is evidence of recent changes in range expansion for several dolphin species in the North Sea region. One such case is the (common) bottlenose dolphin *Tursiops truncatus*, off the northeast coast of Scotland. Here they are at the northern limit of their distribution. The causes behind this increase 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



WHITE-BEAKED DOLPHIN
Lagenorhynchus albirostris

ATLANTIC WHITE-SIDED DOLPHIN
Lagenorhynchus acutus

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).

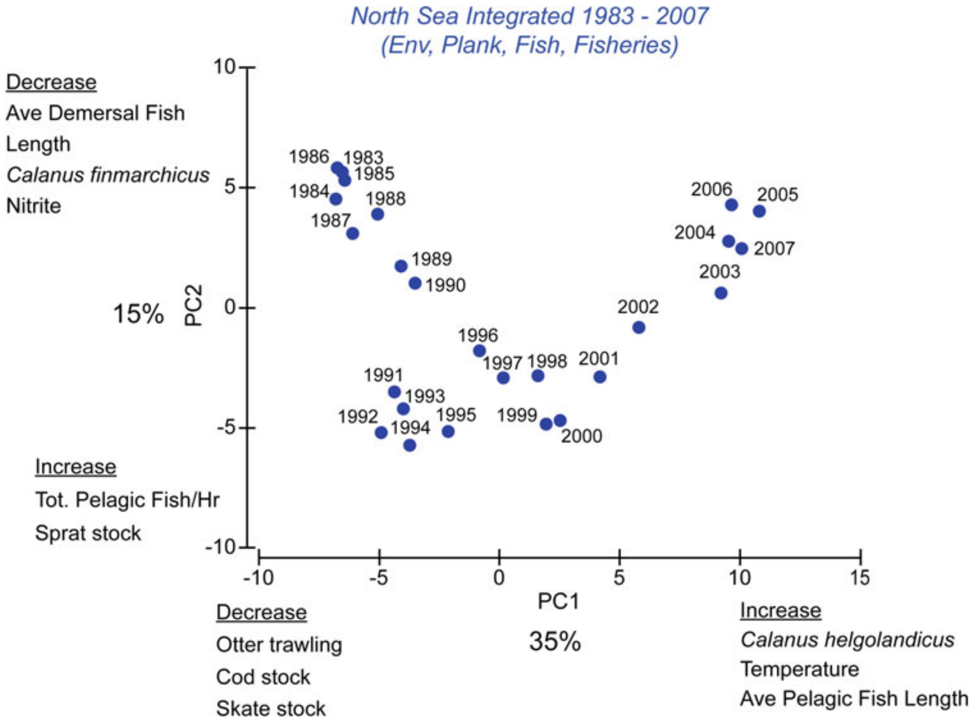


Fig. 8.13 Principal component analysis performed on an integrated data set comprising 106 separate state and pressure variables representing several components of the North Sea ecosystem between 1983 and 2007

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

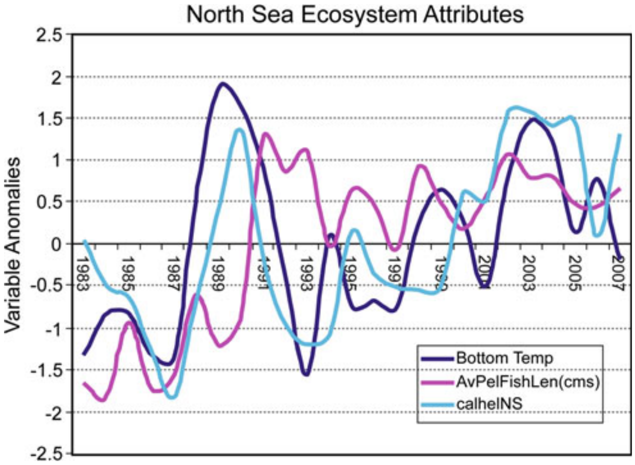


Fig. 8.14 Trends in state of three 'key' components of the North Sea ecosystem; bottom temperature, *Calanus helgolandicus* abundance and average pelagic fish length between 1983 and 2007 (ICES 2009)

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).

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9 Environmental Impacts—Coastal Ecosystems

Jan P. Bakker, Andreas C.W. Baas, Jesper Bartholdy, Laurence Jones, Gerben Ruessink, Stijn Temmerman and Martijn van de Pol

Abstract

This chapter examines the impacts of climate change on the natural coastal ecosystems in the North Sea region. These comprise sandy shores and dunes and salt marshes in estuaries and along the coast. The chapter starts by describing the characteristic geomorphological features of these systems and the importance of sediment transport. Consideration is then given to the role of bioengineering organisms in feedback relationships with substrate, how changes in physical conditions such as embankments affect coastal systems, and the effects of livestock. The effects of climate change—principally accelerated sea-level rise, and changes in the wind climate, temperature and precipitation—on these factors affecting coastal ecosystems are then discussed. Although the focus of this chapter is on the interaction of abiotic conditions and the vegetation, the potential impacts of climate change on the distribution of plant species and on birds breeding in salt marshes is also addressed. Climate impacts on birds, mammals and fish species are covered in other chapters.

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9.1 Introduction

This chapter examines the impacts of climate change on the natural coastal ecosystems in the North Sea region. These comprise sandy shores and dunes and salt marshes in estuaries and along the coast. The chapter starts by describing the characteristic geomorphological features of these systems and the importance of sediment transport. Consideration is then given to the role of bioengineering organisms in feedback relationships with substrate, how changes in physical conditions such as embankments affect coastal systems, and the effects of livestock. The effects of climate change—principally accelerated sea-level rise, and changes in the wind climate, temperature and precipitation—on these factors affecting coastal ecosystems are then discussed. Although the focus of this chapter is on the interaction of abiotic conditions and the vegetation, the potential impacts of climate change on the distribution of plant species and on birds breeding in salt marshes is also addressed. Climate impacts on birds, mammals and fish species are covered in other chapters.

9.2 Geomorphology of Sandy Shores and Coastal Dunes

9.2.1 Distribution and Composition

Andreas C.W. Baas, Gerben Ruessink

The North Sea Basin is ringed by sandy shores and coastal dune fields developed from sedimentary deposits on nearly all sides, except the north-east. The sandy shores include most of the Belgian, Dutch, and Danish coasts as well as various parts of the English North Sea coast, where they alternate with muddy and soft rocky coasts, as well as gravel-dominated coastlines. Extensive dune fields are found along the entire coast of Belgium and the Netherlands, along the sequence of Wadden Sea barrier islands to the Elbe Estuary and up along the entire west coast to the northwest coast of Denmark. These sandy shorelines and dune fields constitute a regional complex developed out of sediment delivered mainly from the Rhine-Meuse delta into the coastal zone, transported via longshore currents following the sweep of the semi-diurnal tide anti-clockwise around the south-eastern coastlines of the North Sea Basin, and being accumulated and driven inland from the beaches by the dominant westerly winds. Coastal dunes along the western Danish coastline cover approximately 800 km^2 (Doody and Skarregaard 2007), while 254 of the 350 km of the coastline of the Netherlands is fronted by approximately 450 km^2 of coastal dune fields extending in some places up to 11 km inland (Doing 1995). Sand dunes also fringe most of the 65 km long coastline of Belgium, covering approximately 38 km^2 and with widths of a few kilometres to less than 100 m, although more than 50 % of the coast has been urbanised (Herrier 2008). The western side of the North Sea Basin is also lined by dune fields along the east coast of the United Kingdom, although these are of a less continuous nature (Doody 2013). Significant dune presence can be found along the northeast of East Anglia, along most of the Lincolnshire coast, isolated stretches along the Yorkshire and Northumbrian coast, and more extensive dune fields along the south-eastern coast of Scotland. The North Sea coastal dunes in the UK are smaller and less extensive than their continental counterparts, because sediment delivery to the coastal zone is from smaller regional catchments (the Thames, the Wash, the Humber), and the easterly winds that propel the dune development are generally weaker and less frequent. A tally of dune fields between Dover and Shetland included in the Sand Dune Vegetation Survey of Great Britain (Dargie 1993; Radley 1994) amounts to 93 km^2 (although a significant proportion of dune fields in Scotland are managed as golf courses).

9.2.2 Current Stressors and Management

In general, sandy shores are alongshore elongated sand bodies whose yearly to decadal evolution is primarily driven by waves and wind. Cross-shore and/or alongshore gradients in sand transport cause coastal morphology to change, reflected by erosion or accumulation of sand. According to a recent EU study of coastal geomorphology and erosion (Eurosion 2004), a large proportion (20–26 %) of the North Sea sandy shores is currently experiencing erosion and, as a consequence, is heavily affected by human activities, such as the presence of hard coastal defence measures (seawalls, groynes) or of regular sand nourishments. It is, however, important to realise that coastal erosion or accretion may vary on a wide range of temporal and spatial scales. A study by Taylor et al. (2004), for example, has shown that the bulk of the North Sea coast of England steepened due to erosion and coastal squeeze over the course of the entire 20th century. On a decadal scale, a coast may gently (typically, a few metres per year) accrete or erode, which is often due to small but persistent gradients in alongshore sediment transport. Shorter-term variations around the decadal trend are often significantly larger, and can be due to episodic erosion events (e.g. dune erosion during a storm) or to the alongshore migration of sand bodies (e.g. Ruessink and Jeuken 2002). Coastal changes may be due to long-period variability and oscillations in wave and storm climate unconnected to climate change (Hadley 2009).

The vast majority of coastal dune systems around the North Sea Basin are tightly managed and controlled for the purpose of various socio-economic and ecoservices (see Electronic (E-)Supplement S9). Along the coasts of Belgium and the Netherlands especially, the main purpose of management has been to preserve and, where possible, expand the sand volume of the foredunes to provide coastal flooding protection and more than 40 % of the foredunes have been artificially preserved or established (Arens and Wiersma 1994), usually by dense marram grass *Ammophila arenaria* planting. In the past two decades a more eco-centred concept has slowly been adopted to allow and encourage limited geomorphic re-activation of wind-blown erosion and bare-sand patches to develop a more varied and species-rich coastal dune environment (Arens and Geelen 2006). Other management practices include grazing activities on grey dunes to combat overgrowth of coarse shrubs (e.g. sea-buckthorn *Hippophae rhamnoides*) to preserve biodiversity (Boorman and Boorman 2001) as well as grazing and sod-cutting on species-rich dune grasslands to prevent grass-encroachment due to nitrification from atmospheric nitrogen deposition (Kooijman and Van der Meulen 1996).

9.2.3 Expected Impacts of Climate Change

Climate change could affect both marine and aeolian boundary conditions. In particular, climate change impacts might be felt through accelerated sea-level rise (SLR) and in modifications in the number, severity and location of extra-tropical storms, with associated changes in wind, wave, precipitation and temperature patterns. The potential consequences of climate change on the North Sea Basin sandy shores and coastal dune systems may be separated into direct geomorphic impacts relating to sea forcing (accelerated SLR and changes in wave climate), wind forcing (changes in weather patterns and wind climate), and potential changes in vegetation character and distribution related to overall climatic changes (temperature and precipitation). Consequences for the vegetation are discussed in Sect. 9.3. Some of these direct impacts may be aggravated by adjustment and intensification of human exploitation and management practices.

9.2.3.1 Sea-Level Rise and Wave Characteristics

Historic tide gauge data for the North Sea region from 1900 to 2011 show a mean SLR of 1.5 ± 0.1 mm year^{-1} (Wahl et al. 2013), slightly below the global mean SLR of 1.7 ± 0.3 mm year^{-1} during the latter half of the 20th century (Church and White 2006). Whereas SLR globally appears to have accelerated to 3.3 ± 0.4 mm year^{-1} from 1993 to 2009 (Ablain et al. 2009, see also Chap 3), the Wahl et al. (2013) study suggests that North Sea SLR acceleration in recent decades is not abnormal, but comparable to that of other periods in the last 200 years. Within the North Sea region local differences have been recorded (as indicated in Table 9.1 in Sect. 9.6.1). While the Intergovernmental Panel on Climate Change (IPCC) in its latest assessment (Van Oldenborgh et al. 2013) projects a global mean SLR of 74 cm by 2100 (at a rate of 11 mm year^{-1}), for the 'business-as-usual' Representative Concentration Pathway scenario (RCP8.5), other studies that include semi-empirical forcing models have projected SLR of between 30 and 180 cm by 2100, depending on the model variant (Nicholls and Cazenave 2010). Recent high-end projections suggest that a 1.25 m SLR in the North Sea may be possible by 2100 (Katsman et al. 2011), although the exact magnitude of the rise strongly depends on underlying modelling assumptions.

Studies on the significant wave height H_s in the North Sea (e.g. Grabemann and Weisse 2008; De Winter et al. 2012) project no to small changes along the Dutch-German coast, with magnitudes depending on the type of general circulation model (GCM) or regional climate model (RCM) used and the particular greenhouse-gas emissions scenario adopted, as for example in Fig. 9.1. For example, Grabemann and Weisse (2008), who used the HadAM3H and the ECHAM4/OPYC3 GCM with SRES scenarios A2 and B2, projected a 0.1–0.3 m increase in the 99th percentile of H_s in front of the Dutch coast by the end of the 21st century, while De Winter et al. (2012), using the ECHAM5/MPI-OM and the SRES A1B scenario, found no detectable change in mean wave conditions. This would seem to indicate that model uncertainty in the prediction of H_s is larger than the emission-induced uncertainty, as was found in general for global projections in the latest IPCC assessment (Van Oldenborgh et al. 2013), which reports low confidence in wave projections because of "uncertain storm geography, limited number of model simulations, and the different methodologies used to downscale climate model results to regional scales".

It is important to consider that the wind, and hence wave climate, shows strong natural variability, which poses a difficulty in detecting climate-change induced trends that are smaller than this natural variability. This is especially relevant to wind and wave conditions with high return periods (for example, 1:1–1:10-year return values, or even rarer) that may be most relevant to coastal erosion. Using the 17-member ESSENCE ensemble (Sterl et al. 2008), De Winter et al. (2012) projected a 0.3–0.6 s decrease in the annual wave period T in front of the Dutch coast for the period 2071–2100, as well as a shift in the wave direction of the annual H_s maxima from north-west to south-west. The decrease in T is induced by this wave-angle shift and associated shifts in the fetch; accordingly, the same shift may lead to an increase in T elsewhere in the North Sea Basin. H_s and T with higher return periods, up to 10,000 years, were

Table 9.1 Regional variation in mean sea-level rise (SLR) within the North Sea region (see also Chap. 3)

Area	SLR mm year^{-1}	Period	Source
Europe	1.7	1900–2000	EEA (2012)
	3	1990–2010	EEA (2012)
Wadden Sea	1–2	1900–2000	Oost et al. (2009)
UK east coast	0.5–2.5	1900–2000	Woodworth et al. (2009)
English channel	0.5–2.5	1900–2000	Haigh et al. (2011)
The Netherlands	2.5	1900–2000	Katsman et al. (2008)
German bight	1.2–2.4	1937–2008	Wahl et al. (2011)
	1–2.8	1951–2008	Wahl et al. (2011)
	2.5–4.6	1971–2008	Wahl et al. (2011)
Lower Saxony, Germany	1.7	1936–2008	Albrecht et al. (2011)
Schleswig-Holstein, Germany	2	1936–2008	Albrecht et al. (2011)
Skallingen, Denmark	2.3	1931–1999	Bartholdy et al. (2004)
	5	1980–2000	Bartholdy et al. (2004)

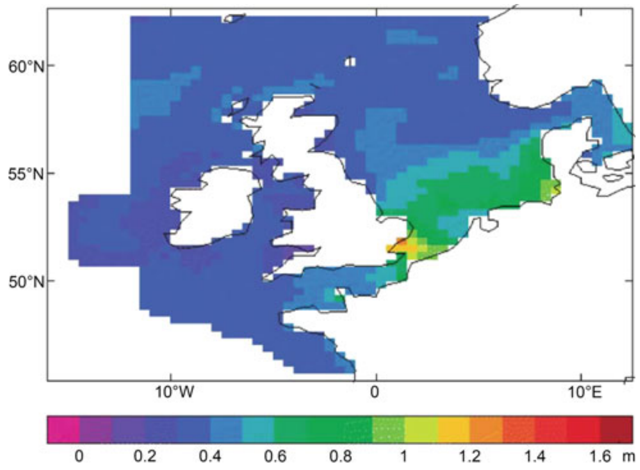

Fig. 9.1 Increase in the height (m) of a 50-year return period extreme water level event, due to combined changes in atmospheric storminess, mean sea-level rise, and vertical land movements, for the SRES A2 scenario, based on the HadRM3H regional atmospheric model and the POL storm-surge model (Lowe and Gregory 2005)

not projected to change significantly at the 95 % confidence level. This also applies to storm surges with similar high return periods (Sterl et al. 2008). In a recent CMIP5 model-comparison study of wind extremes in the North Sea Basin, De Winter et al. (2013) found no changes in annual maximum wind speed or in wind speeds with lower return frequencies for the 2071–2100 period; however, they did find an indication that the annual extreme wind events are coming more often from westerly directions. Thus, these CMIP5 results are not notably different from all earlier CMIP3 (e.g. De Winter et al. 2012) model projections.

The quantitative prediction of the response of sandy shores to climate-change induced effects in the boundary conditions is still under development. The most often used model for the response to accelerated SLR is the Bruun rule (Bruun 1962), a simple two-dimensional mass conservation principle that predicts a landward and upward displacement of the cross-shore profile with SLR (Fig. 9.2). Coastal recession is simply expressed as the product of SLR and the active profile slope, giving typical projected recession distances of 50–200 m depending on profile slope. Although the Bruun rule was routinely used in past decades, its usefulness as a predictive tool is highly controversial (Pilkey and Cooper 2004). For example, the Bruun rule does not include any three-dimensional variability, such as found near engineering structures and tidal inlets, and can thus not be applied in areas with notable gradients in alongshore sediment transport. Also, the Bruun rule predicts sand to be moved offshore during SLR, while overwash and aeolian processes obviously transport sand onshore. Advances have been made in developing more comprehensive conceptual models for understanding and predicting shoreline change in terms of the so-called Coastal Tract (Cowell et al. 2003), but this concept has been aimed at time scales of hundreds to thousands of years. Other more realistic rule-based approaches for predicting shoreline change have been provided by Ranasinghe et al. (2012) and Rosati et al. (2013), but these have not yet been tested on North Sea sandy shores. Beach profile adjustments to accelerated SLR are more likely to involve significant alongshore components and variations as well as greater sensitivities to local changes in sediment budgets (Psuty and Silveira 2010). Even though projections of the North Sea wave climate suggest no to minor change, it is possible that accelerated SLR and changes in wave direction may still aggravate coastal erosion. A modelling study for the UK East Anglian coast, a site with notable alongshore variability in shelf bathymetry, illustrates that

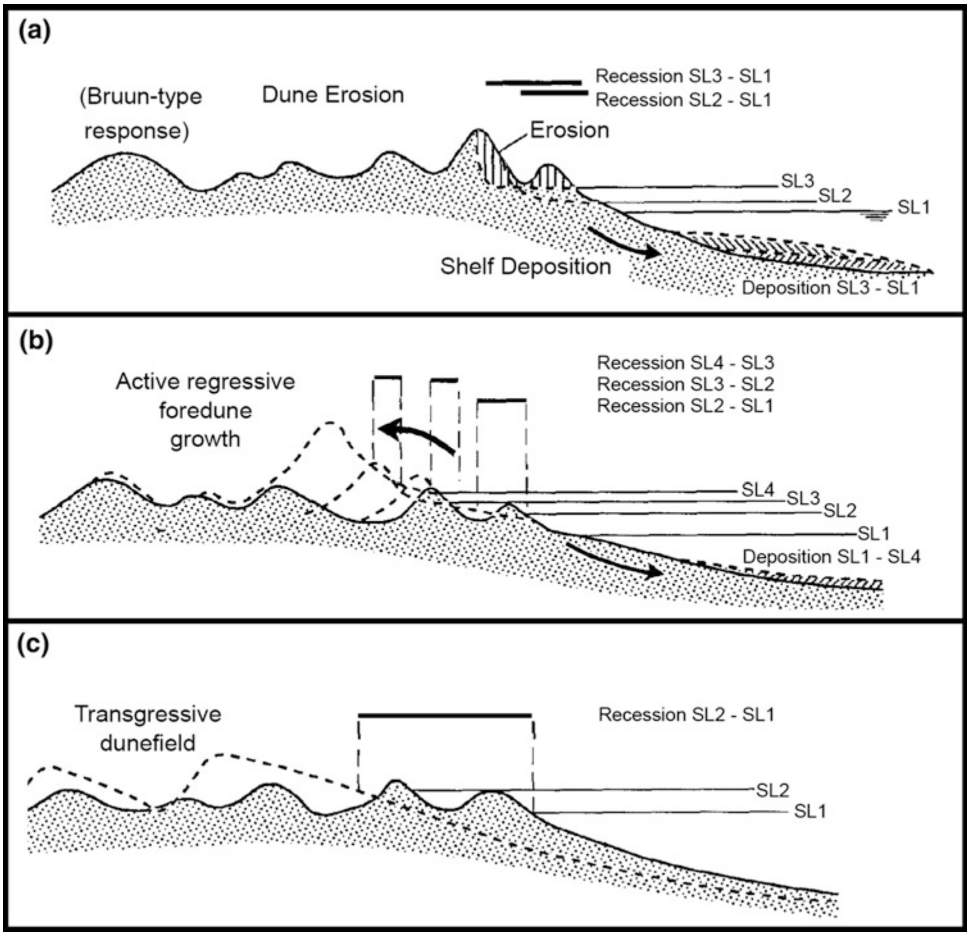

Fig. 9.2 Three potential cross-shore responses to sea-level rise (SLR): **a** Bruun-type response (much disputed) where sediment is redistributed to reach a new equilibrium beach profile; **b** reactivation, growth, and inland migration of foredunes; **c** vegetation cover becomes ineffective leading to a large-scale transgressive dune field (Carter 1991)

inshore wave statistics are sensitive to the trend in SLR and that frequency of occurrence of extreme inshore wave conditions may increase with SLR rates higher than 7 mm year^{-1} (Chini et al. 2010). This, coupled with an increasing occurrence of high water levels by accelerated SLR, may lead to enhanced beach and dune erosion even if wind and wave characteristics remain unaltered under projected climate change; the same effect could also endanger the safety of existing hard coastal defence mechanisms. In a case study for the Dutch coast, De Winter (2014) projected an increase in dune erosion volume by up to 30 % because of a 1-m SLR under unchanged extreme (1:10,000 year) wave conditions. The same case study also illustrated that a change in wave direction by several tens of degrees could lead to a similar increase in dune-erosion volumes as predicted for an approximately 0.4-m rise in sea level, indicating that changes in wind and wave direction are also critically important to coastal response. Such directional changes will also affect the magnitude and, potentially, the sign of gradients in alongshore sand transport, and hence beach width. Current dune-erosion models are primarily based on data collected in laboratory experiments; extensive field validations have, however, not been performed. Furthermore, the models lack descriptions of post-storm coastal recovery by aeolian processes and thus provide an erosion-biased view of coastal evolution. Dunes and beaches are linked in a dynamic and complex sediment exchange system, where losses of sediment from foredunes during storms alternate with inter-storm deposition gains (e.g. Keijsers et al. 2014), potentially leaving the overall shoreline position unchanged in the long term. More frequent storm erosion of the foredune toe may therefore not necessarily result in permanent loss of sediment from the coastal system.

The precise response of the nearshore zone to climatic change and its consequent impact on adjacent coastal dunes is therefore ambiguous and probably subject to substantial regional variation, as in some areas the hydrodynamic boundary conditions may not change very much, while in other areas the coastal sediment budget system will be undergoing complex adjustments. Paradoxically, while sandy beaches in the worst case may get narrower and squeezed between human pressure and accelerated SLR (Carter 1991; Schlacher et al. 2007), the remobilisation and increased dynamics in sediment exchange across the nearshore profile as it is adjusting to SLR may in fact yield an opportunity for reinvigorating coastal dune development

(Psuty and Silveira 2010), as illustrated in Fig. 9.2. Just as during the mid-Holocene, SLR and coastal regression may create opportunities for foredune expansion along some parts of the coastline. This may result from supply of increased amounts of sediment delivered from the adjusting beach profile into the coastal dune system, possibly aided by larger and more frequent storm breach of the dunes, and the potential for greater aeolian sand transport activity in the inland parts of the dune field. This type of landscape response does, however, require the availability of suitable accommodation space for the coastal dune system and in many regions a net landward migration of dunes is arrested by infrastructure and built environment, thus leading to a 'sand dune squeeze' (Doody 2013) and an eventual loss of dune habitat. Coastal squeeze also operates within sites, as the younger, more dynamic habitats including foredunes and yellow dunes may be squeezed against more stable fixed dune grassland, or scrub which occurs in older hind-dune areas. These successionally young habitats are particularly important for many of the dune rare species and, while it is possible for natural remobilisation to occur, it is unlikely under current climatic conditions, since dune mobility is strongly coupled to climate (Clarke and Rendell 2009).

9.2.3.2 Wind Forcing

As previously mentioned, an increase in storminess and associated changes in wind conditions may have implications for the potential of aeolian reactivation of coastal dunes, as well as the wind-blown transport of the additional sediment mobilised as part of beach profiles that are adjusting to accelerated SLR. Regional climate model projections by Beniston et al. (2007) suggest a 5 % increase in the 90th percentile of daily maximum wind speed over most of the North Sea Basin in winter (Fig. 9.3), with storm winds coming from more north-westerly directions.

These projections conflict with the more recent prediction of more south-westerly storm winds by De Winter et al. (2012, 2013). The IPCC meanwhile indicates a "substantial uncertainty and thus low confidence in projecting changes in NH [northern hemisphere] winter storm tracks, especially for the North Atlantic basin" (Van Oldenborgh et al. 2013). The impact of any potential changes in wind climate on the coastal dune fields in the region has not been considered in detail. A shift in dominant wind direction may have a significant impact on the delivery of sediment from the beach into the foredunes due to changes in sub-aerial fetch distance as a function of the local orientation of the coastline (Bauer et al. 2009). For parts of the Dutch and Danish coastline that are aligned SW–NE, for example, a shift to more north-westerly storm winds may therefore result in comparatively shorter fetch distances and less opportunity for aeolian sand transport into the foredunes, as the north-westerly winds will be blowing more perpendicular to the coast. The contemporary geomorphology of the secondary dunes, meanwhile, is aligned to the typical south-westerly winds of the past and the projected shift in wind direction is likely to make it harder for aeolian activity to reactivate dormant blow-outs and parabolic dunes, as it will be acting perpendicular to their main axes and facing greater topographic roughness. Finally, even though there may be an increase in 'drift potential' (the wind power available for aeolian sand transport), its relationship with vegetation cover and associated reactivation of dormant sand dunes shows a distinct hysteresis (Tsoar 2005; Yizhaq et al. 2007), as illustrated in Fig. 9.3. While the future wind climate conditions may become equivalent to those of bare and actively migrating coastal dunes in present-day Israel, for example (as reported in the studies cited here), most North Sea Basin coastal dune fields are situated on the firmly stabilised limb of the hysteresis curve and a reactivation toward active dunes is likely to require more than just an increase in wind power. Recent attempts in the Netherlands to reactivate blowouts and parabolic dunes by removing existing vegetation have so far met with mixed success, with many opened-up sand areas quickly being recolonised and overgrown with vigorous vegetation within a few years (Arens et al. 2013), accelerated by atmospheric nitrogen deposition (Jones et al. 2004). The future change in wind climate may mean that such reactivation attempts become more successful. If not, remobilisation must be assisted by direct management intervention (Arens and Geelen 2006; Jones et al. 2010).

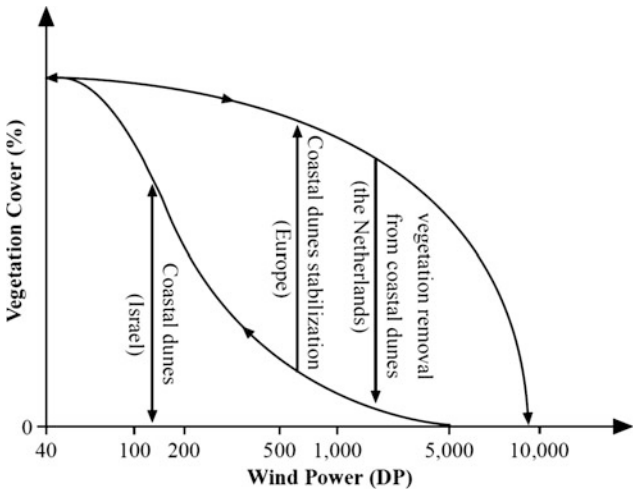

Fig. 9.3 Hysteresis in the relationship between wind power (quantified as a Drift Potential) and the vegetation cover in a coastal dune field (Tsoar 2005)

9.3 Ecology of Sandy Shores and Dunes

Laurence Jones

9.3.1 Climate Change and Dune Ecology

European dune systems have shown constant change over time, with human influences predominating over the last few centuries (Provoost et al. 2011). However, climate change will become an increasingly important influence on dune ecosystems. Climate change is likely to affect coastal dunes in several ways. There will be direct loss of habitat due to accelerated SLR and coastal erosion (see Sect. 9.2), and changes in the climate envelopes affecting the distribution of plant and animal species. There will also be indirect effects through changes in underlying ecosystem processes. These include effects on competition, mediated via plant growth, but also effects on soil development, and groundwater systems which influence the dune wetland communities. This double impact through habitat loss as well as altered climate means that coastal habitats are more sensitive to climate change than the majority of other terrestrial ecosystems. Management of dunes, for example by livestock grazing, may interact with the effects of climate change on the vegetation, but is not discussed here.

9.3.2 Effects of Climate Change on Dry Dune Habitats

General effects of climate change include a lengthening of the growing season, leading to more plant growth where rainfall is not limiting. This is likely to benefit faster growing graminoids and nitrophilous species, and lead to declines in rare species. However, in the drier parts of the North Sea coast such as the Netherlands, increased summer drought may actually reduce the effective growing season, potentially reducing the dominance of some species and allowing other species to flourish. Based on the relationship between drought stress and plant compositional change in Dutch dry dunes (Fig. 9.4), Bartholomeus et al. (2012) suggested that projected increases in the severity of drought may lead to a 15 % increase in the fraction of xerophytes, with potential feedbacks on dune recharge due to reduced evapotranspirative losses (Witte et al. 2012). Levine et al. (2008) predicted an increase in rare dune annuals and Witte et al. (2012) suggested a shift to more xerophytic mosses and lichens and increased cover of bare sand as a consequence of increasing summer drought, with the possible invasion of xeric Ericaceous and broom *Cytisus* species from more southerly European countries. Severe drought has been shown to negatively affect net primary production (NPP) on a European scale (Ciais et al. 2005), and such droughts are predicted to become more frequent.

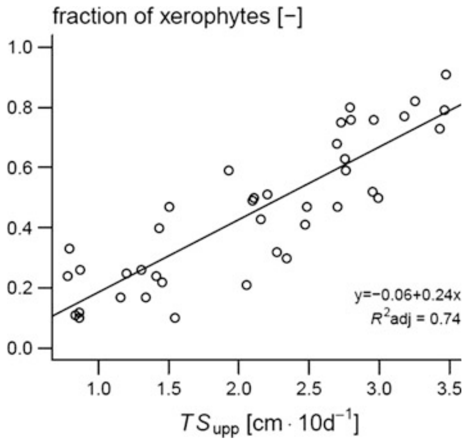

Fig. 9.4 Fraction of xerophytes as a function of the drought stress index TS_{upp} (uppermost transpiration stress) (after Bartholomeus et al. 2012)

The final effects of climate change that may directly impact upon the vegetation that covers most parts of the coastal dune system are changes in temperature and precipitation, and it is here that the great variety of potential climate effects may have a mixture of conflicting positive and negative biological impacts. The Holocene stratigraphic record suggests that warmer and slightly wetter climates in the past have usually resulted in dune stabilisation and full vegetation cover, whereas colder periods with less precipitation, such as the well-documented Little Ice Age, have been associated with more active dune mobility and aeolian sand transport (Pye 2001). The major dune-forming grasses, such as marram grass and sand couch *Elytrigia juncea*, may generally grow better in a CO_2-enriched environment, and may also benefit from the projected 10–15 % increase in precipitation forecast for north-western Europe (Carter 1991). This precipitation is expected to arrive in more extreme and variable events, however, and the potentially drier summers with higher temperatures and greater heatwave risks may also result in greater wildfire incidence in the grasslands covering much of the coastal dune fields, exposing soil to wind erosion and enabling potential dune reactivation. Changes in seasonal temperature and rainfall patterns may also induce changes in species composition. Greater winter precipitation appears to facilitate scrub proliferation and overgrowth, such as sea-buckthorn, while summer droughts have an adverse impact on species diversity in dune slacks through lowering of the water table (Doody 2013). For vegetation on the back beach and foredune toe, meanwhile, simulation studies suggest that accelerated SLR and the narrowing of the beach may constrain plants to such a narrow area that successional processes break down (Feagin et al. 2005). Many of these effects may be difficult to distinguish from more direct anthropogenic impacts, such as grazing, nitrification, groundwater extraction, and changes in land management.

9.3.3 Effects of Climate Change on Wet Dune Habitats

Dune wetlands (slacks) are low-lying depressions between dune ridges, usually in seasonal contact with the water table. They are a highly biodiverse habitat, containing many rare species including plants, invertebrates, and vertebrates (Jones et al. 2011). In addition to the direct influence of temperature, rainfall and length of growing season on plant growth, dune wetlands are highly sensitive to changes in hydrological regime. They are often nitrogen (N) and phosphorus (P) co-limited and dune slack vegetation is dependent on hydrological regime (groundwater level, and seasonal and interannual fluctuations) and groundwater chemistry, particularly buffering capacity (Grootjans et al. 2004). The majority of dune slack plant species of high conservation value are dependent on early successional dune slacks with a high buffering capacity and low nutrient status, and which disappear as slacks decalcify or accumulate nutrients.

9.3.3.1 Groundwater Level

Both accelerated SLR and coastal erosion will lead to a change in dune groundwater tables due to impacts on the hydraulic gradient, with water tables rising (SLR), or falling (steepening of the hydraulic gradient due to coastal erosion). In Denmark it is suggested that slacks which are currently dry will become wetter due to accelerated SLR (Vestergaard 1997). However, some studies suggest that changes in recharge due to altered spatial and seasonal patterns of rainfall and evapotranspiration will have greater effects on groundwater levels than SLR or coastal erosion (Clarke and Sanitwong Na Ayutthaya 2010). In north-west England, dune water tables are predicted to fall over the next 50 years due to negative climate effects on recharge (Clarke and Sanitwong Na Ayutthaya 2010), and this is likely to apply to the majority of English dunes on the North Sea coast. In the Netherlands, recharge is predicted to change relatively little, with either slight decreases or alternatively moderate increases if feedbacks of reduced vegetation cover on the water balance are taken into account (Witte et al. 2012). A modelling study in Belgium assumed there would be increases in recharge to dune groundwater, driven primarily by increased winter precipitation (Vandenbohede et al. 2008). There is as yet little consensus on the likely effects of climate change on dune aquifer recharge and therefore a need for further work on this topic. There have also been very few studies on the impacts of changing water tables on the flora and fauna of dune wetlands. Van Dobben and Slim (2012) using a study of land subsidence due to gas extraction on the barrier island of Ameland in the Netherlands as an analogue for accelerated SLR, suggested that dune vegetation would move towards dune slacks (i.e. become wetter). In the UK, Curreli et al. (2013) showed that differences in mean water table level of only 20 cm differentiate between dune slack vegetation communities, with 40 cm separating the wettest and the driest communities. Based on predictions of falling groundwater levels for a west coast UK dune system (Clarke and Sanitwong Na Ayutthaya 2010), although outside the area of this assessment, Curreli et al. (2013) suggested that climate change may alter what are currently wet slack communities to dry slack or even dry dune grassland by the 2080s (Fig. 9.5). Changes in water table levels are also likely to affect breeding success of the Annex II listed natterjack toad *Epidalea calamita* which requires slacks to dry out in summer to avoid colonisation by fish predators and competitors, but needs water levels to be maintained long enough for the tadpoles to develop into toadlets. April to July is the critical breeding time for this species.

9.3.3.2 Groundwater Chemistry

Dune groundwater composition is sensitive to atmospheric N-deposition and nitrogen and phosphorus inputs from other sources. In dune groundwater, it has been suggested that above total inorganic nitrogen concentrations of 0.2–0.4 mg TIN l^{-1} there may be adverse impacts on dune slack species and soils (Davy et al. 2010), although this threshold has not been tested empirically in dunes.

Although there is relatively little research into the effects of climate change on dune groundwater chemistry, it could be expected to change in the following ways. Rates of mineralisation of soil organic matter are likely to increase due to higher temperatures (Emmett et al. 2004) and an extended growing season (Linderholm 2006) in the majority of North Sea coastal areas, particularly in the north. This will lead to increased production of both nitrates (NO_3) and dissolved organic nitrogen (DON), inevitably increasing N-leaching fluxes to the groundwater. This may not occur in the southern North Sea area however, due to increased soil-moisture deficits in summer acting to reduce mineralisation. In areas with falling groundwater levels due to climate change, or where there is an influence of external groundwater or surface waters on a site, there is potential for nutrient concentrations entering the site to be higher if these source waters become concentrated due to higher evapotranspiration rates and subsequent reduced runoff and lower river flows. Such a mechanism is suggested for altered water composition of the River Meuse under climate change (Van Vliet and Zwolsman 2008). The opposite may occur in the north of the region where runoff is expected to increase (DiPOL 2012).

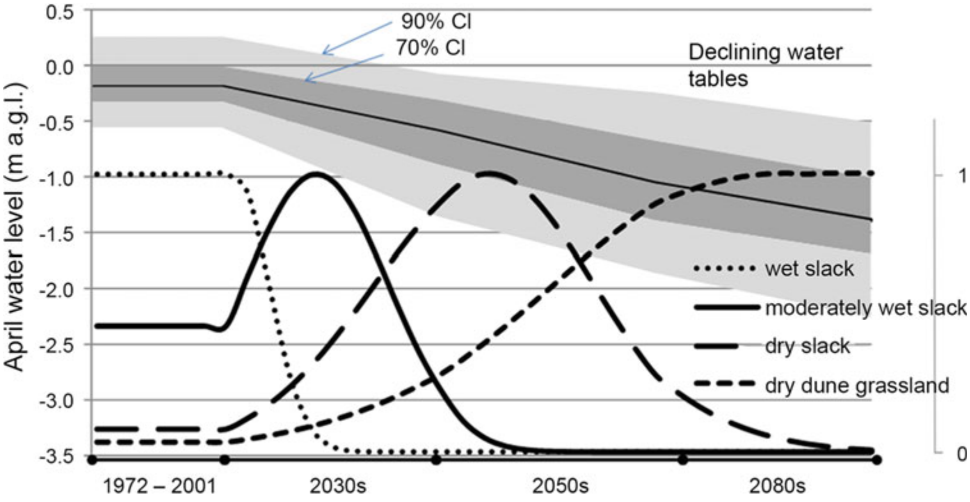

Fig. 9.5 Projections of April groundwater level to the 2080s for a UK site under UKCIP02 medium-high emissions scenario (SRES A2) (Hulme et al. 2002), showing the 70 and 90 % confidence intervals (CI), and corresponding frequency distributions for dune slack communities based on those water levels (after Curreli et al. 2013)

9.3.3.3 Interactions with Hydrological Management

Hydrological management both on- and off-site can affect water composition. A lowering of the water table due to drainage, water abstraction or other causes such as high evapotranspiration from forest, may allow groundwater influx from other sources such as streams or drainage ditches bordering the site or groundwater from inland. The danger is greatest in late summer when dune groundwater tables are at their lowest. These other hydrological inputs to the groundwater may contain high levels of nutrients or other chemicals which affect water composition, particularly if they drain agricultural land. Alterations to the management of hydrological regimes in response to climate change therefore also have the potential to impact dune groundwater chemistry.

9.3.4 Climate Change Effects on Individual Species

Climate change is likely to affect the distributions of individual dune plant species, although there have been relatively few studies on this topic. In Denmark, a study looking at spatial analogues of predicted climate in 2100 suggests that coastal heaths and sand dune vegetation are likely to be vulnerable, particularly the communities “decalcified fixed dunes with *Empetrum nigrum*” (type 2140 according to Annex I of the Habitats Directive; European Commission 1992) and “fixed coastal dunes with herbaceous vegetation” (‘grey dunes’, type 2130) (Skov et al. 2009). The study lists 17 species which may disappear including crowberry *Empetrum nigrum* and sea brookweed *Samolus valerandi*, and 25 coastal species likely to move north into Denmark, some of which may become problem species. In the UK, the Monarch programme modelled changing climate envelopes for a wide variety of species, including some dune species. Generally species ranges shifted northwards and westwards with marsh helleborine *Epipactis palustris* and the natterjack toad potentially gaining climate space in the UK, while the variegated horsetail *Equisetum variegatum* which has a predominantly northern distribution in the UK would lose climate space (Harrison et al. 2001). Note these are predicted changes in climatic envelopes, and do not take into account the subtleties of changing recharge which might affect dune groundwater levels in a different way (see Sect. 9.3.3.3). The more recent BRANCH project modelled changing climate space of 386 plant and animal species, and predicted that the fen orchid *Liparis loeselii* was likely to lose more than 90 % of its climate space by 2080 (Berry et al. 2007). Metzing (2010) modelled the northward shift of the dune grass *Leymus arenarius* in Europe, which would completely disappear from current parts of its range in the southern North Sea areas of Germany, the Netherlands, Denmark and England under the worst-case scenario by 2050 (Fig. 9.6).

9.3.5 Other Climate Change Impacts

9.3.5.1 Invasive Species

There is much evidence in aquatic systems that invasive species may be favoured by climate change. In terrestrial systems, there is far less evidence for this. However, certain plant species such as bird cherry *Prunus serotina* in the Netherlands and Belgium (Baeyens and Martínez 2004) and Japanese rose *Rosa rugosa* in Germany (Isermann 2008) have become highly invasive in dune systems, despite being present on the systems for many decades. It is unclear why their extent has suddenly increased, but changes in climate (warmer winters and fewer severe frosts are one suggestion), while the combination of changing climate and elevated nutrient levels in dune soils due to N-deposition may be a contributory factor. Although invasive species may initially enhance species richness, once tall species become dominant they can outcompete low-statured species, and decrease species richness.

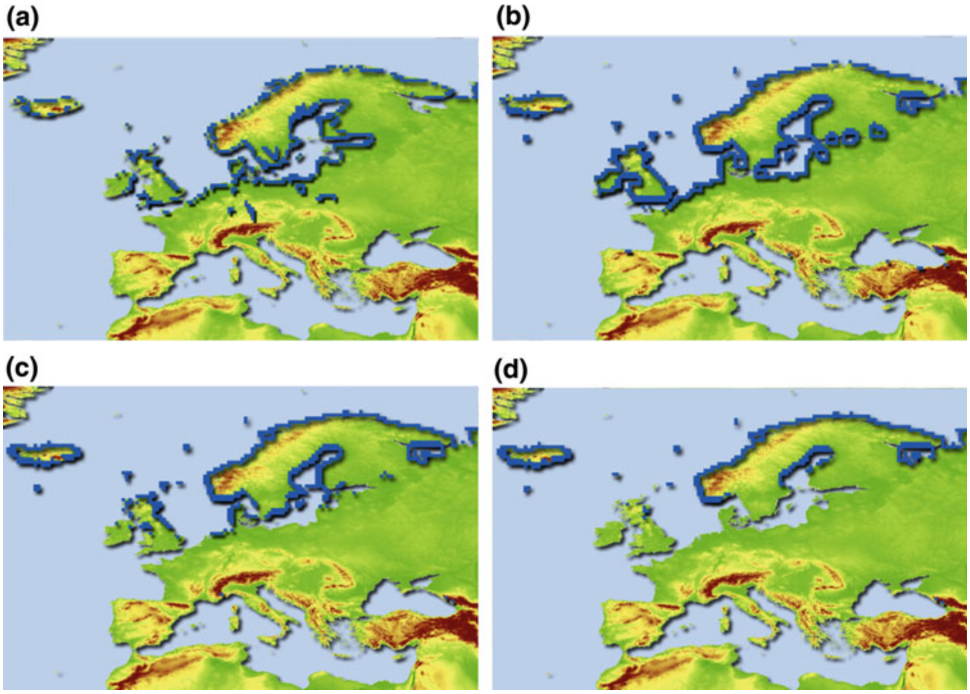

Fig. 9.6 Distribution of the dune grass *Leymus arenarius* in Europe showing: **a**. current distribution, **b**. modelled distribution under recent climate, **c**. distribution under 2050 a best-case climate warming of 1.5 °C and **d**. distribution under a worst-case climate warming of 2.5 °C (Metzing 2010)

9.3.5.2 Impacts on Soils

Where higher temperatures cause greater plant growth, the increased plant production will stimulate soil development through greater litter inputs. Rates of soil organic matter accumulation represent a balance between plant productivity and rates of organic matter decomposition. While the net balance is unknown for many habitats, a dune chronosequence study over the last 60 years linked faster rates of soil development to periods of higher temperatures, and to periods with lower rainfall (Fig. 9.7) (Jones et al. 2008); changes were also correlated with increasing N-deposition. Other changes in soils may include decalcification rates. The rate of leaching of carbonates from dune soils is largely a function of rainfall, therefore changes in rainfall are likely to lead to increases or decreases in decalcification rates of dune soils.

9.3.5.3 Atmospheric Nitrogen Deposition and Interactions with Climate Change

Atmospheric deposition remains a significant source of nitrogen input in many countries around the North Sea, particularly the Netherlands and Denmark. Recent trends in N-deposition in Europe have shown some decline in NO_X emissions and are forecast to decrease further for oxidised nitrogen, but only slightly for reduced nitrogen (Winiwarter et al. 2011). Climate is a strong determining factor in the balance of wet and dry N-deposition, and involves complex interacting processes. Relatively little is known about how climate change may affect N-deposition but is not expected to alter deposition of oxidised nitrogen much (Langner et al. 2005), and it is generally assumed that changes in emissions will have a greater impact on atmospheric deposition than any climate-related effect (Mayerhofer et al. 2002).

Along gradients in atmospheric deposition, studies have shown increased plant production and a decrease in species richness in dunes with higher atmospheric deposition (Fig. 9.8) (Jones et al. 2004; Hall et al. 2011). An increase in biomass occurs above critical levels of 10–20 kg N ha^{-1} year^{-1} in dry dune communities (EUNIS types B1.3, B1.4, B1.5) and above 10–25 kg N ha^{-1} year^{-1} in dune slack

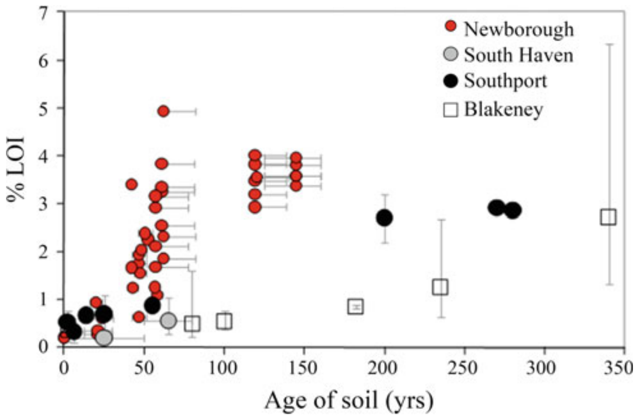

Fig. 9.7 Changes in soil organic matter accumulation in a recent dune soil chronosequence in the UK (Newborough), compared with older UK published chronosequence studies (South Haven 1960; Southport 1925; Blakeney 1922), after Jones et al. (2008)

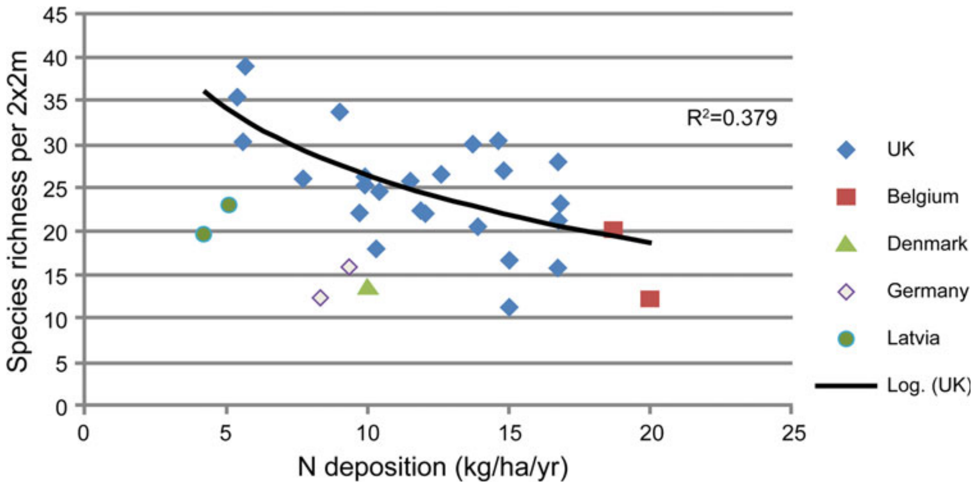

Fig. 9.8 Change in species richness of de-calcified dunes in north-western Europe along a gradient of atmospheric nitrogen (N) deposition (after Hall et al. 2011)

communities (EUNIS type B1.8) (Bobbink et al. 2010). The atmospheric deposition of nitrogen in combination with the release of phosphorous from enhanced mineralisation may result in increased plant production and further spread of grasses (Kooijman et al. 2012).

There is little direct or indirect evidence from dunes of interactions between climate change and N-deposition, although studies in other ecosystems suggest that the combination of higher temperatures and increased rainfall, which are both projected to occur in the northern North Sea dune systems, will lead to faster mineralisation of soil organic matter (Rustad et al. 2001), and therefore faster N-cycling. This may remobilise stored nitrogen in soils and increase leaching of dissolved organic nitrogen (DON) into dune groundwater. There are indications that higher DON concentrations in dune groundwater, which thereby increase the negative impacts of N-deposition are correlated with higher N-deposition (Jones et al. 2002), suggesting that impacts could be worse in areas of high nitrogen inputs. However, in the southern North Sea area where summer soil moisture deficits act to reduce mineralisation rates, there may be less N-leaching into groundwater as a result.

9.4 Fine-Grained Sediment Transport and Deposition in Back-Barrier Areas

Jesper Bartholdy

9.4.1 Physical Conditions

As a shallow semi-enclosed shelf sea, the North Sea imports fine-grained sediment (silt, clay, organic material) from the adjacent North Atlantic. The net import across the transect between Scotland and Norway each year is estimated at 7 million tons and through the Channel at about 14 million tons (Pohlmann and Puls 1993). Due to the generally anti-clockwise circulation in the North Sea, the sediment contribution from the Channel is carried northward where it mixes with sediment of terrestrial origin carried into the North Sea from rivers draining north-western Europe. Part of this flux of fine-grained sediment passes the German Bight close to land and then continues northward as part of the Jutland Current. During this passage, the tidal exchange between the North Sea and the extensive barrier system of the Wadden Sea induces a net landward transport of sediment into the sheltered tidal areas behind the barrier islands.

This import is due to lag effects first described by Postma (1954, 1961, 1967) and Van Straaten and Kuenen (1957, 1958). At high tide, the shift between flood and ebb is slower and involves larger excursions of the water, than the shift between ebb and flood at low tide. Together with the fact that it takes time for a suspended particle to settle out during slack water (*settling lag*) and that erosion/resuspension of a settled fine-grained particle—due to adhesion—demands stronger currents than those in which the particle settled out (*scour lag*), this asymmetry causes a landward shift of sediment for each tidal period. The effect is enhanced by the apparent paradox that the average water depth in a tidal area is smallest during high tide and largest during low tide. A randomly located suspended particle in the exchanged water mass is therefore less prone to settle out during low tide, when only the relatively deep channels are inundated than it is during high tide, where the whole tidal area is inundated with a relatively small mean water depth. A quantitative model of the involved processes during settling and resuspension of sediment particles in tidal currents have shown that *scour lag* is by far the most important mechanism concerning import of fine-grained sediment into the Wadden Sea (Bartholdy 2000). Calibrated on the basis of

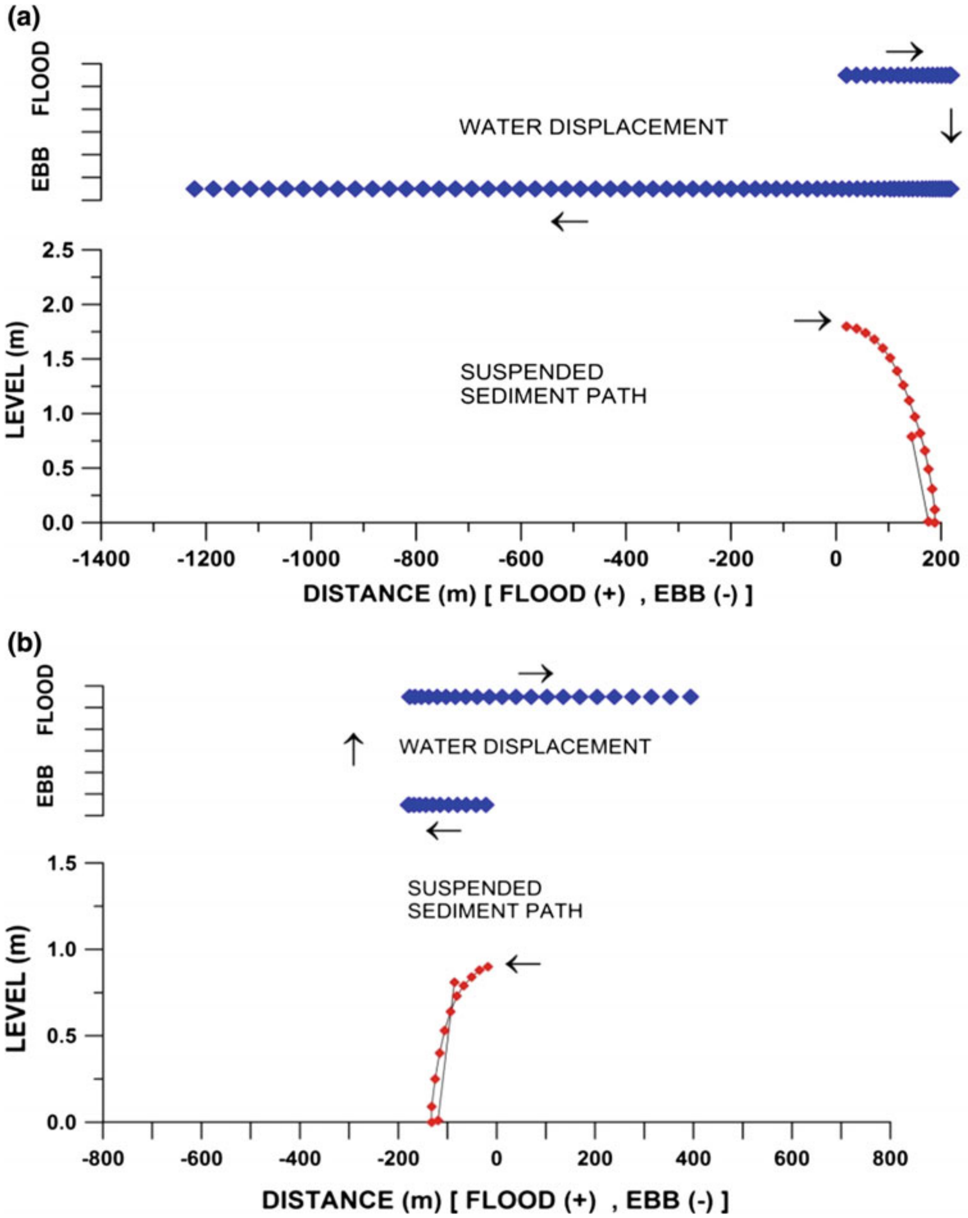

Fig. 9.9 Principals of the import of fine-grained material to tidal areas due to settling lag and scour lag. **a** The location of a water parcel (*blue*) and sediment particle (*red*) is tracked at time intervals of 100 s over a high tide period in the inner part of a tidal area. The tracking takes place from the time the particle starts to settle (at 0 m) to the time it is resuspended (at −1200 m). During the period when the particle settles out, it is transported a distance of 200 m inland (settling lag). From here it is stable on the *bottom* until the water parcel which delivered it has moved 1200 m seawards of the zero point (scour lag). First when the original water parcel has moved to here, current velocity at the location of the settled particle is large enough to resuspend it. Thus, the combined effect of settling lag and scour lag is a shift of the sediment particle to be suspended in a new water parcel located (200 + 1200 m) 1400 m inland. **b** The same dynamics over the low water period in the tidal inlet. Here the settling lag is about 120 m and the scour lag about 400 m. Combined, the seaward shift is therefore (120 + 400 m) 520 m. The joint shift over both flood and ebb is thus (1400–520 m) 880 m in an inland direction (after Bartholdy 2000)

the dynamic conditions in the tidal area Grådyb in the Danish Wadden Sea, the model showed a typical net landward migration on the order of 1 km for each tide due to lag effects (Fig. 9.9).

As a consequence of the lag effects, fine-grained sediments concentrate and form mud flats in inner parts of the Wadden Sea. During storms where wind tide increases the water level and waves resuspend fine-grained sediments from these mud deposits, adjacent salt-marsh areas get inundated by turbid water and sedimentation of fine-grained sediment takes place on the marsh surface during high tide slack water. Because of the sheltering salt-marsh plants, resuspension of

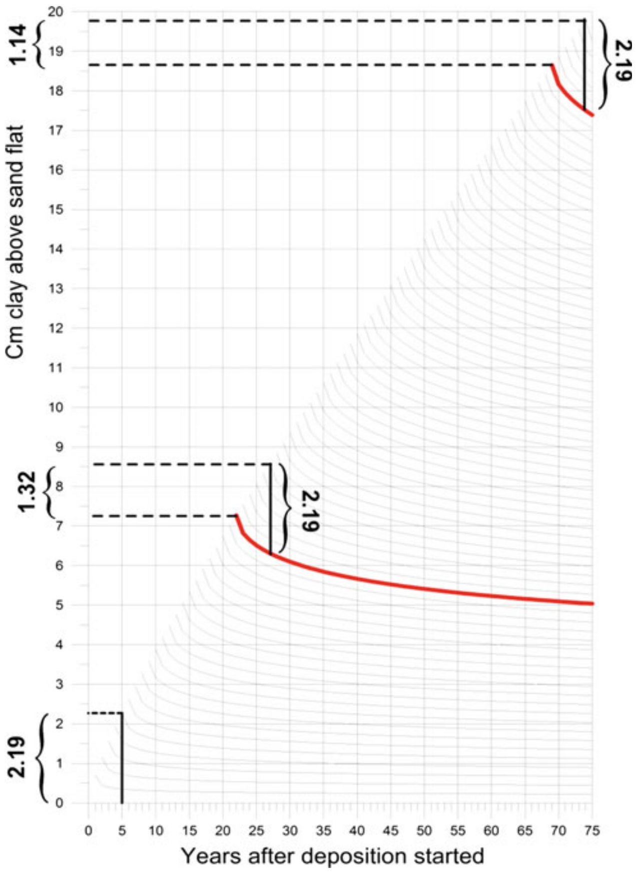

Fig. 9.10 Autocompaction in a salt marsh deposition on top of an incompressible sand flat. The accumulation rate is a constant 1.7 kg m^{-2} year^{-1}. The *semi-horizontal lines* represent yearly locations of former salt-marsh surfaces in the sediment column. The *left-hand* end of these *lines* represents the salt-marsh surface location above the sand flat at the year of deposition. After five years of deposition, the salt-marsh thickness above the sand flat is 2.19 cm. The *two red lines* represent years where the salt marsh was marked by a tracer. As it appears five years of deposition also add 2.19 cm on top of the marker horizon; but because of compaction the absolute level increase of the salt-marsh surface, 70 years after deposition, is only about half of this amount, 1.14 cm (after Bartholdy et al. 2010a)

the settled particles is impeded in the succeeding ebb current, and salt marsh therefore forms the end destination of silt, clay and organic material introduced into the Wadden Sea from the North Sea and local sources. The contribution from the North Sea is by far the largest concerning the net deposition. A combined sediment budget based on results from Pejrup et al. (1997) and Pedersen and Bartholdy (2006) for the four northernmost tidal areas in the Wadden Sea (Lister Tief, Juvre Dyb, Knude Dyb and Grådyb) covering an area of 855 km^2 including salt marshes, shows an accumulation of fine-grained material of 230,000 t year^{-1} of which 64 % is derived from the North Sea, 14 % from primary production, 12 % from local rivers, 9 % from coastal erosion and 1 % from atmospheric deposition.

Once deposited on the salt-marsh surface, the fine-grained sediment consolidates due to autocompaction (e.g. Cahoon et al. 1995, 2000). This process causes the bulk dry density to vary from the top layer downwards as a logarithmic increasing function (Bartholdy et al. 2010a). Because of this, it can be misleading to measure salt-marsh accumulation by means of level/thickness change alone. Bartholdy et al. (2010a) showed that on the Skallingen back-barrier marsh in the Danish Wadden Sea, a constant accumulation (weight/area/time) can give half of its initial value of accretion (thickness change/time) after about 70 years of sedimentation (Fig. 9.10).

Sand is also found in salt marshes. Most of it is mobilised from adjacent sandy tidal flats and deposited on the salt marsh during storms. Not many direct measurements have been carried out on the effects of a storm surge on sediment transport. On 3–4 December 1999 during a storm surge at the back-barrier marsh of Skallingen, the suspended sediment concentration (SSC) on the intertidal flats increased from 10 to 200 mg l^{-1}, and the mobile layer of the intertidal flat was removed. The estimated sediment deposition on the salt marsh was 0.15 mm. This is only about 50 % higher than that of a previously monitored storm, and corresponds to <10 % of the annual deposition at the site (Bartholdy and Aagaard 2001). These authors concluded that the effects of storms on deposition depend on the season as well as the sequence of previous import and high-energy events. One extreme periodic storm can be of less importance for annual variations in salt-marsh deposition than more frequent minor surges (Bartholdy and Aagaard 2001; Bartholdy et al. 2004). During deep storms, flooding wave energy may be too strong to be affected by the local vegetation structure and hence prevent settlement of sediment, or may even cause erosion (Silva et al. 2009). Apart from the quantity of material deposited during storm surges, its composition may also be affected. The occurrence of storms can be reflected in the grain-size distribution of the deposited sediment (Allen 2000). The occurrence of dated thin sand layers at the back-barrier marsh of Schiermonnikoog (Netherlands), suggests that storms capable of depositing sand in the marsh occur about every decade (De Groot et al. 2011). Storm-related coarse-grained layers and sand deposits may occur at various locations within a salt marsh. At the back-barrier marsh of Schiermonnikoog, sand layers occur on 20 % of the marsh area and are partly associated with the local sources of the sand (i.e. marsh creeks, the salt-marsh edge and washovers). In total, sand layers contribute less than 10 % of the volume of marsh deposits on Schiermonnikoog (De Groot et al. 2011). The back-barrier marsh of Skallingen contains about 15 % sand (Bartholdy 1997). Deposition of sand layers after storm surges has also been reported from intertidal flats and salt marshes in the Leybucht on the mainland coast of Germany (Reineck 1980).

9.4.2 Effects of Climate Change

9.4.2.1 Sea-Level Rise

Studies on the development of salt marshes in relation to climate change almost exclusively deal with their ability to survive different SLR scenarios. As a rule, the critical level for salt-marsh survival is taken to be close to the mean high tide (MHT) level, usually considered as the level describing the border between the pioneer zone and the lower marsh (see Fig. 9.16 in Sect. 9.6). Assessments of salt-marsh survival are normally based on accretion models built on the basis of the continuity equation for salt-marsh sedimentation (e.g. Allen 1990). French (1993) added different types of semi-empirical equations of deposition, usually based on either a constant characteristic concentration of suspended sediment in the flooding water or concentrations positively correlated with the MHT level (e.g. Temmerman et al. 2003; Bartholdy et al. 2004). The organic component of salt marshes in the Wadden Sea is usually 10–20 %, of which the major part is deposited together with the mineral part of the sediment. An additional source of organic material, the so-called belowground production, is small and either incorporated in the model calibration or added as a constant value.

French (1993) estimated the organic contribution to accretion for a British salt marsh to be about 0.2 mm year^{-1}. Running this type of model for the Skallingen back-barrier marsh, sedimentation was shown to correlate with the North Atlantic Oscillation (NAO) winter index which explained about 63 % of the variation in the period 1970–1999 (Bartholdy et al. 2004). Using an improved version of the model, Bartholdy et al. (2010b) modelled the distribution of salt-marsh sedimentation on the Skallingen back-barrier marsh (Fig. 9.11) and analysed its vulnerability to different SLR scenarios. This type of assessment is either based on a balance between SLR and salt-marsh accretion or on identifying the SLR during which the salt marsh will survive a certain number of years. The latter approach is most common, as the time it takes to reach a genuine balance can be unrealistically long for a constant SLR scenario (e.g. Fig. 9.12). It was found for the Skallingen salt marsh that for the next 100 years, the salt marsh could survive a SLR of about 4 mm year^{-1} while a SLR of 6 mm year^{-1} would drown the inner part, and the outer part—the salt-marsh edge—would just survive. For a salt marsh further south on the German island of Sylt, Schuerch et al. (2013) found a similar although considerable larger mean SLR of close to 20 mm year^{-1}. Both values are considered realistic for Wadden Sea salt marshes.

Predictions of this type depend primarily on the amount of sediment available in the close vicinity of the salt marsh, and this can vary considerably from place to place. This parameter can also vary in time, and represents the most obvious source of error in such assessments. As all models

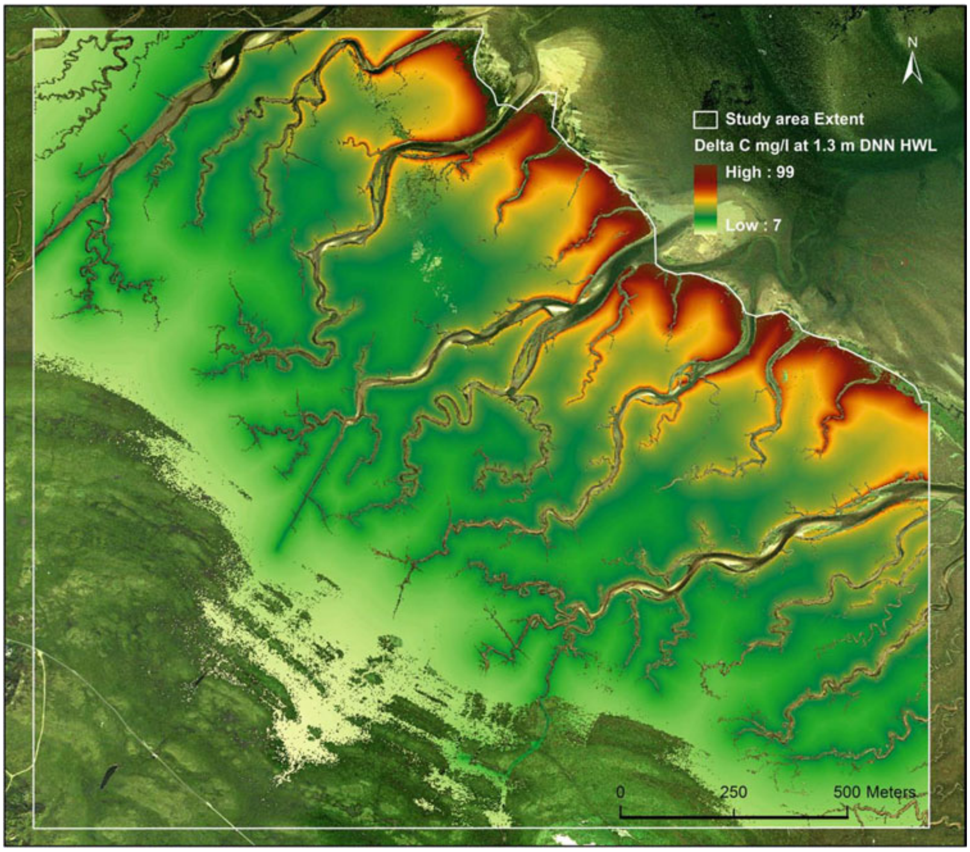

Fig. 9.11 Distribution of the typical deposition of suspended sediment in flooding water over the Skallingen back-barrier marsh at a high water level of 1.3 m Danish Normal Nul DNN (with about 0.5 m of water inundating the salt marsh). This level is the most effective high water level in terms of both frequency and concentration in relation to salt-marsh deposition. The map is superimposed on an aerial photo visible outside the modelled area and in the salt-marsh creeks (after Bartholdy et al. 2010b)

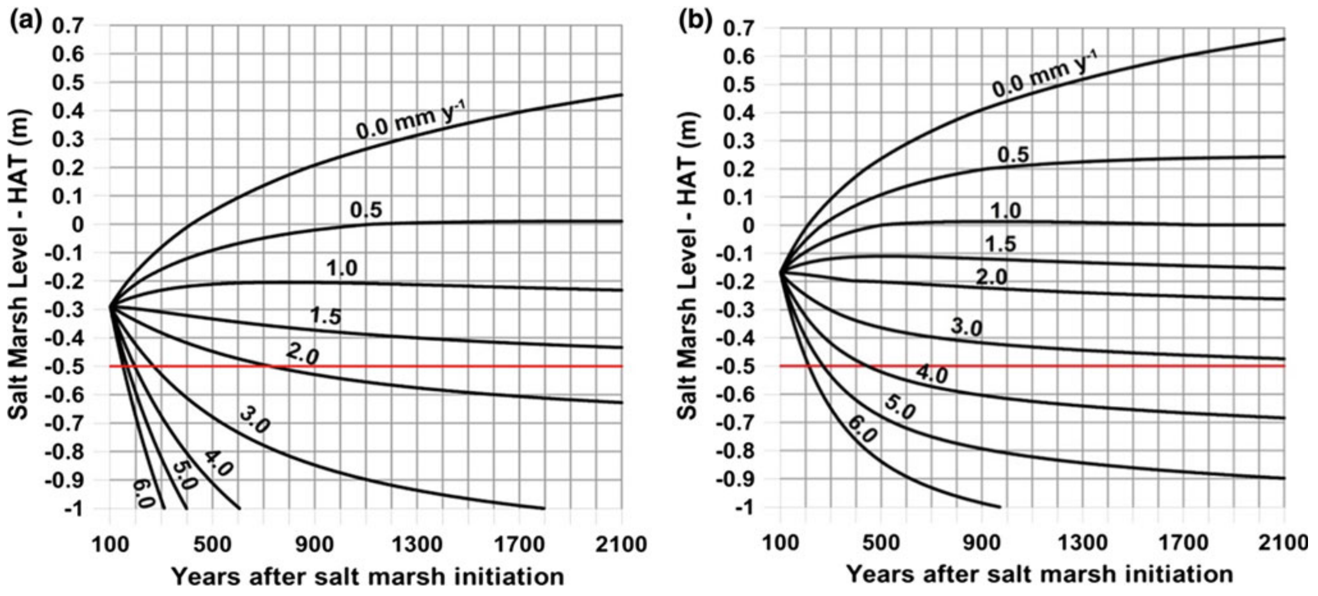

Fig. 9.12 Modelled salt-marsh level at the Skallingen back-barrier marsh minus the highest astronomical high tide level (HAT) for different sea-level rise (SLR) scenarios. A difference between the two of −0.5 m represents the mean high tide level, and is regarded as the lower limit for salt-marsh growth. The start time of 100 years is chosen because the salt marsh is about 100 years old. **a** Conditions characteristic of the central section of the back-barrier marsh. **b** Conditions characteristic for the area close to the salt-marsh edge (Bartholdy et al. 2010b)

are based on a calibration related to actual conditions, they will not make correct predictions of salt-marsh sedimentation if the sediment supply should for whatever reason change over time. The above-mentioned results, however, do not indicate any immediate threat to Wadden Sea salt marshes in general, including back-barrier marshes and mainland marshes. Slow-growing marshes such as that on the Skallingen peninsula, may become threatened in 50 years or so if SLR accelerates to much over 5 mm year^{-1}.

9.4.2.2 Wind Climate

In addition to sediment availability, sediment dynamics (and thus ultimately changes in for example, wind climate) can also play an important role in salt-marsh sedimentation. A major feature related to this is illustrated by the difference between the Wadden Sea and similar areas on the east coast of the USA. Both areas are subject to salt-marsh formation but the salt marshes are very different. In the Wadden Sea, livestock can graze on salt marshes in summer, something which is impossible in the soft mud of the salt marshes in Georgia, for example. The reason for this is the wind-tide effect which is present in the Wadden Sea and absent in Georgia. Because of this, salt marshes in the Wadden Sea quickly grow higher than the highest astronomical tide (HAT), something that never happens in Georgia (Bartholdy 2012). The dry firm summer salt-marsh areas above HAT in the Wadden Sea, therefore appear totally different from the frequently inundated, soft and unsuitable for livestock-grazing salt marshes of Georgia. The two salt-marsh types can therefore be regarded as occurring at opposite ends of a continuum of salt-marsh types directly affected by climate change in terms of changes in wind climate.

9.5 Estuaries: Geomorphology and Sediment Transport

Stijn Temmerman

9.5.1 General Properties

Major estuaries around the North Sea include the Western Scheldt (Belgium and the Netherlands), Eastern Scheldt (the Netherlands), Ems-Dollard (the Netherlands and Germany), Weser (Germany), Elbe (Germany), Firth of Forth (UK), Humber (UK), and Greater Thames (UK). Although historic human modification of these estuaries is very important (see Sect. 9.5.2), their geomorphology is generally characterised by an overall funnel-shaped, landward converging form, including landforms such as subtidal channels, sub- and intertidal sandy shoals or bars, intertidal mudflats and intertidal marshes (ranging from salt, brackish to freshwater tidal marshes) (Fig. 9.13) (Seminara et al. 2001; Prandle 2004; Dronkers 2005; Van Maanen et al. 2013). In the most downstream, wider part of the estuaries the subtidal channel system often comprises multiple channels, including flood and ebb channels, which develop as a consequence of the

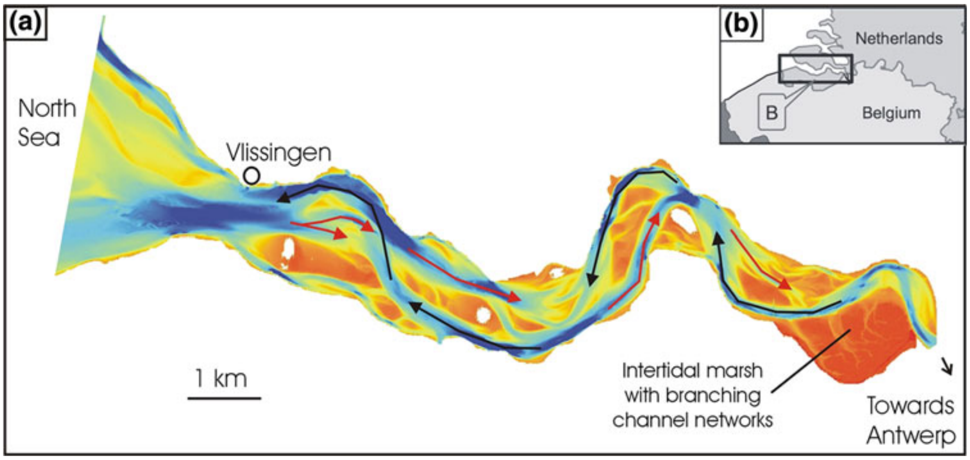

Fig. 9.13 Typical example of a North Sea estuary, the Scheldt estuary, SW Netherlands and Belgium. **a** General location. **b** Bathymetry of the most downstream section of the estuary (up to the Dutch-Belgian border). *Red areas* indicate intertidal flats and marshes; *yellow* and *blue areas* indicate subtidal areas; *darker blue* indicates deeper areas. Flood and ebb channels are indicated with *red* and *black arrows*, respectively. *Note* as for almost all estuaries around the North Sea, human modification of the estuary is important mainly due to large historical embankments of intertidal areas (around 100,000 ha over the last 1000 years) and channel dredging (deepening of sills between the North Sea and port of Antwerp)

semi-diurnal alternating flood and ebb flow directions and inertia in the water movement (Fig. 9.13). More upstream, estuarine channel width and depth decrease and the multiple channel system generally converges towards a single channel system. Branching channel networks typically develop where extensive intertidal flats and marshes are tidally flooded and drained (Fig. 9.13). The most downstream section may transition into a back-barrier tidal lagoon system such as in the Wadden Sea area (e.g. Ems-Dollard, Weser, Elbe) with back-barrier marshes.

The coarse-grained bedload transport is most intense in the subtidal channels and therefore is most determining for the morphodynamic evolution of these channels, while the suspended sediment is more important for the evolution of the intertidal mudflats and marshes. As a consequence of (1) the tidal pumping of sediments, (2) estuarine circulation due to stratification or partial mixing of salt seawater and fresh river water, and (3) settling and scour lag effects as described for the Wadden Sea (see also Sect. 9.4), the more downstream part of estuaries is generally dominated by a net landward transport of sediments of a marine origin; while in the most upstream part of estuaries there is an input of terrestrial sediments through rivers that discharge into the estuary. As a consequence of these converging sediment transport directions, and in combination with flocculation processes, the SSC typically reaches a maximum in the so-called estuarine turbidity maximum (ETM) zone (Fig. 9.14) (e.g. Dyer 1997). The existence of an ETM is well-documented for most estuaries in the North Sea region (e.g. Uncles et al. 2002), and may have important implications for the estuarine ecosystem, because turbidity controls the depth of light penetration into the water column and thereby the potential limitation of primary production by phytoplankton if turbidity is too high (e.g. Cloern 1987). Furthermore, the SSC determines the capacity of intertidal mudflats and marshes to grow with SLR by sediment accretion (more details in Sect. 9.5.3.1).

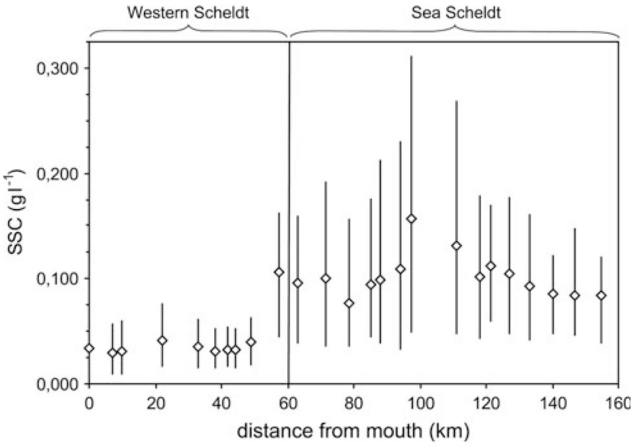

Fig. 9.14 Time-averaged longitudinal variation in suspended sediment concentration (SSC) along the Scheldt estuary, calculated from monthly monitoring data for 1996–2001, showing the presence of an Estuarine Turbidity Maximum (ETM) zone at around 100 km from the estuary mouth in the North Sea. *Error bars* represent the 10th and 90th percentiles of all SSC measurements at a station (after Temmerman et al. 2004)

The SSC may also depend on sediment surface stability depending on biological controls. These can be divided into biostabilisation and biodestabilisation, with sediment surface stability ultimately dependent on the balance between the two competing sets of processes. This balance varies spatially, both vertically within the tidal frame and horizontally along the estuarine salinity gradient, and temporally, on seasonal, interannual and perhaps longer timescales. These patterns have implications for estuarine morphology; strong biostabilisation will lead to a flatter profile because flood and ebb tidal pulses will be less effective on intertidal flat surfaces. Conversely, destabilisation will lead to lower critical shear stresses for erosion and thus result in steeper profiles. In general, biostabilisation is associated with microorganisms and biodestabilisation with a benthic macrofauna. Thus, for the Humber estuary (UK), Wood and Widdows (2002, 2003) developed a simple (if unvalidated) cross-shore model incorporating biostabilisation (in the form of chlorophyll *a* content) and bioturbation (from the burrowing bivalve Baltic tellin *Macoma balthica*). The model suggests that the erosion or deposition driven by natural fluctuations in biota densities are as large as the changes caused by variations in tidal range and currents over a spring–neap cycle or are equivalent to a doubling of the external sediment supply. Seasonal variations in the density of stabilising diatoms can alter the magnitude of net deposition by a factor of 2 and interannual changes in *Macoma balthica* density change deposition by a factor of 5. In a UK climate change scenario, milder winters result in lower springtime recruitment of *Macoma*, leading to lower rates of bioturbation at mid-intertidal levels and lower sediment supply to the upper intertidal zone and its fringing salt marshes (Wood and Widdows 2003).

Using the same two biotic groups, Paarlberg et al. (2005) extended Wood and Widdows (2002) approach, showing that changes in bioturbation and stabilisation by microphytobenthos can potentially alter the mud content and elevation (by 5–10 cm) of shoal banks in the Western Scheldt estuary (Netherlands). In fact, field observations in the Western Scheldt estuary show that two stable sedimentological states are present at intermediate levels of bed shear stress, either a bare surface with low silt content or a high silt content supporting a high density of diatoms. This bimodal pattern results from the feedback links between the biota and silt content. Diatom growth rates are enhanced by the nutrients present in silt-rich sediments and diatom resuspension falls as diatom density increases, favouring the accumulation of silts. Loss of diatom cover sets this dynamic in reverse (Van de Koppel et al. 2001).

9.5.2 Human Impacts

Human impacts on estuarine geomorphology are particularly significant in the North Sea region. A general phenomenon is the historical reclamation of intertidal flats and marshes in many estuaries, since Medieval and even Roman periods. As a result the present-day area of intertidal flats and marshes is only a tiny fraction of the original area. For example, in the Western Scheldt estuary around 100,000 ha of intertidal areas—mostly marshes—have been reclaimed by seawall building since 1200; nowadays only around 2800 ha of marshes and 8000 ha of intertidal flats (i.e. 10 %) remain (Meire et al. 2005). Apart from the direct impact on the reclaimed land, the geomorphology of the remaining estuary will also react. The large reduction in intertidal areas may considerably reduce the volume of an estuary and hence its tidal prism (the volume of water within the estuary between high and low tides). Due to the reduced tidal prism and tidal currents, the long-term response of the estuary is that channels may fill with sediments and remaining intertidal mudflats in front of the seawalls may silt up promoting the succession towards marshes (e.g. Townend 2005). Extreme cases exist where progressive historical land reclamation resulted in a cascading effect and almost complete silting up and disappearance of the estuary (e.g. Zwin estuary towards Bruges, Belgium). In other cases, estuaries are still responding to historical land reclamation and estuarine sediment infilling may be expected to continue over coming decades. In still more cases, other processes may have compensated for the loss of tidal prism and land reclamation may not induce as much estuarine sediment infilling. As De Swart and Zimmerman (2009) concluded in an extensive review, interactions between intertidal and channel morphodynamics are complex and still not fully understood.

More recent human impacts include the dredging and canalisation of estuarine channels, because many estuaries in the North Sea region provide access to major harbours, including the ports of Rotterdam (Rhine-Meuse), Antwerp (Western Scheldt), and Hamburg (Elbe). Channel deepening reduces hydraulic friction, while land reclamation reduces the water storage capacity of estuaries. As a combined effect tidal penetration has increased in many estuaries (e.g. Friedrichs and Aubrey 1994). An increase in tidal range may increase the stirring of fine-grained sediments and so increase SSC towards highly turbid conditions, such as observed in the Ems estuary (e.g. Van Leussen 2011).

Other human impacts since the 1950s include the building of flood defence structures, such as storm surge barriers (e.g. Eastern Scheldt barrier; Thames barrier) and even the complete closure of estuaries by dams (e.g. Dutch Delta works). In the Eastern Scheldt estuary, the storm surge barrier seriously affects the sediment budget: as the tidal prism is reduced, the channels tend to fill in, but because marine import of sediments is restricted by the storm surge barrier, the intertidal flats inside the estuary experience erosion and sediments are redistributed towards the channels.

9.5.3 Future Expectations

9.5.3.1 Sea-Level Rise

Aspects of climate change that are expected to affect the geomorphology of estuaries include accelerated SLR, increased storminess, and increased fluctuations in freshwater discharge. SLR is of particular concern for the geomorphology and ecology of intertidal flats and marshes. In some parts of the world (e.g. Mississippi Delta; Chesapeake Bay; Venice Lagoon), sediment accretion rates are not enough to compensate for relative SLR (i.e. eustatic SLR combined with local land subsidence), which has resulted over the last century in extensive die-back of marsh vegetation and conversion of marshes and mudflats into open water (e.g. Kearny et al. 2002). A recent study combining five state-of-the-art models of marsh sedimentation in response to SLR, revealed that marshes with a low tidal range and low SSC (<20 mg l^{-1}) are especially at risk from submergence by average SLR projections (Kirwan et al. 2010). Based on Fig. 9.15, and given the large tidal ranges (2–6 m) and generally high SSC values (mostly >20 mg l^{-1} and up to several hundreds of milligrams per litre) for estuaries around the North Sea, the risk of marsh submergence by SLR is low for the coming century. For example, for the Western Scheldt estuary (average SSC ~40 mg l^{-1}; mean tidal range ~4 m), marshes are expected to drown in the long term only if the rate of SLR increases to 50 mm year^{-1}, which is far more than expected by 2100 (Temmerman et al. 2004). In theory, SLR may also affect estuarine sediment regimes, as it may increase the landward penetration of tides and hence of the ETM, but only if morphodynamic changes in the estuary are assumed to be zero; however, estuarine morphodynamic changes and human impacts are likely to exert much more control over estuarine sediment regimes than SLR.

9.5.3.2 Storms

Although the precise effects of climate warming on increasing frequency and intensity of storms is subject to debate in the scientific literature, there is growing consensus that climate warming is expected to increase the intensity of extreme tropical and extra-tropical storms for many coastal areas worldwide (e.g. Knutson et al. 2010), including the North Sea (e.g. Knippertz et al. 2000; Leckebusch and Ulbrich 2004; Donat et al. 2010). Increasing storminess may have geomorphological effects as wind waves during storms may affect erosion and sedimentation processes, especially on intertidal flats and along marsh edges (e.g. Callaghan et al. 2010 and see Chap. 18). Wind waves are most important in the seaward, wider parts of the estuaries, where water surface and wind fetch length are longer so that higher storm waves can be generated, while in the more landward, smaller parts of the estuaries smaller wind waves are expected. For several North Sea estuaries, including the Greater Thames area (UK) and the Western Scheldt estuary (Netherlands), lateral erosion of the edges of intertidal flats and marshes has been reported and partly attributed to wind wave erosion (e.g. Van der Wal and Pye 2004; Van der Wal et al. 2008), which might increase with increasing storminess due to climate change. However, these studies also highlighted that the wind-wave climate is not the only variable explaining the patterns and rates of lateral marsh erosion, but that other factors also play a major role, including the larger-scale morphodynamic changes in estuarine channel position, which may be affected by human impacts such as dredging and disposal of sediments (e.g. Cox et al. 2003). Several studies also address the role of self-organising mechanisms, driven by feedbacks between marsh vegetation, sediment deposition and erosion, and wave hydrodynamics, leading to cycles of lateral marsh extension and lateral marsh erosion, that are not solely driven by external forcing factors such as storminess (Van de Koppel et al. 2005; Chauhan 2009; Mariotti and Fagherazzi 2010).

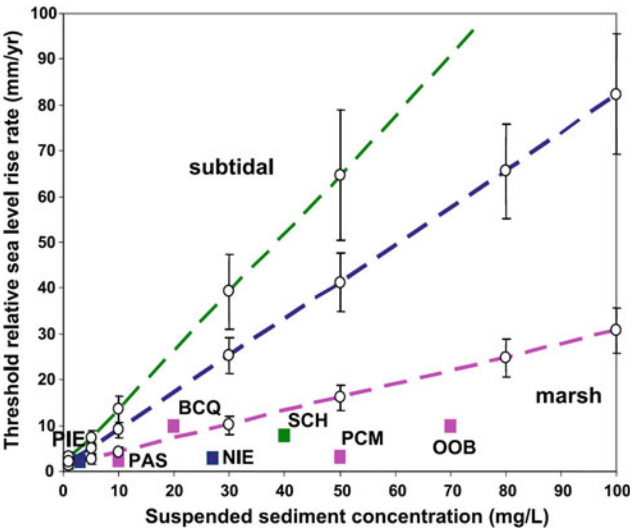

Fig. 9.15 Predicted threshold rates of sea-level rise, above which marshes are replaced by subtidal environments as the stable ecosystem. Each line represents the mean threshold rate (±1 SE) predicted by five models as a function of suspended sediment concentration and spring tidal range. The *hatched line* denotes thresholds for marshes modelled under a 1 m tidal range (*pink*), a 3 m tidal range (*blue*), and a 5 m tidal range (*green*). For reference, examples have been included (denoted with *square markers*) of marshes worldwide in estuaries with different rates of historical sea-level rise, sediment concentration, and tidal range. (*PIE* Plum Island Estuary, Massachusetts; *PAS* Pamlico Sound, North Carolina; *BCQ* Bayou Chitique, Louisiana; *NIE* North Inlet Estuary, South Carolina; *SCH* Scheldt Estuary, Netherlands; *PCM* Phillips Creek Marsh, Virginia; *OOB* Old Oyster Bayou, Louisiana) (after Kirwan et al. 2010)

9.5.3.3 Precipitation

According to the latest IPCC assessment, winter precipitation (October–March) in central and northern Europe (including the North Sea region) could be up to 40 % higher than present-day by 2100 (this value includes the 5th to 95th percentiles of precipitation projections for all IPCC scenarios) (Van Oldenborgh et al. 2013). For summer (April–September), climate models project a change in precipitation of −10 % to +20 % by 2100. Although the range of projections is quite large, the IPCC projections clearly suggest a future increase in precipitation during winter, with a smaller increase or even a slight decrease, during summer. Larger fluctuations in freshwater river discharge may affect the terrestrial sediment supply to estuaries. More intense rainfall events, especially during winter, may induce larger soil erosion events within the river catchment of estuaries (e.g. Poesen et al. 2003), and so may increase the terrestrial sediment supply to estuaries, potentially contributing to higher SSC values in the ETM zone (see also Chaps. 11 and 13). However, it should be emphasised that in terms of runoff and sediment supply to estuaries and the coast, human impacts such as changes in land use within the river catchment of estuaries are often as important as or even more important than changes in precipitation (Syvitski et al. 2005).

9.5.3.4 Human Impact

It must be stressed that human impacts such as channel deepening for harbour accessibility and flood defence and shoreline protection structures on geomorphology and sediment transport in estuaries are very likely to continue over the coming decades, and may dominate, exacerbate or compensate for the potential impacts of climate change. Channel deepening is likely to exacerbate the increase in tidal range and landward tidal wave penetration over coming decades, increasing risk of sediment resuspension and a potential shift towards hyper-turbid conditions such as happened in the Ems estuary in the Netherlands over past decades (Winterwerp 2011). One particular example of mitigation of climate and human-induced impacts is the conversion and restoration of formerly reclaimed land into intertidal flats and marshes in the UK (so-called managed coastal realignment schemes, such as in the Humber and Blackwater estuaries) (French 2006b) and Belgium (the Sigma plan in the Scheldt estuary) (Maris et al. 2007). Other types of ecosystem-based adaptation to climate change (‘soft engineering’), that are starting to be implemented, include the creation of oyster reefs and sand supply on tidal flats such as in the Eastern Scheldt estuary (e.g. Temmerman et al. 2013). Although such schemes provide multiple benefits in the form of ecosystem services (see E-Supplement S9) (e.g. flood storage, erosion protection, water quality regulation, carbon sequestration, fisheries production), societal opposition against conversion of reclaimed land into intertidal flats and marshes may be important and effects on changing tidal conditions in the estuary must be considered (see Temmerman et al. 2013 for a review).

In the Scheldt estuary, up to 3000 ha of historically reclaimed land are designated for conversion into floodplains, of which about 1500 ha are tidal marshes (Broeckx et al. 2011). The new intertidal areas have two objectives: to store extra water and attenuate landward propagating storm surges, thus reducing flood risk in the hinterland; and to provide ecosystem services such as water quality improvement and habitat restoration. Effects on the sediment budget of the estuary may also be expected (Maris et al. 2007). For example, in the Belgian part of the Scheldt estuary, the tidal marsh area is expected to increase from around 420 ha at present to almost 2000 ha by 2030. A pilot project showed that sediment accretion processes are already occurring in the newly created marshes at rates (per surface area) comparable to those on natural marshes (Vandenbruwaene et al. 2011), and so the completion of the whole marsh restoration scheme could reduce the risk of increasing SSC and turbidity within the estuary. Similar tidal marsh creation projects on formerly embanked land have been realised over the last few years and are planned for the near future in other estuaries around the North Sea, in particular in the Humber and Greater Thames estuaries (UK), where this management approach is called ‘managed coastal realignment’ (e.g. French 2006b; Turner et al. 2007).

The positive outcome of this management approach of tidal marsh creation on formerly reclaimed land should stimulate the wider implementation of this approach in other estuaries around the North Sea as a sustainable and cost-effective manner to mitigate climate- and human-induced impacts.

9.6 Salt Marshes

Jan P. Bakker

9.6.1 Distribution and Dynamics

Salt marshes occur along an elevational gradient from the intertidal flats to middle and high marsh with an associated change in the composition of the vegetation (Fig. 9.16). Vegetation-sedimentation feedbacks are only one of the many potentially important interactions (Fig. 9.17) (Nolte et al. 2013a). The main external controls of sediment deposition are sea level (hydroperiod) and sediment supply. The latter is strongly related to the SSC. Interactions between the physical and biological features of salt marshes

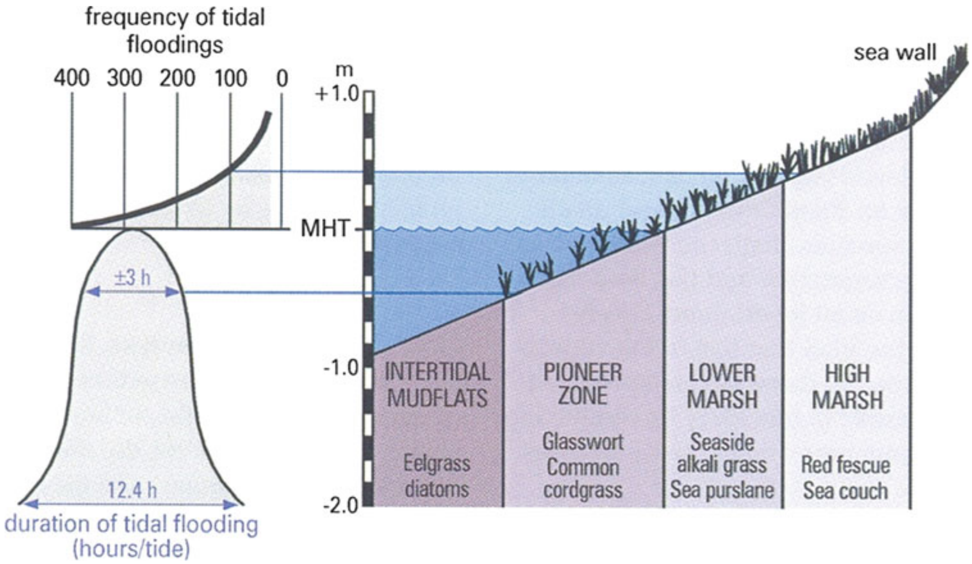

Fig. 9.16 Zonation of salt marshes in relation to the duration and frequency of tidal flooding and marsh elevation for the western German Wadden Sea. On back-barrier marshes the seawall is replaced by dunes (modified after Erchinger 1985). Eelgrass *Zostera* spp., glasswort *Salicornia* spp., common cordgrass *Spartina anglica*, seaside alkali grass *Puccinellia maritima*, sea purslane *Atriplex portulacoides*, *red fescue Festuca rubra*, sea couch *Elytrigia atherica* are the dominant plant species. They may be replaced by other species in the northern North Sea region. Wind flood (Windflut) is defined as 92 cm + MHT, storm flood (Sturmflut) as 198 cm + MHT, hurricane flood (Orkanflut) as 275 cm + MHT. During a period of 20 years, they occur $n \leq 10$ times, $10 > n \leq 0.5$, and $0.5 > n \leq 0.05$, respectively, in the western German Wadden Sea (Niemeyer 2015)

are also important. The accumulation of plant biomass can play an influential role in sediment deposition. Human impacts such as ditching or management practices such as livestock grazing (and then soil compaction) can also affect processes related to hydrodynamics, vegetation composition, and sediment deposition.

Although many salt marshes tend to have a ‘natural’ appearance, some along the mainland coast result from human interference. Salt marshes emerged about 2500 years BP after the last glacial period. Apart from small-scale embankments from the Roman period onward, most of the coastline became protected by seawalls about 1000 AD, thus reducing brackish marshes further inland and disconnecting them from the salt marshes. Peat reclamation along the coastline and subsidence behind the seawalls combined with sudden falls in the human population due to disease in the Medieval period, made the embankments vulnerable to attack by the sea. This resulted in societal collapse and a subsequent inability to maintain the seawalls that protected the embankments (Wolff 1992). This resulted in embayments such as the Lauwerszee, Dollard (the Netherlands), Leybucht (Germany), and subsequent new salt-marsh development. In past centuries, extensive areas of salt marsh have been embanked for coastal protection and agricultural exploitation (Dijkema 1987). Currently, a decline in the pioneer zone and increase in the high marsh zone in the Wadden Sea has been reported (Esselink et al. 2009). Since the 1960s it has not been economically viable to embank salt marshes for agricultural use (Wolff 1992). Accidental de-embankments after storm surges have occurred since the 19th century, and deliberate de-embankments in north-western Europe since the 1990s (Esselink et al. 2009). In terms of their future survival, it is important to understand the extent to which salt marshes can keep pace with the projected acceleration in SLR. An extreme episodic storm surge may destroy the vegetation at the marsh edge and cause the formation of a cliff (Van de Koppel et al. 2005). Feedbacks between sediment, vegetation and wave hydrodynamics may result in the formation of new marshes (see Sect. 9.5.3.2). Estuarine marshes in south-east England suffer from erosion. An overview of erosion rates revealed a net loss in area between 1973 and 1998 of about 1000 ha, or 33 %. Recent erosion rates (1988–1998) have been slower however (Cooper et al. 2001) and the area covered has recently (2006–2009) increased, resulting in a loss of ‘only’ 750 ha since 1973 (Phelan et al. 2011).

Lateral erosion can result in a narrowing of salt marshes, or coastal squeeze (Wolters et al. 2005a), particularly in the case of a short foreshore (Bouma et al. 2014) (see also Chap. 18). The potential loss of salt-marsh area through erosion from the seaward edge appears unrelated to the sedimentation processes in the salt marsh itself, but is determined by sedimentation in the pioneer zone, thus allowing dynamic rejuvenation of the lower salt marsh (Boorman et al. 1989; Dijkema et al. 2010), as in the case of a wide foreshore (Bouma et al. 2014). A wider foreshore will

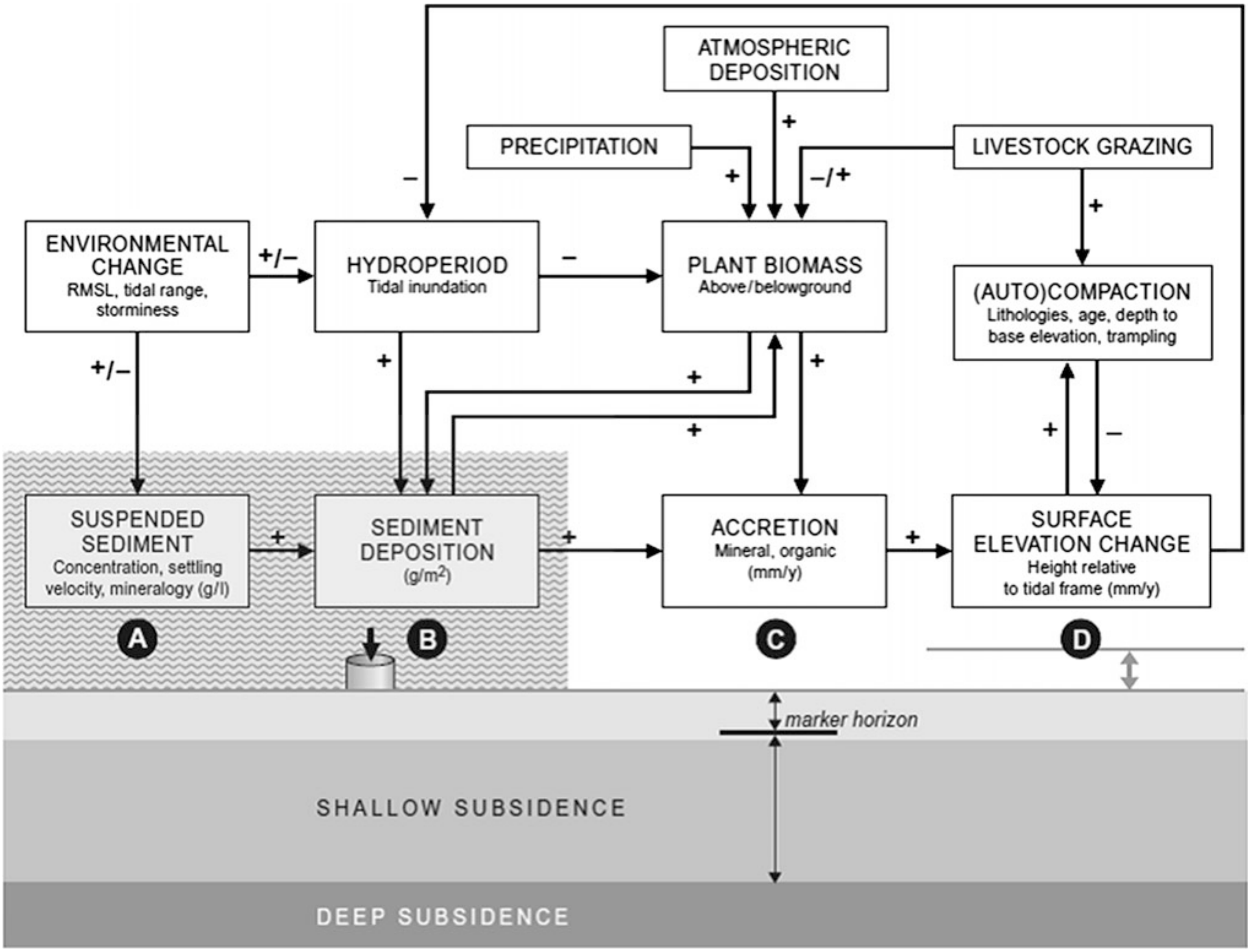

Fig. 9.17 Factors affecting sedimentation and accretion processes in coastal marshes. The letters *A*, *B*, *C*, and *D* indicate the main factors considered in the review (after Nolte et al. 2013a)

inherently offer more space for intertidal ecosystems. Moreover, a wider foreshore will generally have weaker wave energy gradients than a narrower foreshore, thereby making it easier for epibenthic ecosystems to establish. As a result, both the maximum and minimum widths of an intertidal habitat will have a positive relationship with the size of the foreshore (Fig. 9.18). Self-organisation of this type is enhanced by the wave reduction of up to 60 % attributed to vegetation compared to bare soil (Möller et al. 2014). Sea-edge erosion may result in large-scale cliff erosion. If cliff erosion is not prevented by groynes, marshes established from sedimentation fields may disappear in the long term (Dijkema 1994).

The area covered by salt marshes in the North Sea region has increased following accidental de-embankments after breaching of the seawall or summerdike during storm surges, such as occurred in 1953. Accidental de-embankments took place at 35 sites in north-western Europe before 1991. After 1991, deliberate de-embankment took place at 29 sites, and there are plans to increase this number. The de-embanked sites ranged from less than 1 ha to over 500 ha. The total area amounted to more than 5600 ha (Wolters et al. 2005b). Half of the deliberate de-embankments were carried out for habitat restoration and a quarter for flood defence (see E-Supplement S9 for ecosystem services) (Fig. 9.19).

Past SLR is not the same along the entire coastline of the North Sea, nor is it constant over time (Table 9.1 in Sect. 9.2.3.1). Global mean SLR was about 1.7 mm year^{-1} for the 20th century as a whole, but was higher at about 3 mm year^{-1} over the last two decades. These data hold for most of the European coasts, but with variations due to local land movement, either positive or negative (EEA 2012). Mean SLR for the North Sea region over the past 20 years[1] is 1.4 ± 0.4 mm year^{-1}. A recent analysis of data from Dutch

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[1] http://ibis.grdl.noaa.gov/SAT/SeaLevelRise/slr/slr_sla_nrs_free_all_66.pdf.

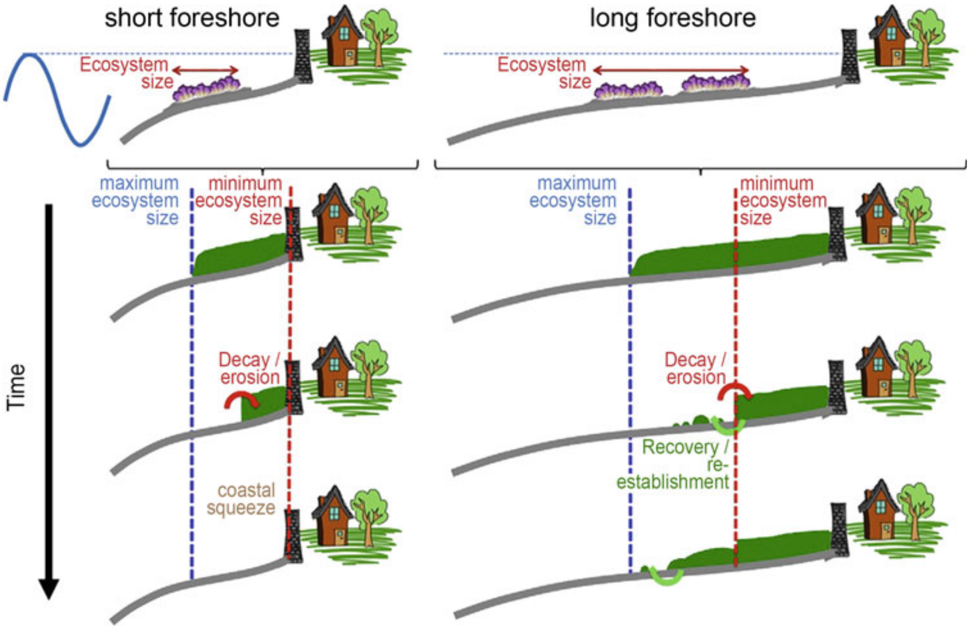


Fig. 9.18 Schematic illustration of the relation between foreshore dimensions and the maximum and minimum widths of an intertidal ecosystem with wave-attenuating aboveground (epibenthic) structures. The maximum and minimum widths relate to the borders reached by intertidal ecosystems with cyclical dynamics: the minimum width is the size of the ecosystem that will maintain, whereas everything between the maximum and minimum will vary over time. A sufficiently wide foreshore is important to enable epibenthic intertidal ecosystems to go through natural cycles of decay and re-establishment (cf. Van de Koppel et al. 2005), without experiencing coastal squeeze. On a narrow foreshore, re-establishment of degrading epibenthic ecosystems may be hampered by gradients in wave energy that are too strong (Bouma et al. 2014)

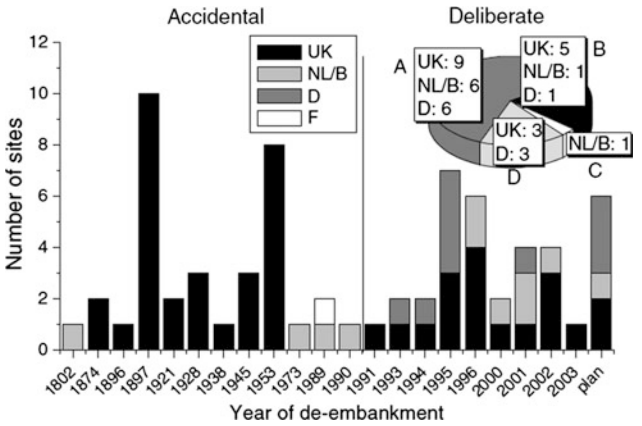


Fig. 9.19 Timing and causes of salt marsh de-embankment by country. **a** habitat creation or restoration; **b** flood defence; **c** gaining experience; **d** unknown (Wolters et al. 2005b)

tidal stations does not show an acceleration in SLR between 1990 and 2010 (Dillingh et al. 2012). SLR can be affected by vertical land movement. This varied from −1.3 to 0.1 mm year^{-1} over the period 1843–2009 in the German Bight (Wahl et al. 2011) and from −1.1 to −0.5 mm year^{-1} in the English Channel through the 20th century (Haigh et al. 2011).

Not only has mean SLR changed over time, but MHT has also varied in different locations and over different periods (Table 9.2). For a given area, the rate of change in MHT was sometimes higher that SLR, sometimes lower, or was even negative.

9.6.2 Sedimentation and Accretion in Intertidal Marshes

Whether coastal marshes can cope with accelerated SLR depends on the change in surface elevation, which in turn depends on availability of sediment (SSC), over marsh tidal events, and autocompaction. These interact with plant biomass and exploitation of salt marshes by livestock grazing (Fig. 9.17). Rates of surface elevation change (SEC) of a broad sample of allochthonous marshes in north-western Europe and North America range from a few millimetres per year to several centimetres per year. There is no obvious trend with tidal range, but the envelope of variability is wider at larger tidal ranges. The sites included no evidence for SEC deficit (i.e. the difference between rates of SEC and SLR) with the exception of a single system (French 2006a).

Accretion and SEC are both often expressed as an average for a given area, including a range on individual measurements. Salt marshes along the mainland coast of the North Sea region reveal higher rates of accretion or SEC than those on barrier islands (Table 9.3).

Table 9.2 Regional variation in change in mean high tide (MHT) within the North Sea region

Area	Change in MHT, mm year^{-1}	Period	Source
Wadden Sea	2–2.5	1950–2000	Oost et al. (2009)
Germany–mainland	4.2	1965–2001	Jensen and Mudersbach (2004)
Germany–islands	3.5	1965–2001	Jensen and Mudersbach (2004)
Ameland, Netherlands	6	1963–1983	Dijkema et al. (2011)
	0	1983–2010	Dijkema et al. (2011)
New Statenzijl, Dollard, Netherlands	5.7	1890–1910	Esselink et al. (2011)
	1	1910–1954	Esselink et al. (2011)
	6	1955–1983	Esselink et al. (2011)
	−0.3	1983–2009	Esselink et al. (2011)

Table 9.3 Regional variation in mean rates of accretion (AC), surface elevation change (SEC) or a combination of the two on salt marshes in the North Sea region

Area	AC/SEC mm year^{-1}	Period	Source
Mainland			
Friesland, Netherlands	11–29 SEC	1984–2010	Dijkema and Van Duin (2012)
Peazemerlannen, Netherlands	9–14 SEC	1996–2010	Dijkema and Van Duin (2012)
Groningen, Netherlands	8–14 SEC	1984–2010	Dijkema and Van Duin (2012)
Dollard, Netherlands	7–10 SEC	1984–2003	Dijkema and Van Duin (2012)
Schleswig-Holstein south, Germany	2–3 SEC	1998–2009	Suchrow et al. (2012)
Schleswig-Holstein north, Germany	5–9 SEC	1998–2009	Suchrow et al. (2012)
Hamburger Hallig, Germany	4–17 SEC	1996–2009	Stock (2011)
Back-barrier			
Stiffkey, UK	6.5 AC/SEC	1995–1998	Cahoon et al. (2000)
Terschelling, Netherlands	1.3 AC/SEC	1995–1998	Van Wijnen and Bakker (2000)
Schiermonnikoog, Netherlands	0–3 AC/SEC	1995–1998	Van Wijnen and Bakker (2000)
Rømø, Denmark	2.6 AC	1980–2003	Pedersen and Bartholdy (2006)
Fanø, Denmark	2.8 AC	1980–2003	Pedersen and Bartholdy (2006)
Skallingen, Denmark	2.4 AC	1980–2003	Pedersen and Bartholdy (2006)
Skallingen, Denmark	1.4 AC/SEC	1995–1998	Van Wijnen and Bakker (2000)

Data on the age of salt marshes in Table 9.3 are not often available. In contrast, age data are available for back-barrier marshes and these indicate decreasing SEC with increasing age of the marsh (Van Wijnen and Bakker 2001). SEC was 2.5 mm year^{-1} on a marsh of up to 15 years in age, around 1.5 mm year^{-1} on a marsh of 30 years in age, and around 0 mm year^{-1} on a marsh of 100 years in age (Fig. 9.20). Decreasing SEC in older marshes may indicate autocompaction (see Sect. 9.4).

In addition to regional differences in SEC, there are also local differences from high marsh to intertidal flats. At the barrier island of Langli, Denmark, an accretion rate of −1 mm year^{-1} (2001–2009) was recorded on the high marsh and 0.5 mm year^{-1} on the low marsh (Kuijper and Bakker 2012). On the mainland marsh of the Dollard estuary in the Netherlands, the accretion rate was 9–16 mm year^{-1} at 10 cm + MHT and 0–8 mm year^{-1} at 55 cm + MHT over the period 1984–1991 (Esselink et al. 1998). Plots at 20–60 cm + MHT revealed a SEC of 5–9 mm year^{-1}, while plots at 70–80 cm + MHT showed only 1 mm year^{-1} for the period 1996–2009 in the mainland marsh of Hamburger Hallig on the German coast. Rates of accretion or SEC were generally higher near the salt-marsh edge in both mainland and back-barrier marshes (Table 9.4). However, this was not found at the southern side of Hamburger Hallig, indicating strong local differences (Stock 2011). Rates were higher on mainland marshes than back-barrier marshes (see also Table 9.3).

The rate of accretion also declines away from creeks and ditches in the mainland marshes of the Dollard; 15 mm year^{-1} next to a creek and 2 mm year^{-1} (over 1984–1991) at 20 m from the creek at a distance of 750 m from the marsh edge (Esselink et al. 1998). Apparently water with very little sediment in suspension inundates the marsh far from the

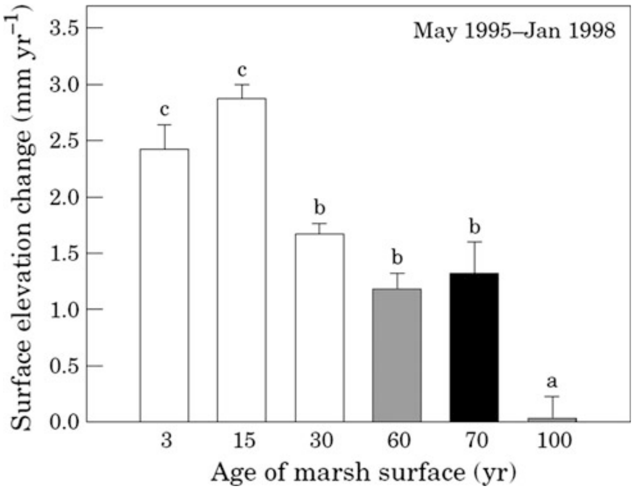


Fig. 9.20 Marsh surface elevation change at 40 cm + MHT in the late 1990s over a three-year period in salt marshes at various successional stages on the ungrazed back-barrier marshes of Schiermonnikoog, the Netherlands (*open bars*), Terschelling, the Netherlands (*grey bar*) and Skallingen, Denmark (*black bar*). Different letters indicate significant differences ($p < 0.05$) (Van Wijnen and Bakker 2001)

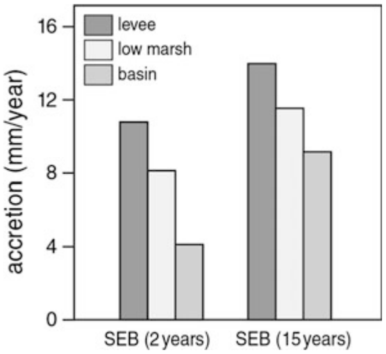


Fig. 9.21 Comparison of accretion rate using Sedimentation Erosion Bar (SEB) measurements for 2 years and 15 years. Measurements took place on levees, in the low marsh, and in basins at the Peazemerlannen mainland salt marsh in the Netherlands. The two-year measurements represent a period without winter storms (Nolte et al. 2013a)

edge. Sediment trapping at the marsh edge is enhanced by plants causing wind wave attenuation (Möller 2006).

Data from a broad sample of allochthonous marshes in north-western Europe and North America, reveal only weak positive linkages between SSC and mean tidal range (French 2006a). Variability in SSC is dependent on the weather conditions. In the eastern Wadden Sea in the Netherlands, SSC of up to 100 mg l^{-1} was recorded during most tides, but could increase to 800 mg l^{-1} during periods of strong western winds (Kamps 1962). Elevated SSC due to wave re-suspension correlates with strong westerly wind events. These local meteorological events seem to overrule sea level and tidal range (French 2006a). An increase in extreme sea level during storm surges in the southern North Sea was found over the period 1850–2000 (Weisse et al. 2012). Wave activities can re-mobilise sediment, especially with onshore winds. However, surges are not always accompanied by strong onshore winds.

Spatial differences in accretion are also found. On the levees, low marsh and depressions in the mainland marsh of Peazemerlannen in the Netherlands, the rate of accretion was higher during a period that included winter storms than periods without (Nolte et al. 2013a) (Fig. 9.21). Most sediment originates offshore (see Sect. 9.4.1), the rest is mobilised from adjacent intertidal flats during storms.

Measurements of SEC over six years along the mainland coast of Friesland in the Netherlands, revealed many floodings of the salt marsh with high tides plus storm surges $\geq$0.90 m + MHT in the period 2002/03–2006/07. A positive relationship was found between the cumulative water column per storm year above the salt marsh and annual SEC for the high marsh (0.57–0.85 m + MHT) and low marsh (0.24–0.34 m + MHT) (Fig. 9.22). Esselink and Chang

Table 9.4 Average rates of accretion (AC) or surface elevation change (SEC) on salt marshes within the North Sea region, at different distances from the salt-marsh edge

Area	AC/SEC (mm year^{-1}) distance to edge		Period	Source
Mainland				
Dengie Peninsula, UK	22 (50 m)	11 (200 m)	1981–1983	Reed (1988)
Hamburger Hallig, Germany	17 (50 m)	4 (650 m)	1996–2009	Stock (2011)
	22 (50 m)	1–2 (1000 m)	1995–1999	Schröder et al. (2002)
Schleswig-Holstein, Germany	8 (100 m)	4 (400 m)	1988–2009	Suchrow et al. (2012)
Dollard, Netherlands	12–16 (50 m)	2–5 (800 m)	1984–1991	Esselink et al. (1998)
Back barrier				
Langli, Denmark	0.5 (50 m)	−1 (150 m)	2001–2009	Kuijper and Bakker (2012)
Norfolk, UK	4.5 (50 m)	3.4 (200 m)	1986–1991	French and Spencer (1993)
Skallingen, Denmark	4.2 (50 m)	1.6 (750 m)	1948–1998	Bartholdy et al. (2004)

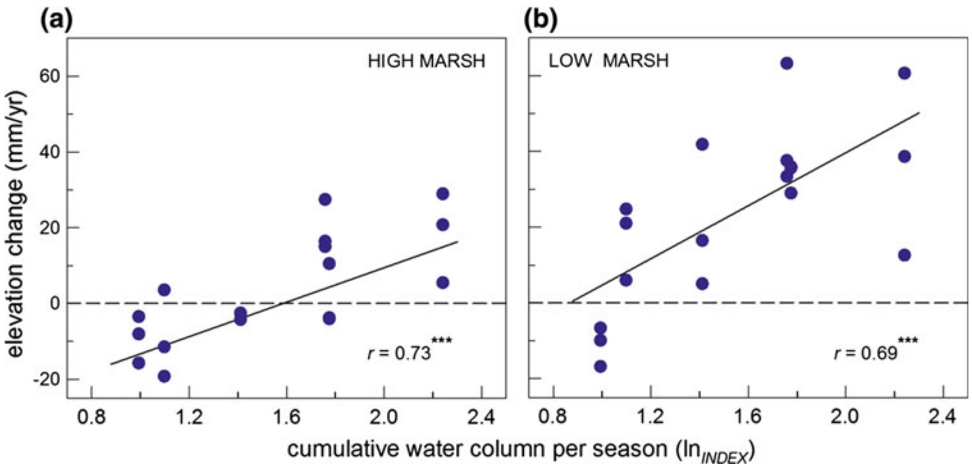


Fig. 9.22 Relation between the annual surface elevation change of the salt marsh and the cumulative water column above 0.9 m + MHT for each storm year (index) along the mainland coast of Friesland in the Netherlands between 2002 and 2007 for the high marsh (**a**) and the low marsh (**b**). Regression lines are based on a joint regression-analysis of the various stations, each station includes three replicates (after Esselink and Chang 2010)

(2010) were able to separate years with various cumulative water columns above the marsh. They found the SEC was 3.8 mm year^{-1} in the high marsh and 31.8 mm year^{-1} in the low marsh in the period 2002–2005, but 4.6 mm year^{-1} in the high marsh and 13.1 mm year^{-1} in the low marsh in the period 2005–2007, which includes the storm surge of 1 November 2006 with a high tide of 2.4 m + MHT compared to average high tides of MHT. Hence, Esselink and Chang (2010) concluded that storm floods contribute strongly to accretion of sediment, but that a hurricane flood does not always result in extra accretion, and may even result in less SEC at the low marsh.

A thick layer of very turbulent water during a hurricane flood might prevent settlement conditions for sediment. Vegetation plays an important role in the accretion of sediment. This was demonstrated in the estuarine Dollard salt marshes in the Netherlands. Both vegetation density and height positively affected accretion rates (Esselink et al. 1998).

9.6.3 Salt–Marsh Ecosystems

9.6.3.1 Plants and Natural Herbivores

Deposited sediment can contribute to SEC, it also contains nitrogen. The nitrogen pool of the rooting zone of 50 cm is positively correlated with the thickness of the clay layer on back-barrier marshes (Olff et al. 1997). In turn, N-mineralisation is positively related to the nitrogen pool (Bakker et al. 2005).

Plant productivity on salt marshes is considered to be limited by nitrogen. N-limitation on lower and higher marshes was demonstrated in west-European salt marshes by Jefferies and Perkins (1977). Nitrogen accumulates during succession in the nitrogen pool of organic matter in the increasing layer of sediment and decaying plants and roots, and N-mineralisation increases with age of the marsh (Van Wijnen et al. 1997). This can be enhanced by the current high rates of atmospheric nitrogen deposition. Although the quantity of plant biomass increases during succession, the quality (more stems that are less palatable) decreases. Hence, the numbers of small herbivores such as winter-staging geese and resident hares and rabbits decrease during succession, after peaking in early successional stages (Van de Koppel et al. 1996). These smaller herbivores need livestock to facilitate for them (Bos et al. 2005).

9.6.3.2 Livestock Grazing

Livestock grazing on European salt marshes can be traced back a couple of millennia (Davy et al. 2009). Older back-barrier marshes are grazed by livestock as mainland marshes. Traditionally many salt marshes were intensively grazed by sheep or cattle (see E-Supplement S9 for ecosystem services). As a result the majority of these marshes were covered by an extremely short homogeneous vegetation of seaside alkali grass *Puccinellia maritima* or red fescue *Festuca rubra* (Kiehl et al. 1996). In the 1980s, grazing by livestock was reduced by up to 60 % on back-barrier marshes and up to 40 % in mainland marshes in the Wadden Sea in 2008 (Esselink et al. 2009). Alongside this change in management regimes there has been an increase in the abundance of the late-successional tall grass species sea couch *Elytrigia atherica* on several salt marshes along the North Sea coast, for example on the Wash, UK (Norris et al. 1997), Schiermonnikoog in the Netherlands (Van Wijnen et al. 1997) and Schleswig-Holstein in Germany (Esselink et al. 2009). There are high numbers of geese and hares on livestock-grazed salt marshes, and low numbers on long-term ungrazed marshes along the coasts of the Wadden Sea (Bos et al. 2005). When grazing ceased, intensive ditching was often discontinued. This resulted in a wetter marsh and reduced spread of sea couch (Veeneklaas et al. 2013).

At the Leybucht, Germany, SEC of 17 mm year^{-1} (1980–1988) at 40 cm + MHT was measured in cattle-grazed marsh, but was higher at 23 mm year^{-1} in the abandoned marsh (Andresen et al. 1990). SEC was about 7 mm year^{-1} over 1996–2009 on ungrazed or low-density grazing on mainland marshes of Hamburger Hallig, Germany. It was however, reduced to 4 mm year^{-1} at sites with high grazing density (Stock 2011). In mainland marshes of the Dollard estuary, intensively grazed sites showed accretion rates of about 8 mm year^{-1} and little-grazed sites about 12 mm year^{-1} over 1984–1991 (Esselink et al. 1998). In Schleswig-Holstein, grazed sites showed an SEC of 3–4 mm year^{-1} and ungrazed sites 8 mm year^{-1} over 1988–2009 (Suchrow et al. 2012). Grazing reduces SEC. However, this is not due to a lower input of sediment in grazed sites, but to an increase in the bulk density of the soil in both a back-barrier marsh (Elschot et al. 2013) and in mainland marshes (Nolte et al. 2013b).

9.6.4 Climate Change and Salt Marshes

9.6.4.1 Sea-Level Rise

Back-barrier marshes with a low vertical accretion might be affected by SLR earlier than mainland marshes with a higher vertical accretion. With little sediment input and continuous SLR, a salt marsh gets wetter, thus preventing the spread of the late successional sea couch *Elytrigia atherica* on Hamburger Hallig even without livestock grazing (Esselink et al. 2009). On the back-barrier marsh of Schiermonnikoog, sea couch has been replaced by the reed *Phragmites australis*, far from the salt-marsh edge (Veeneklaas et al. 2013). This suggest that on broad salt marshes geomorphological changes may occur, resulting in growing differences in elevation, that is, high salt-marsh edge and creek bank levees, and lower depressions between creeks. Especially at the foot of dunes releasing fresh seepage water, brackish conditions can develop.

Accelerated SLR is believed to affect the zonation of salt-marsh plant communities: high salt-marsh communities should turn into lower salt-marsh communities (see Fig. 9.16) (Dijkema et al. 2011). Accelerated SLR can be modelled, but it is not known what will actually happen in reality. An unintended experiment (unique in the North Sea region) taking place as a result of natural gas extraction for energy on the back-barrier salt marsh of Ameland in the Netherlands, may give some idea. Gradual soil subsidence of up to 35 cm by 2050 is expected close to the extraction point (Dijkema 1997). After 25 years, the maximal subsidence is about 25 cm. Near the salt-marsh edge, subsidence is totally counteracted by accretion, with an SEC of zero. About 300 m from the marsh edge, only 4 cm accretion was measured, thus an SEC of −21 cm (Fig. 9.23). Permanent plot data show no decrease in the late successional grass sea couch. At the scale of the salt marsh, however, data from repeated vegetation mapping do show some decrease in the sea couch community (Dijkema et al. 2011). To date, there has been little change in the zonation of plant communities. The future will show whether 25 cm subsidence is sufficient to cause vegetation change, or whether there is a time lag in the response of the vegetation.

Observations of vegetation composition, elevation, soil chemistry, net precipitation, groundwater level, and flooding frequency over the period 1986–2001 were used to predict future changes at the transition between salt marsh and dune due to the combination of ongoing soil subsidence and climate change at the barrier island of Ameland. Climate change was characterised by increases in mean sea level,

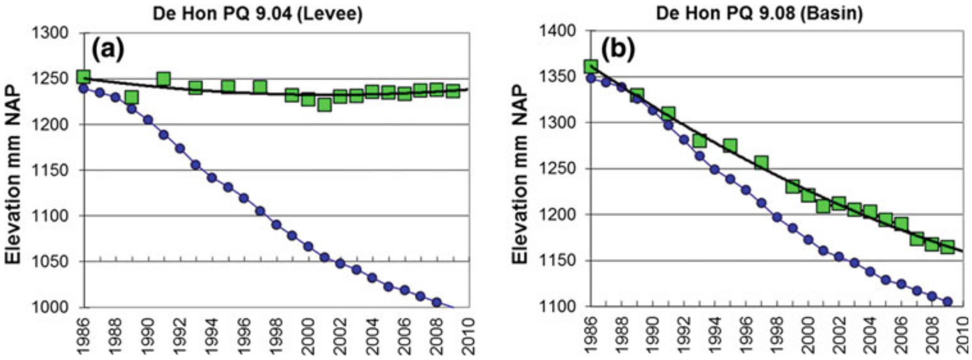


Fig. 9.23 Surface elevation change in the period 1986–2009 (*green*) resulting from soil subsidence due to natural gas extraction (*blue*) and accretion measured near the salt-marsh edge on a creek bank levee (**a**) and about 300 m from the salt-marsh edge in a depression (**b**) (after Dijkema et al. 2011)

storm frequency and net precipitation. Using multiple regression, changes in the vegetation could be subdivided into (1) an oscillatory component due to fluctuations in net precipitation, (2) an oscillatory component due to incidental flooding, (3) a monotonic component due to soil subsidence, and (4) a monotonic component not related to any measured variable but probably due to eutrophication. The changes were generally small during the observation period (1986–2001), but the regression model suggests large changes by 2100 that are almost exclusively due to SLR. Although SLR is expected to cause a loss of plant species, this does not necessarily imply a decrease in nature conservation interest; while common species may be lost rarer species may persist (Van Dobben and Slim 2012).

Comparison of the zonation of beetles and spiders in present mainland salt marshes, and laboratory experiments with enhanced SLR, suggested that species of the lower marsh will move to higher elevation, but species of the higher marsh are unable to escape to higher elevations owing to the barrier of the seawall. These results were interpreted as an example of coastal squeeze (Irmler et al. 2002). Similarly, the lowest-lying vegetation zones will increase at the expense of upper vegetation zones in salt marshes in Denmark with enhanced SLR, according to modelling studies (Moeslund et al. 2011). However, this finding contradicts the previously mentioned results of soil subsidence through gas extraction, which showed no change in the vegetation (Dijkema et al. 2011).

9.6.4.2 Precipitation and Temperature

Although annual deviations from long-term averages are important, there is a general trend of increasing precipitation and rising temperature in the North Sea region. Changes in precipitation may affect plant production (De Leeuw et al. 1990) and plant communities, especially those above MHT (De Leeuw et al. 1991). Long-term trends in precipitation are discussed in Chap. 2 (past) and Chap. 5 (future projections).

Critical loads of atmospheric nitrogen deposition indicate the threshold amount at which ecosystems change dramatically by encroachment of grasses and subsequent loss of species. The empirical range of critical atmospheric nitrogen deposition for 'Pioneer and low-mid salt marshes' has been adjusted in the most recent review (Bobbink et al. 2010) to 30–40 kg N ha^{-1} $year^{-1}$. This range is considered as expert judgment for EUNIS type A2.64 and A2.65. The critical deposition load is now 22 kg N ha^{-1} $year^{-1}$ (1571 mol N ha^{-1} $year^{-1}$) for salt marshes in the Netherlands (Van Dobben and Slim 2012).

Accelerated SLR will have impacts perpendicular to the coastline. In contrast, temperature may have effects parallel to the coastline. The distribution of plant species of salt marshes and dunes may shift along the coast. Based on present patterns of distribution, annual temperature and winter precipitation, Metzing (2010) proposed a model to predict changes in distribution resulting from climate change. An increase of 2.5 °C in annual temperature and 15 % more winter precipitation by 2050 is projected to result in a loss of 16 % of plant species in the Wadden Sea (see also Sect. 9.3.4).

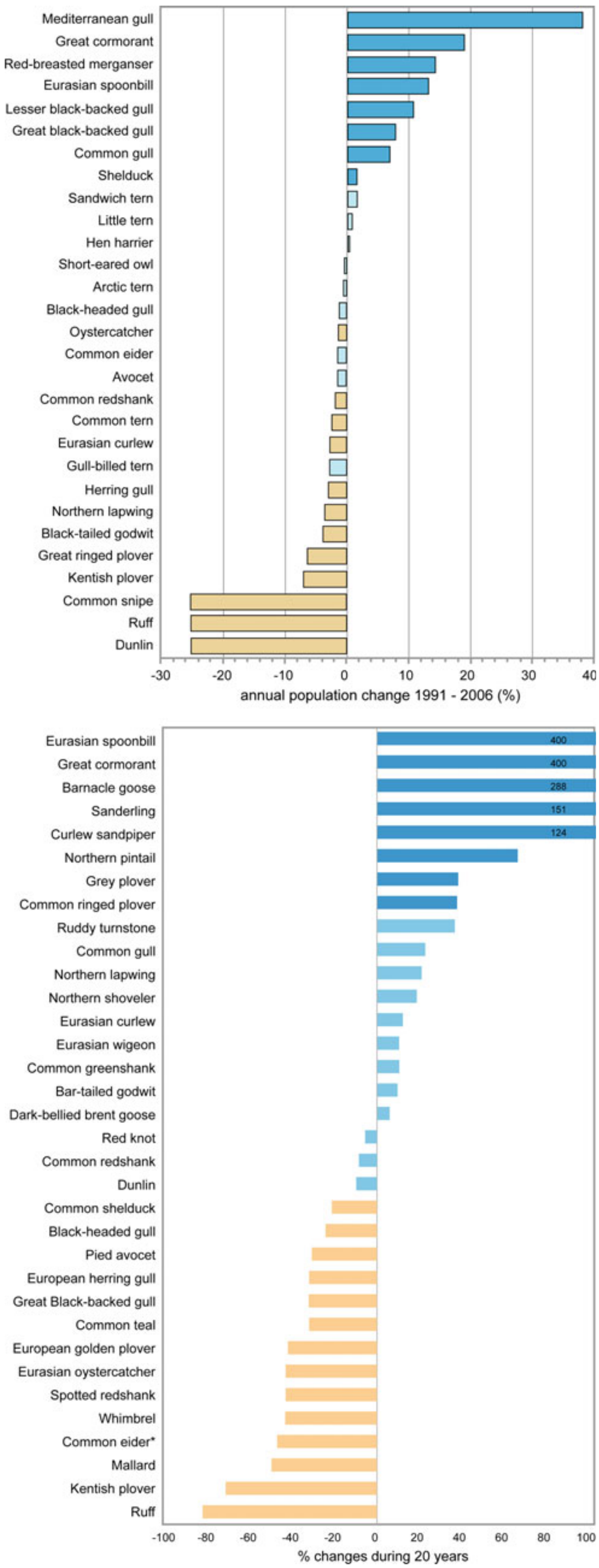
9.7 Coastal Birds

Martijn van de Pol

Coastal birds are typically distinguished from seabirds in that they rely heavily on coastal areas for their food instead of the open sea, although the distinction is not always clear-cut. Coastal and seabirds are phylogenetically closely related and many are part of the same order of Charadriiformes. When discussing the impact of climate change on coastal birds, a rather broad definition of coastal birds is taken here by not only including the large group of waders (sometimes also called shorebirds), but also by including other species that depend heavily on coastal areas for feeding, such as Eurasian spoonbills *Platalea leucorodia*, common eider duck *Somateria mollissima* and various species of terns, geese and gulls. The focus is not on birds that use coastal habitat solely for the purpose of breeding (such as some songbirds).

Since by definition coastal birds rely on coastal areas for their food, they live in the vicinity of coastal shallow waters such as estuaries and intertidal flats and can breed on sandy shores and salt marshes (cliff coasts are generally the domain of seabirds). A substantial proportion of all coastal birds in the North Sea region breed locally, but many others are migratory (e.g. geese) that breed elsewhere (e.g. Arctic), and only use estuaries around the North Sea to overwinter. This distinction between resident and migratory birds is important, as migratory birds may also be impacted by climate change outside the North Sea region.

There is overwhelming evidence from around the globe that the distribution and population size of many bird populations are changing as a direct result of climate change (for an overview see Møller et al. 2010). Around ten species of coastal birds (both breeding and migratory) are declining in parts of the North Sea, such as the Wadden Sea that spans the Netherlands, Germany and Denmark (Fig. 9.24) and estuaries in the United Kingdom (Risely et al. 2012). The functional diversity, however, does not decline (Mendez et al. 2012). But because coastal birds are rarely used as a model system to investigate the effects of climate change, very little is known about the general role that climate change may play in causing changes in numbers of coastal birds in the North Sea region (Ens et al. 2009). Nor is it well understood which species are likely to be adversely affected by climate change and which are likely to benefit.



◀ **Fig. 9.24** Recent changes in numbers of breeding (*top*) and migratory (*bottom*) coastal birds in the Danish-German-Dutch Wadden Sea estuary. *Dark blue columns* indicate species with significant, increasing numbers; *light blue columns* indicate species with stable numbers and orange columns indicate species with significant, decreasing numbers (Koffijberg et al. 2009; Laursen et al. 2010)

Nevertheless, one of the aims of this section is to illustrate that although current knowledge about the climate change impact on coastal birds is limited, recent and future climate change are expected to profoundly affect coastal avian communities.

This section focuses on the few available studies on coastal birds from the North Sea region, supplemented by studies from outside the area to help with interpretation. This involves a consideration of those aspects of climate that might be changing and how these may affect coastal birds (Sect. 9.7.1), a review of the ways in which bird populations may respond to climate change, such as the timing of key annual events (migration and egg laying) and changes in reproduction and survival (Sect. 9.7.2), and an examination of how changes in coastal bird population numbers and in distribution range are interpreted in the light of direct and indirect influences of recent climate variability (Sect. 9.7.3).

9.7.1 Effects of Climate Change on Birds

Weather variables such as air and sea temperature, and amounts of precipitation are changing. Intra- and interannual variability in these weather variables, temporal autocorrelation and the frequency of extreme events can also change over time, which may all affect population dynamics of coastal birds (Van de Pol et al. 2010a, b, 2011). However, climate may not change at the same rate throughout the year or in different parts of the world, and this can lead to phenological mismatches in food webs (Visser 2008) and require readjustment of migration schedules (Bauer et al. 2008).

Global warming is causing both air and water temperatures to rise. Air temperatures directly affect the energetic expenditure and thereby food requirements of birds, particularly in small species during winter (Kersten and Piersma 1987). Many benthic and fish species that are prey items of coastal birds are strongly dependent on sea temperatures for growth, reproduction and survival (see also Chap. 8, Sect. 8.4). Severe winters can cause high mortality among many invertebrates, but these same cold winters can also cause shellfish to lose less body mass (Honkoop and Beukema 1997) and result in a good spatfall (Beukema 1992). Thus, it has been suggested that global warming is already

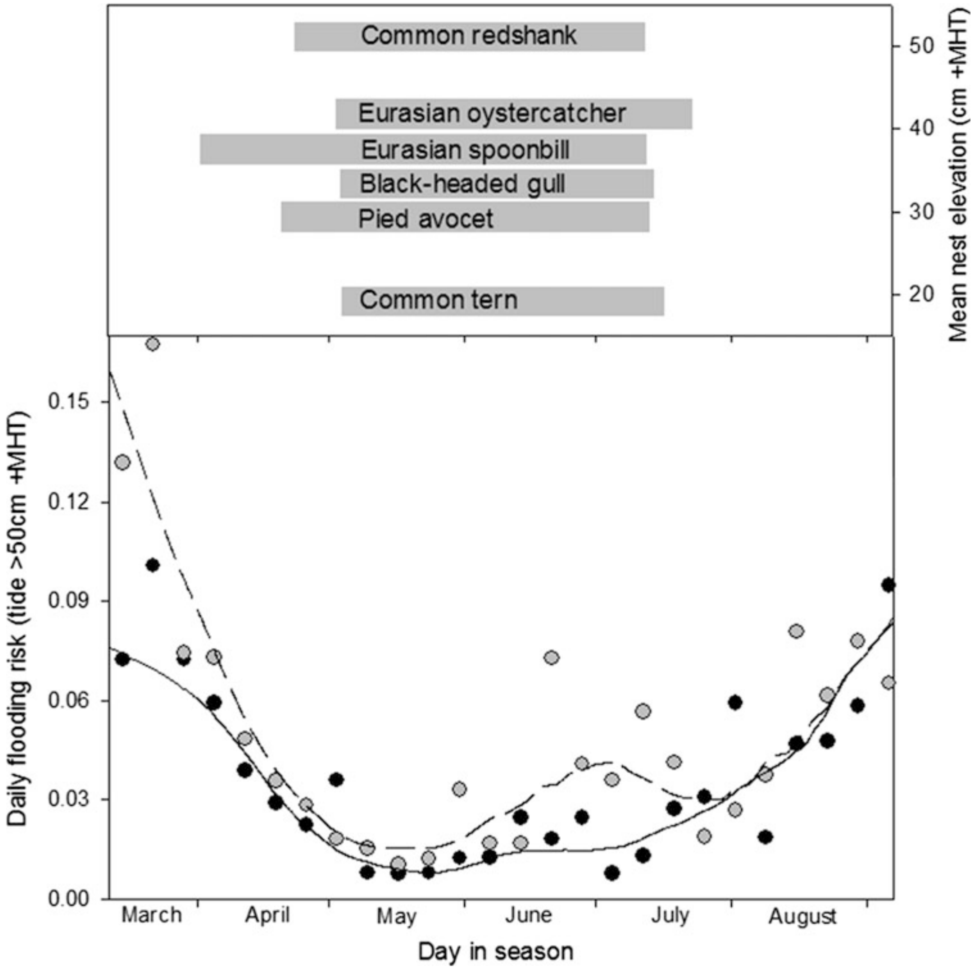


Fig. 9.25 Period during which birds have nests that are sensitive to flooding (eggs or young chicks in the nest) and the mean nest elevation (compared to Mean High Tide) of six salt-marsh breeding species (*upper*). Increase in daily flooding risk of the lower parts of the salt marsh from 1971–1989 (*black circles*) to 1990–2008 (*grey circles*) (*lower*) (Van de Pol et al. 2012)

causing reduced recruitment of shellfish (Beukema and Dekker 2005; Beukema et al. 2009) and a shift in benthic community structure towards less cold-resistant species (e.g. Schückel and Kröncke 2013). Furthermore, invasion of exotic warm-water species, such as Pacific oyster *Crassostrea gigas* which is eaten by few birds, may result in increased competition for existing benthic species (Diederich et al. 2004).

Global warming also causes sea water to expand and land ice to melt thereby directly causing sea levels to rise. Accelerating SLR can have various consequences. The inundation time of intertidal flats may increase or flats used as feeding grounds may become completely inaccessible if sedimentation does not keep up (Flemming and Bartholomä 1997). Accelerated SLR in combination with changing wind patterns (there is currently no definitive evidence in this region for the latter due to the challenge of down-scaling future wind states from coarse resolution climate models) (Van Oldenborgh et al. 2013) can also affect breeding populations on land, as many bird species nest on low salt marshes and beaches that are susceptible to tidal (storm) flooding during the breeding season (Fig. 9.25; Hötker and Segebade 2000; Van de Pol et al. 2010a). Over the long-term, SLR may result in loss of breeding habitat if boundaries such as dunes or seawalls mean that salt marshes cannot move landwards (‘coastal squeeze’; Sect. 9.2.3).

Extreme events may also change in frequency and/or magnitude (Jentsch et al. 2007). In the Netherlands, precipitation and temperature extremes are expected to increase, with more heat waves in summer and higher temperature minima in winter and higher temperature maxima in summer, respectively (KNMI 2014). For example, global warming is expected to decrease the frequency of extremely cold winters in which ice sheets form on intertidal flats. Ice sheets make feeding areas inaccessible and if conditions prevail for long periods, they are known to result in large-scale frost migration and mass mortality of coastal birds (e.g. Camphuysen et al. 1996).

9.7.2 Responses to Climate Change

Individual birds may respond in various ways to a changing environment. Changes in the timing of reproduction (Crick

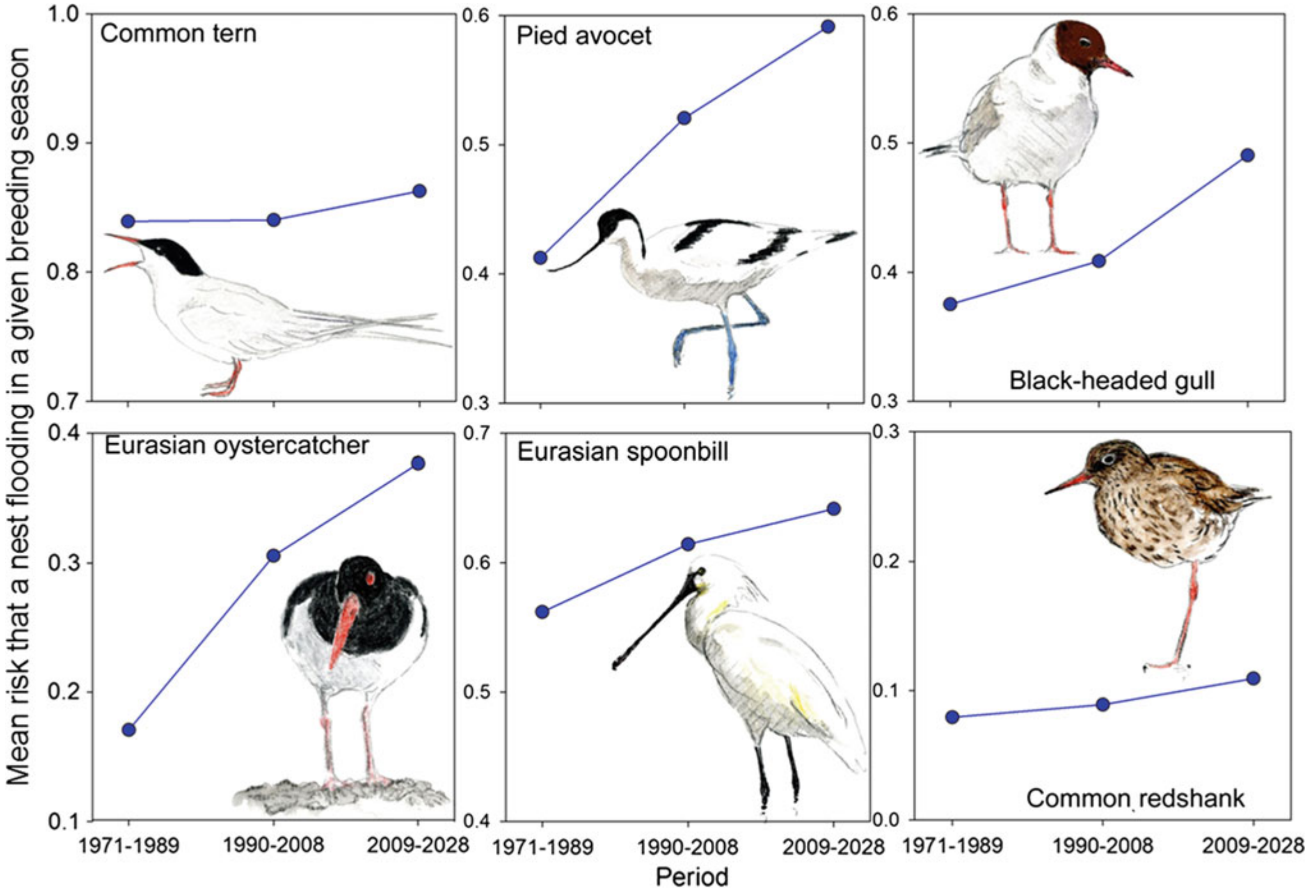


Fig. 9.26 Mean probability that a nest will flood at least once in a given breeding season, calculated for recent years (1990–2008), and projections for earlier (1971–1989) and future periods (2009–2028) based on model projections for sea-level rise and flooding risk that assume birds do not adjust their nest site selection adaptively (Van de Pol et al. 2010a). Please note that the range of the *y*-axis varies between panels

and Sparks 1999) and migration (Cotton 2003) have been most widely reported, since adjusting timing is a flexible way to alter the climatic conditions experienced. If birds cannot alter their timing sufficiently or climate change makes historically adaptive cues maladaptive, then populations may suffer (Visser 2008). Focusing on coastal birds, there appears to be no general pattern in how timing of egg laying has responded, with for example northern lapwings *Vanellus vanellus* showing no response over the past decades, while egg laying in Eurasian oystercatchers *Haematopus ostralegus* advanced in response to increased rainfall, and in ringed plovers *Charadrius hiaticula* advanced in response to rising temperatures (Crick and Sparks 1999).

Studies have also identified various cases where interannual variability in demographic rates was associated with climatic variability. The most common pattern is that annual juvenile and/or adult survival is strongly positively related to winter temperatures in many coastal birds (e.g. Peach et al. 1994; Yalden and Pearce-Higgins 1997; Atkinson et al. 2000). By contrast, a review has suggested that populations of nidifugous species (i.e. most waders) might be more strongly influenced by climatic conditions during the breeding season via effects of summer climate on reproduction (Sæther et al. 2004). A specific example of strong effects of summer climate on the reproduction of a community of coastal birds occurs when salt marshes become flooded during periods of strong wind, which can lead to catastrophic failure of a given breeding season. However, the degree to which species are affected by such events depends strongly on their existing nesting preference and elevation (Fig. 9.26), as well as on their potential to respond to increased frequency of summer flooding events (about which virtually nothing is known).

9.7.3 Changes in Bird Numbers and Distribution

Although there is some evidence that key life-history traits and demographic rates are changing potentially as a direct

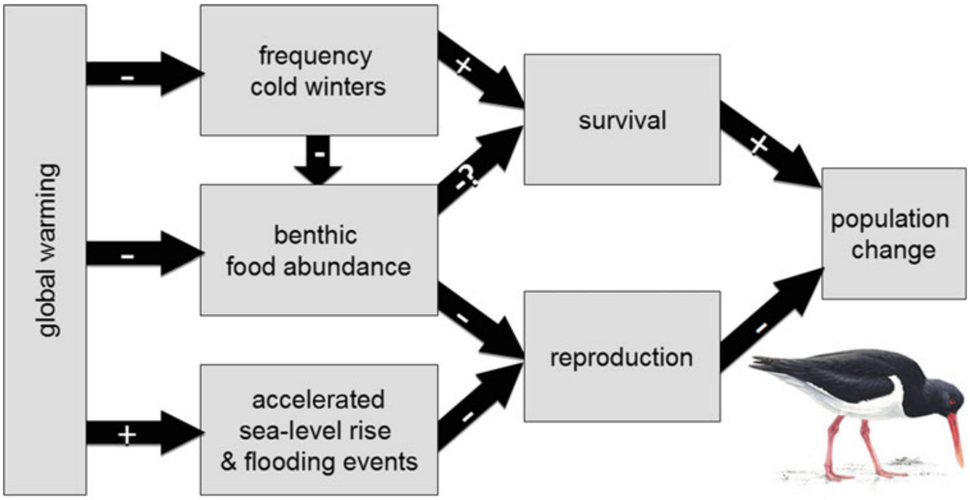


Fig. 9.27 Schematic illustration of how different aspects of a changing climate affect different demographic rates in Eurasian oystercatchers (Van de Pol et al. 2010a)

result of changes in climate variables, it remains very difficult to predict from these patterns what the population consequences of a changing climate might be. The reason for this is two-fold. First, many aspects of the weather (temperature, rainfall) are changing and not necessarily at the same rate throughout the year and in the same area. To assess the impact of climate change as a whole it is necessary to have good knowledge of all major climate drivers affecting bird populations. Second, different parts of the life-cycle may be affected by climate change, and not necessarily in the same direction. This implies that to predict how climate change will affect the population size of a species, requires a thorough understanding of which demographic rates are affected and how this in turn will affect population dynamics. In some cases, even strong climate dependency of demographic rates may not necessarily translate into changes in population size, for example in species with strong density-regulation (Reed et al. 2013).

An example of how complex the situation might be is shown in Fig. 9.27 for Eurasian oystercatchers breeding on a salt marsh on the Wadden Sea island of Schiermonnikoog (Van de Pol et al. 2010a, b, 2011). The frequency of exceptionally cold winters is predicted to decrease in this area, which is expected to result in an increase in both juvenile and adult survival. However, these warmer winters are also expected to reduce the benthic food stocks on which oystercatchers rely for their reproduction. Reproduction is expected to be further negatively affected by the flooding events that have become more frequent and higher in recent decades, especially during the breeding season (Figs. 9.25 and 9.26). Taking all these relationships together it is a priori unclear whether the local population will benefit or suffer, and a population model needs to be built that includes effects on demographic rates across the entire life-cycle in order to establish whether oystercatcher numbers are likely to benefit from climate change (Van de Pol et al. 2010b). This example also illustrates that even though reproduction is likely to be negatively affected by climate change, this does not mean that population numbers will also be reduced. Since reproduction and survival might be affected in opposite directions by different aspects of climate change predicting how population numbers will respond is not straightforward. Translating local population dynamics to meta-population dynamics is even more difficult, as climate does not affect all populations equally (e.g. some salt marshes are more susceptible to flooding than others due to geographic variation in elevation and compensatory sedimentation rates; see Sect. 9.6.2).

Finally, most coastal birds are already affected by many other (anthropogenic) threats, such as changes in land use (see, for example, effects of livestock grazing or abandoning on the vegetation of salt marshes in Sect. 9.6), predation, eutrophication, fisheries and disturbance (Koffijberg et al. 2009), and these other threats may interact with or add to the effects of climate change and thus make it difficult to isolate the contribution of climate change to changes in bird numbers (especially if multiple factors change synchronously over time). For example, as illustrated in Fig. 9.28, when looking at the effects of accelerated SLR on the flooding risk and nesting success of birds, the effects of local soil subsidence due to natural gas extraction may act in a similar cumulative way. Alternatively, the effect of changes in land use may interact indirectly with climate-related SLR via an indirect pathway and feedback loop. Specifically, salt marshes grow vertically in response to more frequent flooding due to sedimentation, but the rate of sedimentation increases with vegetation height, which in turn is affected by the land use in terms of mowing or grazing regimes (see Sect. 9.6).

Direct observations of changes in population numbers are another source of information on how coastal bird populations respond to climate change, although due to the lack of knowledge about the underlying demographic mechanisms, it

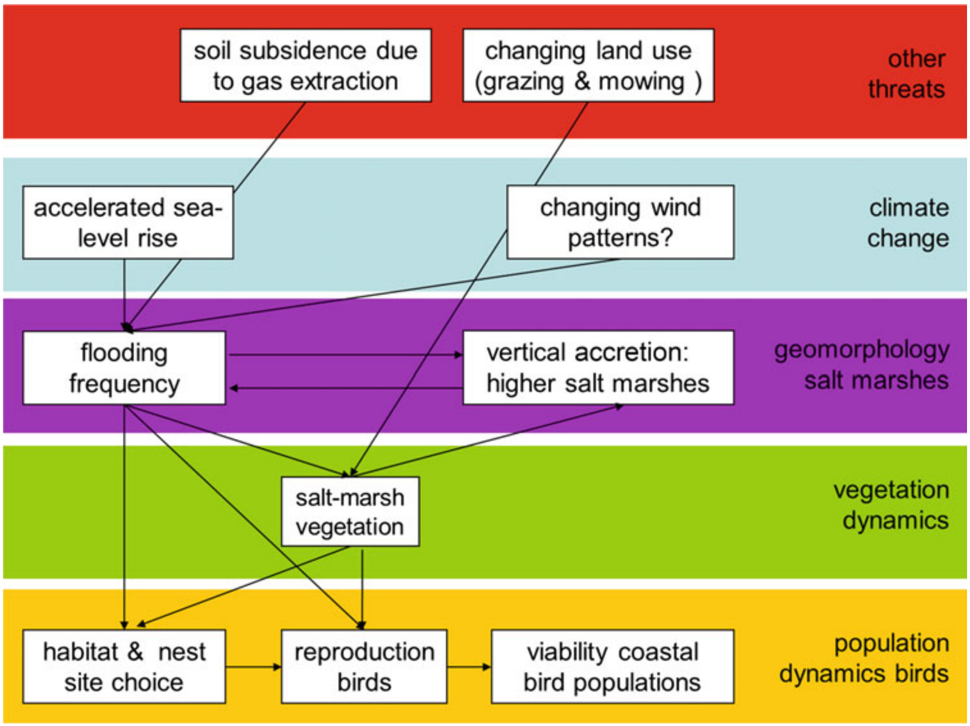


Fig. 9.28 Schematic overview of how specific aspects of climate change and other anthropogenic threats may have cumulative or interactive effects on coastal birds (after Van de Pol et al. 2012)

may be difficult to make reliable predictions for the future. Notwithstanding there is now a strong indication that climate fluctuations are a key driver of population dynamics for coastal birds in Europe's largest estuary, the Wadden Sea. For a striking 30 out of 34 migratory species, changes in meta-population numbers were associated with changes in spring temperatures and/or the NAO index (Laursen et al. 2010). However, the direction of the relationship varied widely among species, and it remains unclear why this is the case.

On a larger scale there have been some clear patterns in observed changes in the distribution of coastal birds, which have been largely attributed to global warming (Ens et al. 2009). It was shown for waders wintering in the United Kingdom that warmer winters led to a shift from wintering on the Atlantic coast (where winters are mild, but food is poor), to wintering on the North Sea coast (where winters are generally more severe, but food supplies are higher) (Austin and Rehfisch 2005). The range shift was especially clear in the smaller species that are affected most from energy stress when temperatures are low (Kersten and Piersma 1987). It has also been suggested that milder winters allow coastal bird species with a greater range of characteristics to overwinter in British estuaries, such that changes in abundance and functional diversity of the community of shorebirds may both change, but in different ways. Another more recent analysis of waders wintering in Europe confirmed a shift in the centre of the distribution to the northeast during the past 30 years, in line with milder temperatures in these areas (Maclean et al. 2008). And also in the Wadden Sea estuary more birds remain to overwinter in the eastern part during mild winters and may also depart at an earlier date to their northern breeding grounds when springs are warm (Bairlein and Exo 2007).

Predictions have also been made for coastal breeding populations on a European-scale based on climate envelope models with mostly northward shifts in the distribution of coastal birds (Huntley et al. 2008). Although these models form a useful starting point, they do not consider the adaptive potential of species. In fact, some coastal species such as common redshanks *Tringa totanus*, black-tailed godwits *Limosa limosa*, northern lapwings and Eurasian oystercatchers have previously shown that they can be very successful in adapting to new environmental conditions, as evidenced by their extremely successful colonisation of non-coastal agricultural areas over the 21st century (Van de Kam et al. 2004).

9.8 Conclusions

9.8.1 Abiotic Conditions

Accelerated SLR, and changes in the wave climate, storms, and local sediment availability all affect the abiotic conditions of coastal systems. The relative importance of these climate change effects and how they interact is poorly understood. It is even more difficult to separate effects of climate change from natural dynamics and the human impacts such as dredging. Human impacts on the geomorphology and sediment transport in estuaries are very likely to continue in the coming decades, and may supersede, exacerbate or compensate for the potential impacts of climate change. Heavy storms may result in coastal squeeze. This is particularly the case for dunes and salt marshes with a short foreshore, that is, a relatively narrow and steep foreshore.

9.8.1.1 Sandy Shores and Dunes

- The general response of sandy shores to climate change in the coming decades will be difficult (if not impossible) to detect and quantitatively predict as it is most likely to be superseded by local natural and/or human-impacted dynamics. Increased wave heights, storm surges and SLR, coupled with observed steepening of beach profiles and a historical decline in sediment availability due to coastal protection mean less sediment is available to replenish erosion of beach sand.
- Future changes in abiotic conditions of coastal dune systems are more likely to be driven by local anthropogenic impacts and natural variability than attributable directly to climate change. Rate of coastal change is strongly affected by local conditions, such as the effect of offshore bathymetry on inshore wave climate, local sand availability, rather than by regional variability and changes in the wave and wind climate.

9.8.1.2 Salt Marshes

- The SSC of fine-grained material is important for salt marshes to cope with sea-level rise. Salt marshes with a low tidal range and low SSC (<20 mg l^{-1}) are at risk of submergence by average SLR projections. The large tidal ranges (2–6 m) and generally large SSCs (mostly > 20 mg l^{-1} and up to several hundreds of mg l^{-1}) in estuaries make the risk low for marsh submergence by SLR. This also holds for most mainland marshes with or without sedimentation fields. The risk for marsh subsidence by SLR may be higher for back-barrier salt marshes with lower SSC values and tidal ranges.
- There is no single figure for surface elevation change for entire marshes. The position on the marsh is important: distance to source of suspended sediment, namely, edge of salt marsh or creek. Depressions away from the salt-marsh edge and creeks on back-barrier marshes are vulnerable. Surface elevation change is reduced in older marshes as a result of autocompaction, and in grazed marshes as a result of increased bulk density.
- Knowledge of vertical accretion rates at the scale of catchment areas on salt marshes (creeks with their drainage area) in salt marshes is poorly developed. Minor storm floods contribute strongly to accretion of sediment, but a heavy storm flood storm does not always result in extra accretion, and may even result in less surface elevation change at the low marsh and pioneer zone.
- More intensive process studies are needed to elucidate the linkages between tidal marshes and adjacent estuarine and coastal systems.
- De-embankment of summer polders can help to enlarge the area of salt marshes.

9.8.2 Plant and Animal Communities

Plant and animal communities can suffer from habitat loss by coastal squeeze in dunes and salt marshes as a result of high wave energy. This is particularly the case for dunes and salt marshes with a short foreshore. Apart from erosion by storm surges in winter, floodings occurred in summer over past decades with subsequent loss of offspring of breeding birds. Plants and animals are also affected by other aspects of climate change, such as changes in temperature and precipitation and atmospheric deposition of nitrogen. Local populations must deal with invasive species that change competitive interactions. Moreover, natural dynamics such as succession, and management practices such as grazing and mowing have a strong impact on plant and animal communities. The key challenge is not only to identify the exact role of climate change, but also to determine the relative importance of climate change compared to other impacts, and how they might interact.

9.8.2.1 Sandy Shores and Dunes

- On the drier southern North Sea coasts, vegetation of dry dunes will increase in xerophytes and bare sand due to moisture limitation of vascular plants.
- Water levels of dune wetlands are highly sensitive to changes in evapotranspiration and therefore recharge. There is currently little consensus on the effects of climate change but implications for dune slack vegetation could be severe. This is a major knowledge gap.
- Dune groundwater chemistry may become more concentrated with solutes due to lower recharge, or altered chemistry of input waters.
- There are relatively few species-specific climate studies, but most suggest a northward shift in species ranges. At a European-scale this may have few consequences, but distributions within individual countries may change markedly. Changes in climate may favour invasive shrub species such as bird cherry *Prunus serotina* or Japanese rose *Rosa rugosa* with subsequent changes in the food web.
- Atmospheric nitrogen deposition is above the critical level for dry and wet dune systems. Nitrogen is available

in excess and causes increased plant production with subsequent loss of slow-growing plant species. There may be interactions between climate change and the effects of nitrogen deposition, linked to faster growth of competitive species in both situations, and enhanced mineralisation of soil organic matter promoting nutrient availability and leaching of nutrients to groundwater.

9.8.2.2 Salt Marshes

- Minor storm floodings in spring negatively affect breeding birds.
- Plant production is significantly positively related to increased precipitation on salt marshes above MHT. Increased plant production could result in outcompeting low-statured species, and hence a decrease in species richness on marshes with subsequent changes in the food web.
- Some southern species will extend northward as a result of higher temperatures. The number of species extinct or emigrating north is smaller than the number of immigrating from the south. The real change in distribution patterns will differ for different species, for example due to migration rates.
- Atmospheric nitrogen deposition is just below the critical level for salt-marsh communities. When the limiting resource nitrogen is available in excess, plant production can easily increase with higher precipitation and temperature.

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Environmental Impacts—Lake Ecosystems

10

Rita Adrian, Dag Olav Hessen, Thorsten Blenckner, Helmut Hillebrand, Sabine Hilt, Erik Jeppesen, David M. Livingstone and Dennis Trolle

Abstract

The North Sea region contains a vast number of lakes; from shallow, highly eutrophic water bodies in agricultural areas to deep, oligotrophic systems in pristine high-latitude or high-altitude areas. These freshwaters and the biota they contain are highly vulnerable to climate change. As largely closed systems, lakes are ideally suited to studying climate-induced effects via changes in ice cover, hydrology and temperature, as well as via biological communities (phenology, species and size distribution, food-web dynamics, life-history traits, growth and respiration, nutrient dynamics and ecosystem metabolism). This chapter focuses on change in natural lakes and on parameters for which their climate-driven responses have major impacts on ecosystem properties such as productivity, community composition, metabolism and biodiversity. It also points to the importance of addressing different temporal scales and variability in driving and response variables along with threshold-driven responses to environmental forces. Exceedance of critical thresholds may result in abrupt changes in particular elements of an ecosystem. Modelling climate-driven physical responses like ice-cover duration, stratification periods and thermal profiles in lakes have shown major advances, and the chapter provide recent achievements in this field for northern lakes. Finally, there is a tentative summary of the level of certainty for key climatic impacts on freshwater ecosystems. Wherever possible, data and examples are drawn from the North Sea region.

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10.1 Introduction

Freshwaters and freshwater biota are highly vulnerable to climate change (IPCC 2013). The various impacts and threats differ substantially between biomes and among geographical regions, and even within geographical regions hydrological factors and catchment properties will be major determinants of the responses in freshwater ecosystems to climate change. Effects on freshwater resources in agricultural or densely populated catchments for example will differ from those in pristine boreal or alpine catchments. In the North Sea region, water scarcity per se is not seen as the most immediate threat of climate change, with the exception of during summer in some areas. Strong flooding events may pose greater challenges. The North Sea region contains a vast number of aquatic systems, including shallow, highly eutrophic water bodies in agricultural areas; systems highly influenced by the input of terrestrially derived, coloured dissolved organic matter in coniferous areas; and large, deep and oligotrophic systems in pristine, sub-alpine areas. Clearly, the review presented in this chapter cannot cover every aspect related to climate and surface waters in the North Sea region; hence a focus on natural lakes and parameters where there is empirical support for climate change effects, as well as on systems for which long-term data sets exist and for which their responses have major impacts on ecosystem properties such as productivity, community composition and biodiversity. Hydrological effects, wetland effects and past climate effects inferred from paleolimnological surveys are covered elsewhere in this report, although there is no doubt that hydrology will also have strong bearings on water chemistry (e.g. by dilution through increased precipitation) and biota (changed fluxes in key elements like nitrogen, phosphorus, carbon, silicon, iron and calcium), dissolved organic matter and pollutants.

Monitoring the impacts of climate change poses challenges because of the many responses within an ecosystem and the spatial variation within the landscape. A substantial body of research demonstrates the sensitivity of freshwater ecosystems to climate forcing and shows that physical, chemical, and biological lake properties respond rapidly to changes in this forcing (Rosenzweig 2007; Adrian et al. 2009; MacKay et al. 2009; Tranvik et al. 2009; IPCC 2013). Fast turnover times from the scale of organisms to entire lake ecosystems are the prerequisite for these rapid changes. Studies of lake ecosystems have provided some of the earliest indications of the impact of current climate change on ecosystem structure and function (Adrian et al. 1995; Magnuson et al. 2000; Verburg et al. 2003) and the consequences for ecosystem services (O'Reilly et al. 2003). Some climate-related signals are highly visible and easily measured in lakes. For instance climate-driven fluctuations in lake level have been observed on a regional-scale across North America (Williamson et al. 2009), and shifts in the timing of ice formation and melt reflect climate warming at a global scale (Magnuson et al. 2000). Other signals may be more complex and difficult to detect in lakes, but may be equally sensitive to climate or more informative regarding impacts on ecosystem services. Long-term historical records and reconstructions from sediment cores have yielded insight into less visible climate-related changes, thus increasing understanding of the mechanisms driving these changes. In particular, paleolimnological records have been critical for reconstructing the climate record over recent geological periods, making it possible to interpret current climate change and predict its future impacts.

Lake ecosystems are excellent sentinels for current climate change. In this context a sentinel is a lake ecosystem that provides indicators of climate change either directly or indirectly through the influence of climate on the catchment (Fig. 10.1; Carpenter et al. 2007; Adrian et al. 2009; Williamson et al. 2009). The indicators are measureable response variables, such as water temperature, dissolved organic carbon, or phytoplankton composition. Lakes are particularly good sentinels for current climate change for several reasons: they are well-defined ecosystems and studied in a sustained fashion; they respond directly to climate change and incorporate the effects of climate change within the catchment; they integrate responses over time, which can filter out random noise; and they are distributed worldwide and so cover many different geographic locations and climatic regions. However, the large range in lake morphology, geographic location, and catchment characteristics means that broad statements about the ability of lakes to capture the impacts of the current, rapidly changing climate must be made with caution. On the other hand, this also means that there are many different types of sensors in the landscape ranging from small shallow turbid lakes to large, deep, clear lakes that may capture, or provide sentinel information on different aspects of climate change, including temperature and precipitation-related components.

This chapter focuses on both the direct and indirect (e.g. via the catchment) effects of climate change, as well as on internal physical, chemical and biological processes and on the role of temporal scale. Wherever possible, data and examples are drawn from the North Sea region, but for important phenomena where North Sea studies are not available, information is 'borrowed' from other parts of the world.

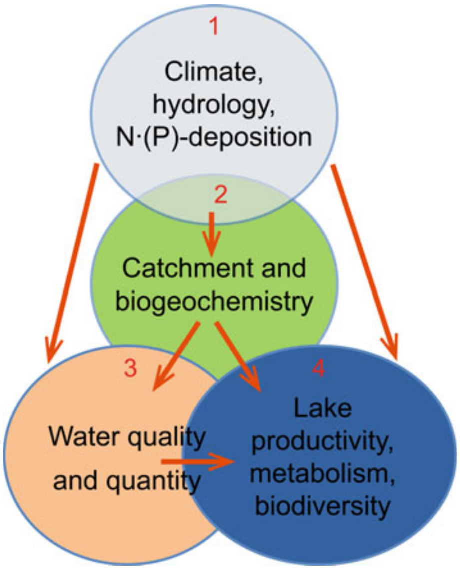


Fig. 10.1 Water and its context: lakes respond to climatic forcing, atmospheric deposition and the properties of their catchments. *1* Atmospheric forcing via temperature, precipitation and deposition of key constituents like nitrogen. *2* The catchment responds to climatic drivers and atmospheric inputs via vegetation and soil processes. *3* This determines the inputs of organic matter, nutrients and key elements determining parameters like retention time, transparency, pH and temperature. *4* The biota respond in terms of phenology, productivity, metabolism, community composition, diversity and food web interactions, to the direct forcing (*1*), catchment properties (*2*) and water properties (*3*)

10.2 Climate Warming and Impacts on Lake Physics

Data-based studies on the impact of climate change on lake temperature began in the early 1990s with the seminal studies of Magnuson et al. (1990) and Schindler et al. (1990). The former demonstrated that near-surface lake temperatures in Wisconsin fluctuate coherently in response to regional climatic forcing, while the latter demonstrated that lake temperatures in the Canadian Experimental Lakes Area were undergoing a long-term increase. Since the 1990s, an increasing number of studies have demonstrated that near-surface lake temperatures can fluctuate coherently over several hundred kilometres (e.g. Benson et al. 2000; Livingstone and Padisák 2007; Livingstone et al. 2010a), and that individual lakes in many parts of the world have been undergoing long-term warming at all depths. Lake warming has been demonstrated in Europe (e.g. Livingstone 2003; Salmaso 2005), North America (e.g. Arhonditsis et al. 2004; Coats et al. 2006; Austin and Colman 2008), East Africa (e.g. O'Reilly et al. 2003; Verburg et al. 2003), Siberia (Hampton et al. 2008) and Antarctica (Quayle et al. 2002). A recent study based on satellite thermal infrared images from 1985 onwards (Schneider and Hook 2010) confirmed that lake surface temperatures have been undergoing a long-term increase over large areas of the northern hemisphere. In an extensive world wide survey of lake's summer surface temperatures O'Reilly et al. (2015) found an average warming trend of 0.34 °C per decade for the period 1985 until 2009.

Modelling studies on strictly dimictic lakes, which are ice-covered in winter and mix twice per year, suggest that surface temperatures will increase faster than deep-water temperatures as a result of climate change (Robertson and Ragotzkie 1990; Hondzo and Stefan 1993). In monomictic lakes, which mix once per year, the divergence between surface and deep-water temperatures is likely to be less strong as a result of heat carry-over in winter (Peeters et al. 2002). However, even in such lakes historical data show that near-surface water temperatures are increasing faster than deep-water temperatures, which implies an increase in thermal stability leading to an increase in the duration of stratification in summer and a corresponding decrease in the duration of homothermy in winter and spring (Livingstone 2003).

At high latitudes or high altitudes, where lakes are generally ice-covered for many months of the year, the more frequent occurrence of mild winters associated with climate warming will imply a general decrease in the duration of ice cover and a corresponding increase in the duration of summer stratification. Since the mid-19th century, there has been a general long-term decrease in the duration of ice cover in northern hemisphere lakes at a mean rate of about 1.2 days per decade (Magnuson et al. 2000), with the rate for individual lakes ranging from 0.9 to 1.7 days per decade (Benson et al. 2012). This decline seems to be accelerating: over the last 30 years, the equivalent is 1.6–4.3 days per decade (Benson et al. 2012). In regions with relatively brief or mild winters, where lakes are ice-covered for a comparatively short period—for instance in southern Sweden, Denmark and northern Germany—increasingly milder winters are likely to result in ice cover becoming intermittent or even disappearing (Livingstone and Adrian 2009; Weyhenmeyer et al. 2011). The disappearance of ice cover from a deep lake, implying a shift in mixing regime from dimixis to monomixis (Boehrer and Schultze 2008; Livingstone 2008), is likely to cause a change in its physical response to further climate warming, as mixing will no longer necessarily occur at the temperature of maximum density (4 °C) before ice-on and after ice-off. However, mixing can still occur at temperatures higher than 4 °C. Deep lakes that are already monomictic will experience individual years in which some form of stratification persists throughout the year, reducing the intensity of mixing and inhibiting deep-water renewal. Thus some deep monomictic lakes may show a tendency towards becoming oligomictic; i.e. will not mix fully every year. Shallow polymictic lakes, which lose their winter ice cover, are likely to undergo permanent mixing during winter.

10.2.1 Lake Water Temperature

Research on lakes within the North Sea region has demonstrated the occurrence of many of the phenomena mentioned in the previous section. In the UK—at the western boundary of the region, where the influence of the North Atlantic is at its greatest—research has focused on the English Lake District, where several decades of data are available from some of the larger lakes. Here, water temperatures both near the surface and in the deep water have been shown to respond coherently to climatic forcing throughout the year (George et al. 2000), with a clear long-term increase recorded in both near-surface temperatures (George et al. 2007a) and deep-water temperatures (Dokulil et al. 2006). Long-term increases in surface water temperatures have also been recorded in lakes in Sweden, at the region's eastern boundary (Adrian et al. 2009), and in northern Germany, at its southern boundary (Adrian et al. 2006, 2009; Wilhelm et al. 2006). It is thus likely that long-term increases in lake temperature are occurring throughout the North Sea region.

It has become evident that the climatic forcing acting on lakes in the North Sea region is extremely large-scale in nature, with the climate prevailing over the North Atlantic playing a major role in determining the physical behaviour of the lakes. Interannual fluctuations in thermal stratification in the lakes of the English Lake District, for instance, are related to north-south displacements of the Gulf Stream, with the early summer thermocline tending to be shallower and more well-defined when the Gulf Stream has its most northern direction (George and Taylor 1995). This effect appears to be related to the effect of the Gulf Stream on wind speed (George et al. 2007b). However, an even more potent determinant of physical lake behaviour is the climate mode known as the North Atlantic Oscillation (NAO), which governs winter weather in western, northern and central Europe to a very large degree (Hurrell 1995; Hurrell et al. 2003) and which is known to play an important role in determining the behaviour of lakes in this region (Straile et al. 2003). This climate mode, which can be considered a regional manifestation of the Arctic Oscillation (AO) (Thompson and Wallace 1998), is associated with interannual fluctuations in the meridional surface air pressure gradient in the north-east Atlantic (between about 35°N and 65°N). A positive NAO index implies a large meridional air pressure gradient, which results in the strong zonal transport of warm, moist maritime air from the North Atlantic towards north-west Europe. In winter, this implies predominantly mild, wet weather in the North Sea region. When the NAO index is negative, however, the eastward transport of warm, moist air from the North Atlantic is much weaker, implying predominantly cold, dry weather in the North Sea region. In lakes throughout northern and central Europe, surface water temperatures, near-bottom temperatures and the duration of ice cover (Fig. 10.2) are correlated to some extent with the winter NAO index (Blenckner et al. 2007).

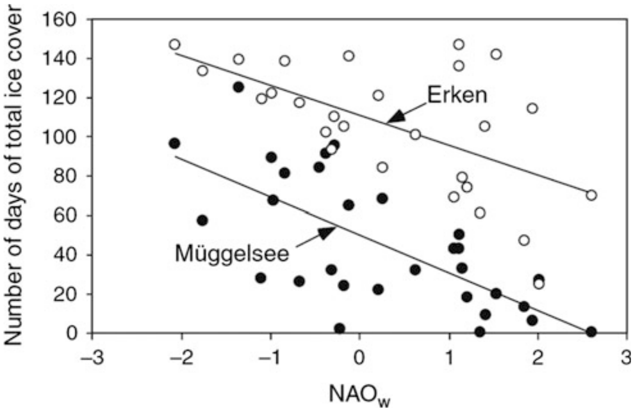


Fig. 10.2 Dependence of the number of days of total ice cover on Lake Erken (southern Sweden) and Müggelsee (northern Germany) on the winter NAO index (NAO$_w$) of Hurrell (1995), based on data from winter 1976/77 to winter 2005/06. Interannual variability in NAO$_w$ explains 35 % of the interannual variability of the duration of ice cover for Lake Erken and 47 % for Müggelsee. The linear regressions (regression lines illustrated) are significant at $p < 0.01$ (from Livingstone et al. 2010b)

In the English Lake District, lake surface temperatures in winter are tightly correlated with the winter NAO index (George et al. 2000, 2004b, 2007a) as, but to a lesser extent, are deep-water temperatures (George et al. 2004b), with the highest correlations being observed in the shallower lakes (George et al. 2004b). Mean annual water temperature of Lake Veluwe, a shallow lake in the Netherlands, is correlated with the winter NAO index (Scheffer et al. 2001), as are the surface water temperatures of Vänern, Vättern, and Mälaren, the three largest lakes in Sweden, in spring (Weyhenmeyer 2004). However, in Mälaren, a morphometrically complex lake with many sub-basins, the significance of the correlation varies substantially among the different sub-basins, suggesting that local lake characteristics can modify the effect of large-scale climatic forcing even on surface water temperature, which apart from the timing of ice-off is probably the lake variable least affected by internal lake processes. In Müggelsee, a well-studied, shallow, polymictic lake in northern Germany, several studies have demonstrated the effect of the winter NAO on lake temperatures (Gerten and Adrian 2000, 2001; Straile and Adrian 2000).

In a comparative study of Müggelsee and two neighbouring lakes, Gerten and Adrian (2001) showed that the winter NAO leaves a signal at all depths in lake temperature, but that the temporal persistence of this signal can differ substantially from lake to lake. Near the surface, the NAO signal is in general confined to late winter and early spring. In the deeper water, however, the persistence of the NAO signal depends on the morphometry and mixing characteristics of the lake. The NAO signal persists only through spring in shallow, polymictic Müggelsee, but throughout much of the following summer in the shallow, dimictic Heiligensee, and throughout the whole of summer and autumn in the much deeper, dimictic Stechlinsee. Thus, although an NAO signal is likely to be present to some extent in the temperature of all lakes within the North Sea region, individual lake characteristics are certain to result in a large degree of variability in the strength and persistence of this signal.

In the context of the NAO, one other phenomenon should be mentioned: the late 1980s climate regime shift. In the late 1980s, an abrupt regime shift occurred in the atmospheric, oceanic, terrestrial, limnological and cryospheric systems in many regions of the world. Evidence suggests that this large-scale regime shift involved abrupt changes in the AO and NAO (Alheit et al. 2005; Rodionov and Overland 2005; Lo and Hsu 2010), had a substantial impact on air temperature in northern Europe (Lo and Hsu 2010), and affected fish populations in the North Sea (Reid et al. 2001; Alheit et al. 2005). It is not surprising therefore that a regime shift in lake temperature in the late 1980s was also detected in Müggelsee (Gerten and Adrian 2000, 2001), and it can be fairly confidently hypothesised that a similar regime shift, at least in lake surface temperatures, is likely to have occurred in many lakes within the North Sea region.

In summer, a more regional approach to determining the effects of climatic forcing on lakes is necessary owing to the smaller spatial scales of the weather systems involved. In the case of the UK, the Lamb synoptic weather classification system (Lamb 1950) has proven useful. For both Windermere, the largest lake in the English Lake District, and Lough Feeagh, a lake located near the west coast of Ireland, the highest lake surface temperatures were recorded during a westerly circulation type in winter (corresponding to a positive NAO index), but a southerly circulation type in summer (George et al. 2007b).

On a multi-annual time scale, large-scale regional coherence is greater in winter than in summer. However, on shorter time scales the opposite appears to be the case. Short-term, high-resolution surface temperature measurements in Scottish Highland lochs (Livingstone and Kernan 2009) show a high degree of regional coherence in daily means from late spring to autumn, but much lower coherence in winter and early spring. Short-term regional coherence is high in summer because the surface mixed layer is thin and surface temperatures respond sensitively to climate forcing, and is high in autumn because surface temperatures are dominated by convective cooling, which is governed by regionally coherent air temperature. Short-term coherence is comparatively low in winter because fluctuations in lake surface temperature are small and may be buffered by partial ice cover, and is low in early spring because the lochs warm up and stratify at different times during the season depending on their altitude and distance from the maritime influence of the Atlantic. This latter effect may be important on the western boundary of the North Sea region, because the ameliorating influence of the Atlantic Ocean acts to increase winter surface temperatures, and hence to reduce the duration of inverse stratification or circulation.

Based on observed air temperature and physical lake characteristics, George et al. (2007b) were able to model well the surface temperatures of the lakes of the English Lake District. Using a regional climate model (RCM) driven by the SRES A2 scenario, they also projected lake surface temperatures in the 2050s. This showed increases of up to 1.1 °C in winter and up to 2.2 °C in summer, with the greatest increase in winter occurring in the shallowest lake, and the greatest increase in summer occurring in the lake with the shallowest thermocline.

10.2.2 Lake Ice Phenology

It is likely that the phenology of ice cover on the lakes of the North Sea region will follow the global trend; with ice-on occurring later, ice-off occurring earlier, and a general reduction apparent in the duration of ice cover (Magnuson et al. 2000; Benson et al. 2012). However, several factors will modify this general trend. Because of the approximately sinusoidal form of the air temperature curve, the dates on which the air temperature falls below and rises above 0 °C, which are crucial for the timing of ice-on and ice-off, respectively, are not linear functions of air temperature. Instead, they are arc cosine functions of air temperature, which implies that the sensitivity of the timing of ice-on, the timing of ice-off, and the duration of ice cover are greater in warmer regions than in colder regions, and so will increase as the climate warms (Weyhenmeyer et al. 2004a, 2011; Jensen et al. 2007; Livingstone and Adrian 2009). Thus, in the North Sea region, the impact of climate warming on lake ice phenology will be disproportionately large in those areas where winters are mild or variable and the duration of ice cover on lakes is already short (i.e. the UK, northern France, Belgium, Netherland, Luxemburg, northern Germany and southern Scandinavia) compared to those areas where winters are consistently cold and the duration of ice cover is much longer (i.e. northern Scandinavia). This is despite the IPCC (Intergovernmental Panel on Climate Change) projections implying that climate warming in winter in northern Scandinavia will be stronger than in the rest of the region (Christensen et al. 2007). In Sweden, several decades of historical data confirm that the timing of ice-off on lakes in the south of the country, where winters are relatively mild, has been responding significantly more sensitively to

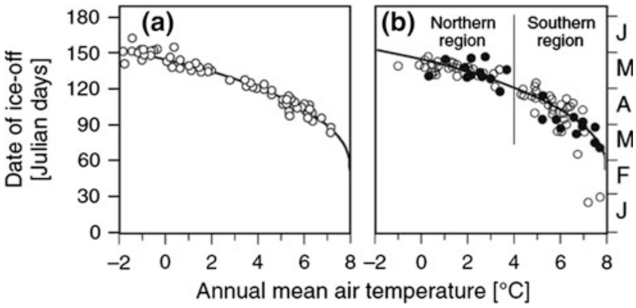


Fig. 10.3 **a** Dependence of the median date of ice-off on annual mean air temperature (1961–1990) for 70 lakes in Sweden. **b** Temporal variation in the relationship between the median date of ice-off and annual mean air temperature for 14 lakes in a northern region of Sweden (61–67°N) and 14 lakes in a southern region of Sweden (56–60°N) for the periods 1961–1990 (*white*) and 1991–2002 (*black*), showing that the form of the relationship is strongly dependent on latitude but not on the time period chosen. Annual mean air temperatures are calculated from July to June, and the curves illustrated are based on the arc cosine model of Weyhenmeyer et al. (2004a) (Livingstone et al. 2010b; after Weyhenmeyer et al. 2004a)

interannual fluctuations in mean winter air temperature than the timing of ice-off on lakes in the north of the country, where winters are longer and more severe (Fig. 10.3; Weyhenmeyer et al. 2004a).

A further study of ice phenology on 54 Swedish lakes during the 30-year IPCC reference period 1961–1990 showed a statistically significant ($p < 0.05$) trend towards earlier ice-off in 47 lakes, with the shift towards earlier ice-off varying between 1 and 29 days (Weyhenmeyer et al. 2005). Again, the shift towards earlier ice-off was stronger in the milder, southern part of Sweden than in the colder, northern part. During the IPCC reference period, the mean air temperature of the northern hemisphere increased by 0.4 °C. This resulted in a shift in the timing of ice-off by ~70 days in southern Sweden, but only ~10 days in northern Sweden. Applying the arc cosine model suggests that interannual variability in the duration of lake ice cover will be far greater in southern Scandinavia, Scotland and northern Germany than in northern Scandinavia (Weyhenmeyer et al. 2011). A more sophisticated probability model applied to Müggelsee, which now shows extremely variable, intermittent ice cover, predicts that the percentage of ice-free winters for this lake will increase from ~2 % now to over 60 % by the end of the 21st century (Livingstone and Adrian 2009).

As for winter lake surface temperatures, the duration of ice cover on lakes in the North Sea region also appears to be strongly related to the NAO. In the case of Müggelsee, 47 % of the interannual variability of the duration of ice cover can be explained statistically ($p < 0.01$) in terms of the interannual variability of the winter NAO index, while for Lake Erken, in east-central Sweden, the equivalent value is 35 % (Fig. 10.2). Even in the UK, where total lake ice cover does not occur frequently, there is evidence that the number of days of partial ice cover is strongly linked to the winter NAO (George et al. 2004a; George 2007).

As well as the duration of ice cover, the timing of both ice-on and ice-off also appear to be determined to some degree by the NAO. For lakes in Sweden, the timing of ice-off is strongly related to the winter NAO while the timing of ice-on shows a weaker relationship to the autumn NAO (Blenckner et al. 2004). These results agree with those of similar studies showing that the winter NAO is an important determinant of ice phenology in the neighbouring Baltic region (Livingstone 2000; Yoo and d'Odorico 2002; Blenckner et al. 2004; George et al. 2004a). As in the case of lake water temperatures, there is evidence to suggest that the late 1980s climate regime shift may have resulted in an abrupt shift in lake ice phenology in the North Sea region: a study of Swedish lakes showed an abrupt shift in 1988/1989 that was substantial in southern Sweden but not in northern Sweden, again emphasising the relative sensitivity of ice phenology in warmer regions to external climatic forcing (Temnerud and Weyhenmeyer 2008).

10.3 Catchment–Lake Interactions

While lakes are commonly seen as closed entities, which is partly true in terms of populations with low or no immigration or emigration, lakes are strongly influenced by catchment properties such as the proportions of forest, bogs, and arable land that serve as major determinants of element fluxes (and water) to lakes. This is however modified by anthropogenic impacts. For example, acidifying elements such as nitrogen (N) and sulphur (S) will modify the catchment export of ions, dissolved organic matter (DOM) and nutrients, and deforestation or afforestation will also have a major impact on the flux of elements to lakes. This is especially striking for nitrogen, where alpine or otherwise sparsely vegetated catchments may have very low N-retention, while forested catchments may retain almost all nitrate (NO_3) and ammonium (NH_4) inputs during the growing season (Hessen 1999).

Different catchment properties have vastly different effects on lakes, even within the North Sea region, and these properties and effects will also be differently modified by climate drivers (Fig. 10.1). Although large, deep and oligotrophic lakes are common in alpine areas of the North Sea drainage basin, the North Sea region is dominated by two major types of lake system and it is these that will be most affected by climate change. These are the boreal lakes generally found in forested, less impacted, catchments with limited input of bioavailable nutrients but high loads of humic substances of terrestrial origin. The other lake type occurs in agricultural areas with higher nutrient loads. Both

Fig. 10.4 Export of coloured dissolved organic carbon (DOC) from wetlands, bogs and forest via rivers (*Photo* D.O. Hessen)

categories of lake/catchment encompass a wide range of size, volume, renewal rates, productivity and community composition.

While catchment responses to climate affect downstream rivers, lakes and ecosystems, hydrology (runoff) also plays a major role both in mobilising and diluting dissolved matter and key elements (such as nitrogen, phosphorus, iron, silicon and calcium). Hydrology also affects the water renewal rate, which has major impacts on the physical, chemical and biological properties of waters. These aspects are less well studied and there is a need for 'bridging the gap' between hydrology and especially aquatic biology.

10.3.1 Boreal Lakes

Rising temperatures and changes in precipitation patterns and amounts will have direct effects on lake ecosystems as well as indirect effects via impacts within the terrestrial catchments (Schindler 2001; Kernan et al. 2010). Atmospheric deposition of nitrogen and sulphur will add to these climate-related impacts on ecosystems (Wright et al. 2010). The well-documented increase in dissolved organic matter in boreal lake ecosystems is one of the most obvious indirect effects (Monteith et al. 2007). This 'browning' is mainly due to coloured dissolved organic carbon (DOC) which absorbs light and so affects lake production at all trophic levels (Karlsson et al. 2009; Xenopoulos et al. 2009) as well as species composition (Watkins et al. 2001). The export of DOC from wetlands, bogs and forest via rivers (Fig. 10.4) to lakes and coastal areas is projected to increase, causing reduced primary and secondary production due to light limitation.

Changes in temperature and precipitation drive seasonal and interannual variations in the export of DOC and nutrients by affecting soil organic matter mineralisation and the production of DOC and mineral nitrogen species (Kalbitz et al. 2000; Hobbie et al. 2002a, b), as well as hydrology within the catchment. On a longer timescale, climate change can allow forests to expand into areas at present under heathland and alpine vegetation (Hofgaard 1997), thereby affecting nutrient retention, nutrient export and soil organic matter pools and quality (Kammer et al. 2009). A major climatic response expected in boreal, coniferous areas is an increase in the concentrations of terrestrially derived DOM and DOC. For a large dataset of boreal lakes (1041 Swedish lakes along a 13° latitudinal gradient), Weyhenmeyer and Karlsson (2009) demonstrated a nonlinear response of DOC to increasing temperature, with the number of days above 0 °C as the major predictor. Analysis of a correspondingly large dataset of boreal Norwegian watersheds within the North Sea region, indicates that even a moderate (2 °C average, downscaled Hadley scenario) increase in temperature with associated increase in precipitation and vegetation density has the potential to increase DOC export substantially (Fig. 10.5; Larsen et al. 2011a, b). For other North Sea regions, especially the UK, reduced deposition of acidifying compounds (notably sulphur) has also been shown to affect DOC concentrations (Evans et al. 2006), although the Nordic studies strongly suggest that climatic drivers like temperature and/or precipitation are the key drivers of rising DOC concentrations in lakes.

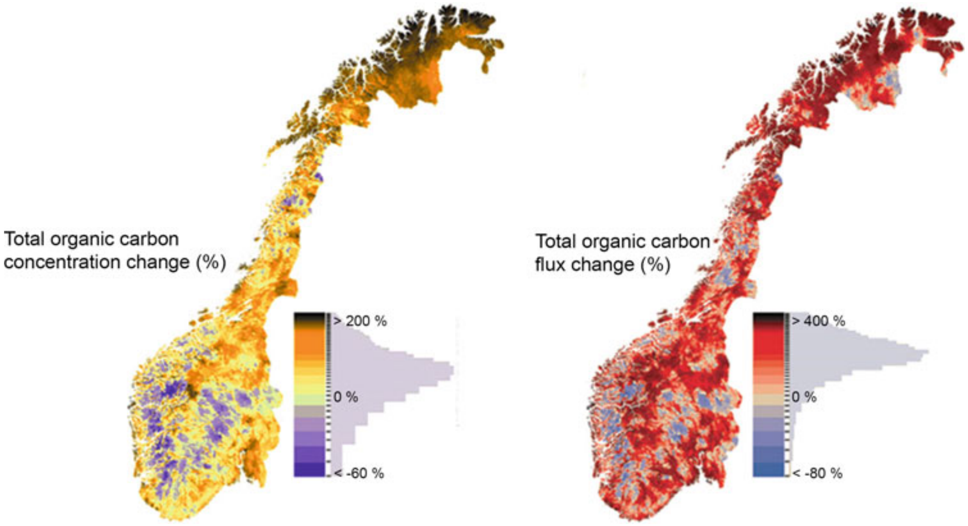


Fig. 10.5 Projected change in total organic carbon concentrations and catchment fluxes at a new steady state based on a downscaled 2 °C increase (Hadley model) (Larsen et al. 2011b)

The ecosystem responses to elevated DOC export may be profound, and may also act in concert with elevated N-deposition and N-export to lakes, which also may increase as a result of elevated N-deposition due to increased precipitation (de Wit et al. 2008; de Wit and Wright 2008; Hessen et al. 2009). This in turn is likely to affect productivity and autotroph community composition; a large survey of US and Scandinavian lakes suggested a transition from N-limitation to P-limitation in many freshwater systems as a result of chronic, elevated N-deposition (Elser et al. 2009).

An increase in allochthonous carbon may fuel microbial production and serve as an alternative food resource for zooplankton (Hessen 1998; Jansson et al. 2007). Changes in water colour and loading of organic carbon may also affect the relative roles of the benthic and pelagic parts of the lake ecosystem, in favour of the pelagic (Ask et al. 2009; Karlsson et al. 2009). However, increased DOC loads are expected to have negative impacts on overall lake productivity. Recent studies from boreal catchments suggest that P-loads especially will decrease in most areas due to increased terrestrial uptake, intensifying P-limitation and in concert with increased light limitation will reduce the overall productivity of boreal freshwaters (Weyhenmeyer et al. 2007; Jones et al. 2012; Thrane et al. 2014). Since DOM may also be a source of phosphorus in pristine catchments, a unimodal response in fish yield over DOC was found for a large number of boreal, Norwegian lakes (Finstad et al. 2014), where an initial stimulus of DOC-associated phosphorus was superseded by light limitation at higher DOC-concentrations.

Hansson et al. (2012) studied how a combination of warming and increased lake colour affects spring plankton phenology and trophic interactions in a mesocosm experiment. Elevated temperature was crossed with increased water colour. Overall, they found temperature to have a stronger effect on phytoplankton and zooplankton abundance than humic substances, but importantly also found synergistic effects between the two stressors. Thermal properties will also be affected by changes in ice cover and basin morphometry (MyLake-model, Saloranta and Andersen 2007), and temperature and reduced nutrients may both induce smaller algal cell size (Daufresne et al. 2009; Hessen et al. 2013) and community changes.

10.3.2 Lakes in Agricultural Areas

While changes in DOC may be the main climatic response in boreal lakes, they will also be affected by changes in nitrogen, phosphorus and silicon loads. The nutrient impact is far more severe in urban or agricultural lakes, however, and such lakes are also more susceptible to catchment erosion promoted by extreme rainfall as well as reduced periods of snow cover or frozen ground in winter. Land use and agricultural practices such as harvesting and fertiliser applications largely determine loads of nutrients and particulate matter to these lakes, but climatic factors, not least precipitation patterns, will add to these effects. Typically the nitrogen load from agricultural areas is expected to increase, but with a seasonal shift to increased N-export in winter, reflecting both land-use practices and climatic change (Jeppesen et al. 2011).

Phosphorus loads will also increase due to higher winter precipitation and erosion, but again the effects of land-use practices will be superimposed on the effects of climate change. The net impact on lake productivity is unclear, not least because increased turbidity has such a profound impact on lake productivity and stability (Mooij et al. 2005; Jeppesen et al. 2011). Specific ecosystem responses in lakes in agricultural areas are addressed in the following sections.

10.4 Ecosystem Dynamics

Climate change is expected to alter community structure and ecosystem functioning within lakes worldwide as well as within the North Sea region. Changes may occur in phenology, species and size distribution, food-web dynamics, life-history traits, growth and respiration, nutrient dynamics and ecosystem metabolism. Temperature-induced changes of this type are expected to interact with the increased nutrient flows resulting from enhanced precipitation and runoff (Blenckner et al. 2007; Jeppesen et al. 2010a; Moss et al. 2011).

10.4.1 Trophic Structure and Function

10.4.1.1 Fish

Several studies indicate that fish community assemblages, size structure and dynamics will change with global warming. A long-term study of 24 European lakes revealed a decline in the abundance of cold-stenothermal fish species, particularly in shallow lakes, and an increase in the abundance of eurythermal fish species, even in deep, stratified lakes (Jeppesen et al. 2012). This occurred despite a reduction in nutrient loading in most of the case studies, supposedly favouring fish in cold-water and low-nutrient lakes. The cold-stenothermic Arctic charr *Salvelinus alpinus* has been particularly affected, showing a clear decline in Lake Elliðavatn in Iceland, Lake Windermere in the UK (Winfield et al. 2010), Lake Vättern in Sweden (Jeppesen et al. 2012), and Scandinavian hydroelectric reservoirs (Milbrink et al. 2011).

Other cold-water-adapted species such as coregonids and smelt *Osmerus eperlanus* are affected at the southern border of their distribution. The harvest of whitefish *Coregonus* spp. has declined substantially in Lake Vättern in Sweden and Lake Peipsi in Estonia (Kangur et al. 2007; Jeppesen et al. 2012). In the UK and Ireland, a decline in the coregonid pollan *Coregonus autumnalis* in recent decades has been attributed to changes in temperature (Harrod et al. 2002). A drastic reduction in the population of smelt has occurred in shallow Lake Peipsi as shown from commercial fishing, with the decline particularly strong in years with heat waves (Kangur et al. 2007; Jeppesen et al. 2012). In contrast, the abundance of eurythermal species, including the thermo-tolerant carp *Cyprinus carpio* (Lehtonen 1996; Jeppesen et al. 2012) is rising in several lakes in the North Sea region (Jeppesen et al. 2012).

It is well-established that high-latitude fish species are not only often larger but also often grow more slowly, mature later, have longer life spans and allocate more energy to reproduction than populations at lower latitudes (Blanck and Lamouroux 2007). Even within species such differences can be seen along a latitudinal gradient (Blanck and Lamouroux 2007) and within North Temperate lakes (Jeppesen et al. 2010b). Thus, changes in life history and size can be expected with warming, and may in fact already have occurred (Daufresne et al. 2009; Jeppesen et al. 2010b, 2012).

10.4.1.2 Plankton

Changes in fish community structure are likely to have cascading effects in lakes, most implying increased predation on larger zooplankton which in turn means less grazing on phytoplankton and so higher algal biomass per unit of available phosphorus (Lehtonen and Lappalainen 1995; Gyllström et al. 2005; Balayla et al. 2010; Ruuhijärvi et al. 2010; Jeppesen et al. 2010a, b; Meerhoff et al. 2012). Decreasing body size has been suggested as a universal biological response to global warming (Gardner et al. 2011; Hessen et al. 2013). However, there is no consensus about the underlying causality.

The predatory effect due to fish that prefer large zooplankton prey could be reversed or partially reversed if the prevailing or additional predators are invertebrates that prefer small prey. In this case, stronger predation at higher temperature would lead to a stronger removal of small species. A shift towards smaller species can also result from stronger resource competition under higher temperatures and competitive advantage for smaller species. Stronger invertebrate predation at higher temperatures has been suggested, particularly for primary producers, because heterotrophic metabolic rates increase faster with rising temperature than photosynthesis (Yvon-Durocher et al. 2011).

Further evidence of warming-induced changes in plankton size structure comes from mesocosm studies that mimic British shallow lakes. In these mesocosms, warming increased the steepness of the plankton community size spectrum by increasing the prevalence of small organisms, primarily within the phytoplankton assemblage. Mean and maximum size of phytoplankton was reduced by about an order of magnitude. The observed shifts in phytoplankton size structure were reflected in changes in phytoplankton community composition, while zooplankton taxonomic composition remained unaffected by warming (Yvon-Durocher et al. 2011). See Sect. 10.6 for more information on responses of lake plankton communities in the context of global warming. Weak changes in the species composition of benthic macroinvertebrates following shifts towards warmer water temperatures were found in Swedish lakes (Burgmer et al. 2007).

10.4.1.3 Cyanobacteria Biomass

Higher phytoplankton biomass, particularly higher biomass of cyanobacteria during summer may be expected as a direct response to enhanced water temperatures and as an indirect response to prolonged stratification. Prolonged stratification causes an increase in internal P-loading (Jensen and Andersen 1992; Søndergaard et al. 2003; Wilhelm and Adrian 2008; Wagner and Adrian 2009b), boosting the decomposition of organic matter and thus oxygen depletion at the water-sediment interface, which further exacerbates the P-release from the sediment (Søndergaard et al. 2003). In polymictic lakes, for example, climate warming extended the periods of stratification, and this lengthening of stratified periods led to more frequent and/or stronger internal nutrient pulses between stratified and mixed periods which again promoted cyanobacteria proliferation during summer (Wilhelm and Adrian 2008; Wagner and Adrian 2009b). In dimictic lakes, on the other hand, longer periods of summer stratification may cause longer periods of nutrient limitation in the epilimnion along with higher water temperature and stronger nutrient pulses during the autumn overturn (Adrian et al. 1995; Huisman et al. 2004; Mooij et al. 2005; Elliott et al. 2006; Jöhnk et al. 2008). Immediate access to the hypolimnetic nutrient pools will be limited to migrating species such as buoyant cyanobacteria species, which are often capable of N-fixation (Reynolds 1984; Paerl 1988). Thus, in addition to causing an increase in algal biomass (particularly for cyanobacteria), climate warming may also lead to a change in ecosystem functionality such as a predominance of species capable of N-fixation (Wagner and Adrian 2009b; Huber et al. 2012).

10.4.1.4 Microbial Loop

How the microbial community and microbial processes are affected by global warming has only been studied in a few large-scale experiments. In mesocosm studies in Denmark the abundance of picoalgae, bacteria and heterotrophic nanoflagellates showed no direct response to experimental warming (Christoffersen et al. 2006). However, experimental warming modified the effects of nutrient addition (Christoffersen et al. 2006; Özen et al. 2013), indicating that interactive effects may be significant in the future given the expected increase in nutrient loading to shallow lakes worldwide (Jeppesen et al. 2009, 2010b; Moss et al. 2011). Increased DOM levels will alter the balance between phytoplankton and heterotrophic bacteria, and thus shift systems (further) towards net heterotrophy (see also Sect. 10.4.4).

10.4.1.5 Macrophytes

Owing to the climate-induced increase in eutrophication there is an increased likelihood of losing submerged macrophytes and thereby shifting shallow lakes from benthic- to pelagic-dominated systems with a consequent reduction in biodiversity. Indications of such developments are based on long-term data of Danish (Jeppesen et al. 2003) and Dutch shallow lakes (van Donk et al. 2003) as well as modelling studies (Mooij et al. 2007, 2009). Moreover, a dominance of filamentous green algae rather than phytoplankton seems possible under elevated temperatures (Trochine et al. 2011). Space-for-time approaches indicate that macrophyte cover will decrease in lakes with fewer days of ice cover, unless nutrient levels also decline (Kosten et al. 2009). Netten et al. (2011) predicted that milder winters may cause submerged macrophytes with an evergreen overwintering strategy as well as free-floating macrophytes, to outcompete submerged macrophytes that die back in winter. Neophytes such as the free-floating species *Salvinia natans* and the submerged species *Vallisneria spiralis* have been shown to be successful under elevated temperatures at the expense of native submerged macrophytes (Netten et al. 2010; Hussner et al. 2014). Mormul et al. (2012) tested the effects of elevated temperature (3 °C) on native and non-native aquatic plant production in mesocosms in combination with ‘browning’ (increased DOC), a potentially important change in the northern hemisphere and found browning to be more important for species invasion than warming. Climate change is likely to have a direct effect if non-native species respond positively to climate change and an indirect effect through species interactions, for example, because browning impairs the growth of native macrophytes and reduces biotic resistance to invasion.

Native competitors of the invasive *Elodea canadensis* were less successful in browner waters indicating a reduced resistance to invasion. Warming of mesocosms in the UK by 3 °C also significantly altered the proportions of three macrophyte species due to a higher growth rate and higher relative abundance of the neophyte *Lagarosiphon major* (McKee et al. 2002). A subsequent trial with temperatures 4 °C higher and higher nutrient concentrations resulted in a dominance of floating duckweed *Lemna* spp. which severely reduced oxygen availability and resulted in a fish kill (Moss 2010). In general, however, there are few long-term studies on the effect of climate change on macrophyte species distribution and invasions, coverage and subsequent effects on other trophic levels in aquatic ecosystems.

For large areas of northern Europe, mass occurrences (‘nuisance growth’) of the macrophyte *Juncus bulbosus* have been recorded (Moe et al. 2013). The reasons for this phenomenon are still unclear, but nuisance growth has been linked with hydrology, carbon dioxide and elevated N-deposition (Moe et al. 2013).

10.4.2 Phenology

The most prominent examples of climate-induced changes in lakes are changes in phenology. Coherent changes in ice phenology (see Sect. 10.2.2), and changes in spring and early summer plankton phenology in the North Sea region in recent years have been attributed to climate change (Adrian et al. 1999; Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Straile 2002) as synchronised by large-scale climatic signals such as the NAO (for a review see Blenckner et al. 2007; Gerten and Adrian 2002a; Straile et al. 2003). While indirect temperature effects such as early ice-off, which improves underwater light conditions have brought forward the start of algal bloom development in spring, direct temperature effects caused changes in the timing of rotifer and daphnid spring maxima (Gerten and Adrian 2000; Adrian et al. 2006; Straile et al. 2012) cascading into an earlier clear water phase (Straile 2002). For zooplankton, phenological shifts were most immediate for fast-growing species such as cladocerans and rotifers (but see Seebens et al. 2007), whereas longer-lived plankton such as copepods showed a lag in response. Copepods responded to altered day-length-specific water temperature affecting the timing of the emergence of resting stages in spring (Gerten and Adrian 2002b; Adrian et al. 2006). In addition, warming-induced accelerated ontogenetic development may enable the development of additional generations within a year as has been shown for copepod species (Gerten and Adrian 2002b; Schindler et al. 2005; Adrian et al. 2006; Winder et al. 2009).

10.4.3 Metabolism

Recent research suggests that global warming tends to shift the metabolic regime of entire lakes toward a dominance of respiration (Allen et al. 2005). This fundamental difference in temperature response between autotrophic and heterotrophic processes may have major implications for biological communities and for ecosystems in general. However, different members of a food web react differently to temperature, for example while cell-division rates may increase with temperature, as may grazing rates and metabolic demands of zooplankton. Thus, the net effect of warming on metabolism is not straightforward also because metabolic rates differ at the species level. As a result, how a changing climate interacts with increased nutrient supply to alter ecosystem metabolism is more uncertain than the change in trophic structure. Although evidence suggests that processes such as deoxygenation, decomposition and denitrification are influenced both by nutrients and by warming, interactions are complex and variable and there are discrepancies in study results about the end result for system components as well as for systems as a whole.

Mesocosm studies in the UK indicated that gross primary production and respiration increase with warming, while results for net production and carbon storage differ. Two experiments (Moss 2010; Yvon-Durocher et al. 2010) showed a marked increase (18–35 %) in the ratio of diurnal community respiration rates and gross photosynthesis for a warming of up to 4 °C. If extrapolated to the large number of shallow northern lakes, this could have immense implications for positive feedbacks in the Earth's future carbon cycle (Moss 2010). However, these UK experiments were all of short duration (less than one year) and may only have described the transient state after warming, which may lead to overestimation of the net release of carbon. Long-term mesocosm experiments will provide more reliable indications about the net effect of warming on ecosystem metabolism (Jeppesen et al. 2010a; Liboriussen et al. 2011), complemented by long-term research and modelling of whole lake ecosystems (Trolle et al. 2012).

10.4.4 Greenhouse Gases and Heterotrophy

Ecosystems not only respond as recipients of climatic change, but also provide feedbacks, not least via greenhouse gases such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O). As previously mentioned, the input of organic carbon to lakes through run-off from the catchment has increased in the North Sea region, inducing changes in water colour (Hongve et al. 2004; Erlandsson et al. 2008) (see also Sect. 10.3). Recovery of soils from acidification and changed hydrological conditions are believed to be important factors determining this development (Monteith et al. 2007). On a somewhat longer perspective, climate effects on hydrology and vegetation density may also promote a substantial browning of boreal surface waters (Larsen et al. 2011a, b).

Autotrophs and heterotrophic bacteria compete for the same essential elements, but utilise different energy sources. While DOC is a major energy source for heterotrophic bacteria, it is also an important absorbent in the photosynthetically active part of the spectrum. DOC thus has negative impacts on primary producers both by competing for photons and by stimulating their major nutrient competitors. Increased levels of terrestrially-derived DOC in concert with reduced availability of inorganic phosphorus in lakes may shift systems further towards net heterotrophy and thus a net CO_2 release (Sobek et al. 2003; Larsen et al. 2011c).

Increased loads of DOM in boreal lakes would also promote anoxia in the deeper water layers, which promotes

CH_4 production and its net flux to the atmosphere (Juutinen et al. 2009). Increased N-deposition in concert with elevated export of DOM may promote export of N_2O (Hong et al. 2015). For lakes in agricultural systems, increased productivity due to increased nutrient inputs from the catchment may promote the net efflux of CH_4 and N_2O (Juutinen et al. 2009; Hong et al. 2015), while the net impact of the CO_2-balance will also depend on lake morphometry and stratification and so is harder to predict.

10.5 Biodiversity

Climate conditions are as important for freshwater biodiversity as for terrestrial and marine biodiversity, and consistently explain a major proportion of the geographic variation in species richness of different freshwater taxa such as amphibians, fish, mammals, crayfish and waterbirds (Tisseuil et al. 2013). Even so, other geographic patterns such as the latitudinal gradient in biodiversity is not as strong in freshwater as it is in the marine or terrestrial realms (Hillebrand 2004). However, these geographic trends (often measured at global to regional scales) cannot easily be transferred into predictions on temporal shifts in biodiversity at regional to local scales under climate change. Freshwater systems are particularly vulnerable to climate change for several reasons: owing to the isolated nature of freshwater habitats embedded in a terrestrial matrix; because climate change has direct influences on local temperatures and temperature-associated factors (such as oxygen saturation); and because many freshwater systems already absorb other anthropogenic stressors such as nutrient loading or an altered hydrological regime (Woodward et al. 2010). This section addresses these issues by reviewing existing information on biodiversity shifts in the North Sea region (Sect. 10.5.1) and deriving more general predictions from theoretical and experimental literature identifying research needs in the North Sea region (Sect. 10.5.2).

10.5.1 Shifts in Biodiversity

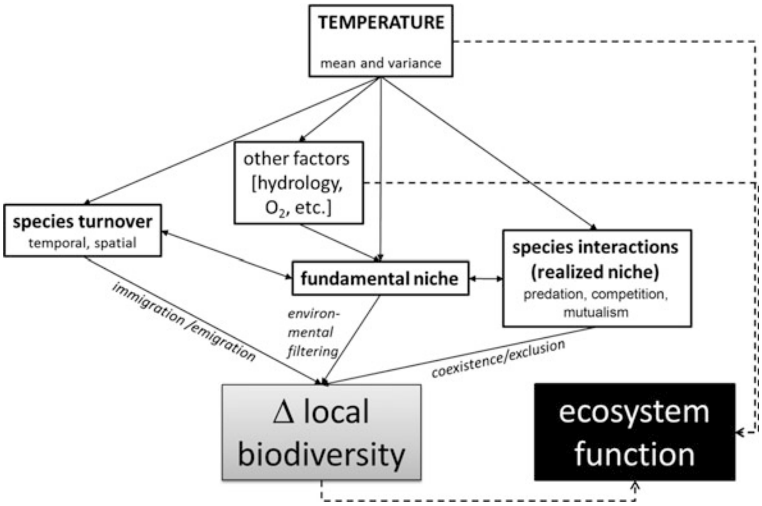
Predicting shifts in freshwater biodiversity in the North Sea region is difficult, because few studies have been explicitly conducted in lentic or lotic water bodies in this region. Predictions concerning future biodiversity are often derived from bioclimatic envelope models, which project future range shifts based on the current distribution of species (Parmesan and Yohe 2003). These models typically predict a northward (and often eastward) shift in ranges, such that warm-adapted species expand their ranges, and the ranges of cold-adapted species narrow.

Although changes in marine biodiversity in the North Sea region have frequently been predicted using this approach (Beaugrand et al. 2002), studies for freshwater systems in this region are rare. The species richness of macroinvertebrates across running waters in Europe has been predicted to decline in the southern North Sea countries (UK, Germany, Netherlands, Denmark), but to increase in the North (Norway) (Domisch et al. 2013). Changes in distribution and diversity have already been observed in some freshwater groups, such as odonates in the UK (Hickling et al. 2005). Other diversity shifts caused by local, climate-related range retractions have been reported for fishes in Iceland (Jeppesen et al. 2010b) and crustaceans in Norway (Lindholm et al. 2012). Correspondingly, analyses of long-term monitoring data on community composition revealed shifts in macroinvertebrate assemblages associated with ambient temperatures in Greenland, Iceland, Norway, Denmark and Sweden (Burgmer et al. 2007; Friberg et al. 2013). However, few long-term monitoring data sets still exist for freshwater systems within the North Sea region.

Thus it seems clear that specialised communities in colder regions around the North Sea have a high potential for reduced biodiversity. Macroinvertebrates in glacier-fed river systems will be characterised by lower local species richness and lower beta-diversity if warming leads to glacier retreat (Jacobsen et al. 2012). In boreal regions of northern Europe, the riparian zones of running waters are predicted to be affected by additive or interactive combinations of higher temperature, increased annual discharge but less seasonal variation in runoff, changes in groundwater supply, and altered ice regimes (Nilsson et al. 2013). Potential consequences for biodiversity can be negative or positive. Negative consequences are likely if the riparian zone narrows, such as by hydrologic changes, and thus species richness locally declines. In contrast, higher temperatures might allow invasion of exotic species leading to higher local species richness. Other types of change include altered disturbance regimes (e.g. altered freezing and thawing regimes during winter), which could foster a more dynamic and species-rich riparian vegetation, but also a more specific and species-poor assemblage of stress-tolerant species.

Floodplain systems around the North Sea coast have been massively altered by human regulation of flow regimes and inundation (Tockner et al. 2010). At the same time, they harbour a diverse fauna and flora shaped by the interaction of different climatic, hydrological and biological drivers as well as by the interaction between aquatic and terrestrial ecosystems with respect to the exchange of water, nutrients and organisms. Climate-induced shifts in flow regime are thus of primary importance for biodiversity. European-scale modelling scenarios predict that North Sea region floodplains will experience moderately higher flow levels

Fig. 10.6 Schematic representation of pathways leading to altered local biodiversity and thus ecosystem function. Main pathways include changes in species pools (species turnover) and on the fundamental as well as realised niches of species



(contrasting with predictions for other regions, such as the Mediterranean floodplains) (Schneider et al. 2013). Consequences for biodiversity remain largely unknown.

Climate-driven changes in biodiversity are very likely to interact with changes associated with other anthropogenic pressures, such as eutrophication (Moss et al. 2009). Some synergistic effects have been found in UK mesocosm studies (Feuchtmayr et al. 2009). For example, warming promoted increased phosphorus concentrations and the frequency of severe benthic anoxia in the mesocosms, with the potential to exacerbate existing eutrophication problems (McKee et al. 2003).

10.5.2 Predictions, Theory and Experimental Studies

Although functional aspects of ecosystem impacts (biomass, productivity, element cycling) under climate change can be predicted with some accuracy (see previous sections), information on shifts in freshwater biodiversity in the North Sea region remains vague (Moss et al. 2009). This is due not only to the scarcity of studies themselves, but also to the focus on larger spatial scales (i.e. regional climate-envelope models on range shifts), which makes predictions for local ecosystems difficult. Information from ecological theory and experiments can help to fill this gap by identifying potential changes in freshwater biodiversity and associated pathways (Fig. 10.6). Local attributes may also be superimposed on large-scale patterns. In an analysis of global lake zooplankton data, Shurin et al. (2010) found increased biodiversity in lakes showing greater temperature variation on different time scales (intra- and interannual). A recent review argued strongly for including temperature variability in climate-change experiments (Thompson et al. 2013).

The survival of a species can be directly impaired if temperatures are shifted beyond the fundamental thermal niche, leading to local extinction (Fig. 10.6). Temperature also affects the fundamental niche of a species with respect to other conditions, which are often directly related to temperature (e.g. oxygen saturation, hydrological regimes, solute concentrations). Indirect consequences of temperature change can be seen in freshwaters from around the North Sea, for example with respect to stratification regimes (Wagner and Adrian 2011) or oxygenation (Wilhelm and Adrian 2008). These changes alter the environmental filtering of colonising species, such that local diversity can increase or decrease depending on the number of species that are precluded or enabled to establish viable populations.

The meta-community context (Leibold et al. 2004) reflects the interplay of dispersal and local processes and will become an important tool to predict future changes in aquatic biodiversity. This is even more likely given that much of the regional biodiversity in aquatic systems is contributed by ponds and shallow lakes as these have high beta-diversity due to their often isolated nature (Scheffer et al. 2006) and provide important ecosystem services such as carbon storage due to their high number (Giller et al. 2004; Downing et al. 2006; Tranvik et al. 2009).

At the same time, there is high potential for small isolated systems to lose species with global climate change (Burgmer and Hillebrand 2011) and spatial dynamics are important for maintaining biodiversity in these systems. Meta-community dynamics can also provide spatial insurance for freshwater ecosystems (Loreau et al. 2003). In a meta-community mesocosm study, colonisation from a regional species pool and higher biodiversity positively affected the recovery of the pond ecosystems from heat stress (Thompson and Shurin 2012).

Changes in species turnover with time reflect changes in biodiversity dynamics, i.e. local immigration and extinction.

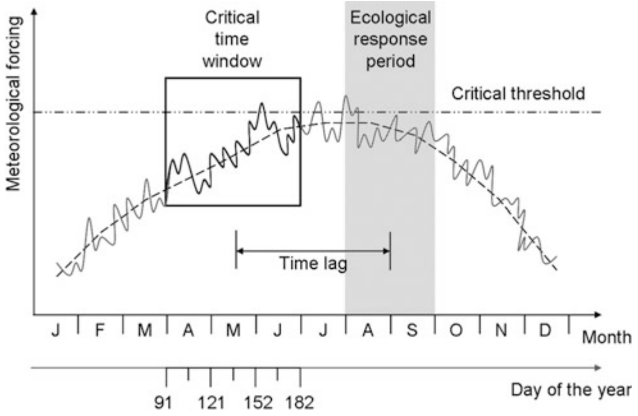


Fig. 10.7 Timing of ecosystem responses to meteorological forcing. Ecological responses are often triggered by changes in critical time windows. The triggering mechanism frequently involves the crossing of critical thresholds in forcing variables (*dashed-dotted line*), and responses tend to occur with a time lag. In this conceptual sketch, analysis at the monthly timescale (*dashed line*) would not be sufficient to detect threshold exceedance, in contrast to analysis at the daily timescale (*solid line*) (Adrian et al. 2012)

Most experiments suggest a more rapid turnover of species at higher temperatures reflecting an acceleration of colonisation–extinction dynamics. In the thermal effluent of a nuclear power plant, higher temperatures resulted in a faster turnover of species composition but without affecting species richness (Hillebrand et al. 2010). Laboratory experiments also indicated faster change in species composition with increasing temperature (Hillebrand et al. 2012). Analysing temporal turnover in community composition could thus be a better means of identifying climate-induced changes in biodiversity than simple univariate measures of biodiversity such as richness or evenness (Angeler and Johnson 2012). Especially because even major changes such as a shift in dominance between functional groups (e.g. from diatoms to cyanobacteria in phytoplankton) might occur without a change in species richness (Wagner and Adrian 2011).

Temperature also modifies species interactions and their consequences for biodiversity (Fig. 10.6). Increased temperatures are often associated with higher rates of consumption (Hillebrand et al. 2009), which can lead to either lower biodiversity (higher mortality) or higher biodiversity (more consumer-mediated coexistence). Competitive interactions are also strengthened by higher temperatures, leading to more rapid exclusion of inferior species—an effect which was shown to depend on consumer presence (Burgmer and Hillebrand 2011). Not only can the strength of interactions be altered by temperature, but also the temporal match of the interacting species through changes in phenology (Berger et al. 2010). Information on temperature-dependent changes in mutualistic interactions in freshwaters is currently missing.

Both experiments and models indicate that warming-induced shifts in biodiversity have functional consequences for ecosystems (Fig. 10.6), among others with respect to primary production, resource use efficiency and temporal stability of ecosystem functions (Hillebrand et al. 2012; Schabhuettl et al. 2013). In a long-term freshwater phytoplankton experiment, temperature-induced reductions in species richness were associated with lower biomass production, and higher extinction rates were associated with higher variability in biomass production (Burgmer and Hillebrand 2011). Similar strong relationships between diversity and resource use efficiency are found in freshwater field data from the UK and Scandinavia (Ptacnik et al. 2008).

10.6 Importance of Temporal Scale

Responses to climate change in lake ecosystems operate on various temporal scales. Physical forces such as variation in temperature and mixing regimes span sub-daily to monthly time scales. Organisms differ in their generation time from daily to yearly time scales (Adrian et al. 2009). Thus, to understand the impacts of single climatic forcing events in the context of longer term dynamics it is necessary to consider not only sufficiently long periods (several decades) but also to consider appropriate small temporal scales within the yearly cycle. For example, ecological variables may respond to meteorological forcing only during short critical time windows, or to short-lived exceedance of ecologically-relevant critical thresholds. Thus, annual, seasonal or monthly climate data may not be enough to capture the thermal dynamics to which organisms actually respond (Fig. 10.7; Adrian et al. 2012).

Members of the grassroots organisation GLEON (Global Lake Observatory Network; www.gleon.org) or the European project NETLAKE (Networking Lake Observatories in Europe; www.cost.eu/domains_ctions/essem/Actions/ES1201) established an international network of automatic stations in lakes to address dynamics of ecosystem properties at sub-hourly scales.

The following sections focus on the role of temporal scale in climate impact research and provide examples of responses at small (sub-daily) to large (decadal) temporal scales, the role of critical time windows, and the significance of exceeding critical thresholds for lakes within the North Sea region (which also applies for lakes throughout the North Temperate Zone).

10.6.1 Critical Temporal Scales

The importance of addressing critical temporal scales in climate impact research has been documented for various lakes in the North Sea region (see Adrian et al. 2012; Sect. 10.2). A closer look at sub-hourly measurements showed that the rate of increase in the daily minima (night-time water temperature) exceeded that of the daily maxima (daytime water temperature) (Wilhelm et al. 2006). The consequences of this day-night asymmetry for the biota are unclear, but may contribute to some of the unexplained changes observed in ecosystem dynamics over time. Day-to-day variation in respiration seems to be common in lakes worldwide, including those in the North Sea region (Solomon et al. 2013). Daily variation in gross primary production explained 5–85 % of the daily variation in respiration. Solomon et al. (2013) found respiration to be closely coupled to gross primary production at a diurnal-scale in oligotrophic and dystrophic lakes, but more weakly coupled in mesotrophic and eutrophic lakes.

Known changes in the thermal regime of lakes in the North Sea region (Sect. 10.2) operate over a broad range of temporal scales, and are closely related to lake morphometry: on sub-daily (Wilhelm and Adrian 2008) to weekly scales in polymictic lakes (Wagner and Adrian 2009b), and on weekly to monthly scales in monomictic or dimictic lakes (Gerten and Adrian 2000; Livingstone 2003). While variation in the timing of spring overturn affects underwater light conditions and thus the start of algal growth (Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Peeters et al. 2007), variation in the timing of summer stratification affects water temperature and internal nutrient loading and subsequent plankton development and species composition in productive lakes (Wilhelm and Adrian 2008; Wagner and Adrian 2011). Differences in water temperature between mixed and stratified periods can be up to 5 °C within days or a just few weeks in summer, favouring thermophilic copepod species for example (Wagner and Adrian 2011).

Changes in phenology in abiotic and biotic variables (see Sect. 10.4.2) operate on time scales of weeks (Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Straile et al. 2003). Thus, in terms of their duration, seasons should be defined by cardinal events within the lake itself, rather than by fixed calendar dates. Important markers successfully used to define phenology-adjusted seasons in lakes include temperature thresholds, ice-off dates, the timing of the clear-water phase, and periods of stable thermal stratification (Rolinski et al. 2007; Wagner and Adrian 2009a; Huber et al. 2010).

Wagner et al. (2012) proposed a seasonal classification scheme tuned to specific hydrographic-sensitive phases for dimictic lakes across a latitudinal gradient: inverse stratification (winter), spring overturn, early stratification and the summer stagnation period. They estimated a mean latitudinal shift of 2.2 days per degree of latitude for the start of these sensitive phases. After accounting for latitudinal time shifts, mean water temperatures during the defined hydrographic cycles were similar in lakes spanning the gradient between 47° and 54°N. Adjusting seasons in this way thus enhances the probability of identifying the major driving forces in climate impacts on lake ecosystems.

10.6.2 Critical Time Windows

Responses to warming trends are often expressed in terms of average changes in temperature on seasonal or annual scales, however species exhibiting short generation times such as planktonic organisms respond only during specific time windows within a season. Shatwell et al. (2008) showed how short time windows can open for cyanobacteria in warm springs in an otherwise diatom-dominated season. They argued that if cyanobacteria attain a critical biomass during that critical time window they can dominate the phytoplankton during summer. In terms of zooplankton, the abundance of cyclopoid (Gerten and Adrian 2002b; Seebens et al. 2009) and calanoid copepods (Seebens et al. 2007) in summer and autumn are determined by conditions in spring—probably related to temperature-induced changes in the emergence of resting stages (Adrian et al. 2006) or short time windows of high food availability which increases offspring survival (Seebens et al. 2009).

Temperature-driven changes in the timing of food availability and of predation by young-of-the-year fish during critical time windows in spring/early summer determined the mid-summer decline in daphnids (Benndorf et al. 2001). More specifically, water temperatures in narrow time windows either before (2.2 weeks) or after the typical clear-water phase (3.2 weeks) affected the start-up populations of summer crustacean zooplankton and explained some of their contrasting success during three hot summers characterised by more or less the same average summer water temperature (Huber et al. 2010).

10.6.3 Critical Thresholds

Threshold-driven responses to environmental forces have gained attention in ecology because of their seeming unpredictability and their potentially large effects at all levels of ecosystems. The crossing of critical thresholds may result in abrupt changes in particular elements of an ecosystem (Andersen et al. 2009; Scharfenberger et al. 2013) or entire ecosystems—the famous example being the alternative stable states of clear versus turbid lakes (Scheffer and

Carpenter 2003). Abrupt changes within ecosystems are already known under warming trends experienced in the recent past for a number of variables spanning abiotic and biotic components, such as nutrients or algal blooms (Wagner and Adrian 2009a; for review see Adrian et al. 2009, 2012). The underlying forces are often unclear, but may involve competition for common resources and the crossing of critical thresholds in the abundance of conspecifics (Scharfenberger et al. 2013) or multiple overlapping environmental forces (Huber et al. 2008).

Critical thresholds are known to have been exceeded within lake ecosystems (Hargeby et al. 2004). For example, Peeters et al. (2007) quantified the exceedance of critical thresholds in spring for several meteorological variables to determine early or late onset of phytoplankton growth in Lake Constance (Germany). In a recent model, Straile et al. (2012) used water temperature phenology as a predictor for *Daphnia* seasonal dynamics in North Temperate lakes. The day of the year when surface water temperatures reached a threshold of 13 °C explained 49 % of the variability of the timing of the spring *Daphnia* maximum in two German lakes (Lake Constance, Müggelsee) and in Lake Washington (USA). The *Daphnia* phenology model also performed well for predicting the timing of the *Daphnia* maxima in 49 lakes within the northern hemisphere—many located in the North Sea region (Straile et al. 2012). Early spawning of zebra mussel *Dreissena polymorpha* in Müggelsee was related to early attainment of the same critical water temperature threshold of 13 °C, known to initiate the first spawning event of the year (Wilhelm and Adrian 2007).

Exceeding direct and indirect temperature thresholds (length of thermal stratification) has been shown to trigger processes such as the onset and magnitude of cyanobacteria blooms (Wagner and Adrian 2009a; Huber et al. 2012). Stratification periods of more than three weeks caused a switch from a dominance of non-N-fixing cyanobacteria to a dominance of N-fixing cyanobacteria species, thus affecting not only biomass of cyanobacteria but also ecosystem functioning (Wagner and Adrian 2009a). In addition to warming-related changes in species composition (Adrian et al. 2009), habitat shifts northward toward temperate-zone lakes over the last few decades have been observed for *Cylindrospermopsis raciborskii*, an invasive freshwater cyanobacterium, originating in the tropics (Padisak 1997). Observations of *Cylindrospermopsis raciborskii* in pelagic populations were found to be temperature-mediated. Filaments emerged in the pelagic habitat when water temperature rose above 15–17 °C in two north German lakes (Wiedner et al. 2007).

10.6.4 Extreme Events

Extreme events, which are expected to become more frequent in the future, are often ecologically more relevant than fluctuations in mean climate. For lakes, extreme events principally refer to exceptionally mild winters, summer heat waves, or extreme storms or heavy rainfall events. For example, an extreme event for a lake that typically freezes in winter would be if the lake did not freeze at all. Based on regional climate model forecasts, Livingstone and Adrian (2009) predicted that the percentage of ice-free winters for a lake in northern Germany would increase from about 2 % at present to over 60 % by the end of the century; see Sect. 10.2.2 for more detail on the frequency of extremely late freeze-up, early break-up and short ice duration. These extremes affect thermal stratification patterns and underwater light conditions, with implications for oxygen conditions and phytoplankton development (see Sect. 10.4.2).

Central Europe has recently experienced extreme heat waves, most notably that of summer 2003. Mean air temperature in summer that year exceeded the long-term average by around 3 °C over much of Europe (Schär et al. 2004). Although heat waves are likely to promote cyanobacteria blooms (Jöhnk et al. 2008), water temperatures above average to the same extent in Müggelsee (Germany) in two recent summers (2003 and 2006) resulted in very different situations: a cyanobacteria bloom in 2006 but a record low cyanobacteria biomass in 2003. This difference was due to the thermal stratification pattern being critically intense only in 2006 (Huber et al. 2012).

Summer fish kills and a change in fish community structure have been attributed to summer temperature extremes in combination with eutrophication in shallow Lake Peipsi (Estonia/Russia) related to a decline in near-bottom oxygen conditions and a decrease in water transparency (Kangur et al. 2013). An extreme rainy period in 2000 caused a strong increase in chemical loading, particularly for organic carbon, in Lake Mälaren (the third largest lake in Sweden) followed by an increase in water colour by a factor of 3.4 and a doubling of spring cryptophyte biomass. This increase in algal mass required changes in the treatment of raw water from Lake Mälaren for the drinking water supply of Stockholm city (Weyhenmeyer et al. 2004b). Extreme summer rain events have also altered CO_2 and CH_4 fluxes in southern Finish lakes, with the systems switching from being a net sink to a net source of CO_2 to the atmosphere (Ojala et al. 2011).

Episodic events of extreme wind speed or rain events exceeding two standard deviations of the seasonal means

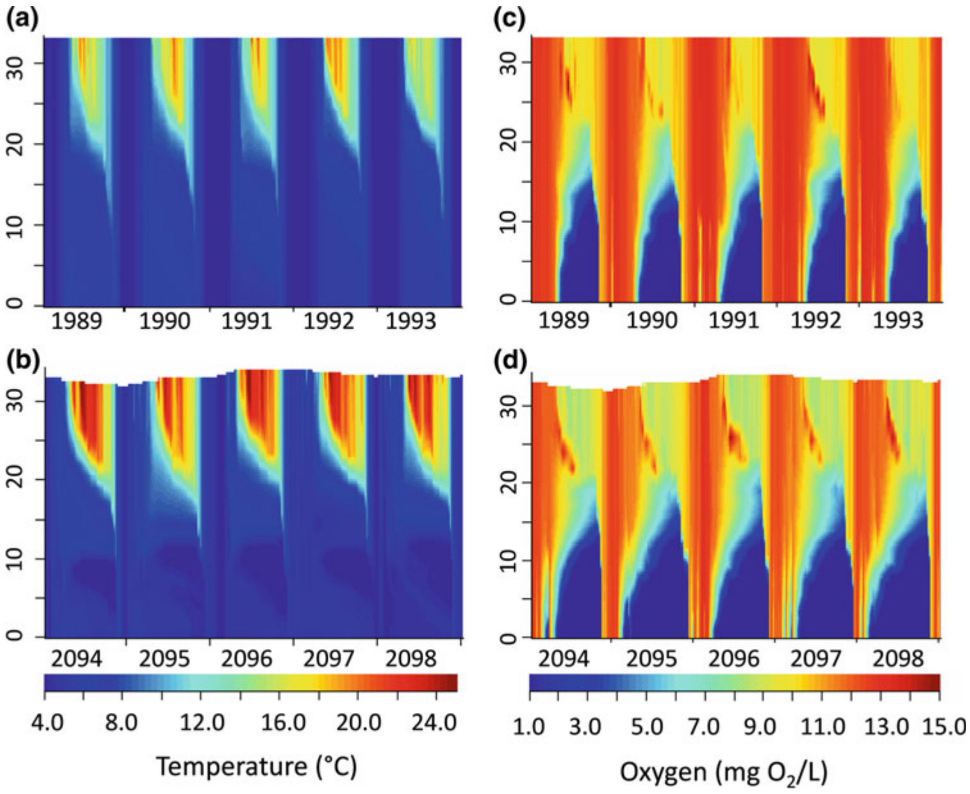


Fig. 10.8 Simulated water temperature for the deep Lake Ravn, Denmark, for current climate (represented by 1989–1993) (**a**) and future climate (represented by 2094–2098) (**b**), and simulated oxygen concentration for current climate (**c**) and future climate (**d**). Simulations were performed using DYRESM-CAEDYM. Future climate forcing was derived by the Danish Meteorological Institute using the regional HIRHAM model and the SRES A2 scenario for Denmark. Y-axis represent water level (m) (D. Trolle, original)

have strong but complex impacts on thermal structure and stability, DOC loading and underwater PAR (photosynthetically active radiation) levels in northern European lakes—the magnitude and direction of change depending on the location of the lake and catchment characteristics (Jennings et al. 2012). A comprehensive summary as to how extreme weather events affect freshwater ecosystems is provided by the British Ecological Society (BES 2013).

10.6.5 Regime Shifts

While ecosystems may be buffered against single short-lived critical threshold exceedance events, gradual changes over longer periods may cause lake ecosystems to switch abruptly from one state to another. The most likely and widespread climate warming-induced shift in lakes will be shifts in thermal regime (see Sect. 10.2). Climate change alters heat redistribution over time (within the annual cycle) and space (vertically within the water column), and eventually leads to transitions in the seasonal mixing regime of a lake much in the sense of scenarios described by regime shift theory (Scheffer and Carpenter 2003).

On the basis of existing climate scenarios, Kirillin (2010) predicted a shift from a dimictic to a monomictic regime in the majority of European dimictic lakes by the end of the 21st century, with the loss of ice cover in the cold season meaning that winter stratification in these lakes would completely disappear. In summer, climate warming has an opposite, stabilising effect that may eventually lead to the mixing regime shifting to a dimictic regime in hitherto polymictic lakes. The ecological consequences of this type of regime shift may be even more far-reaching than for di-/monomictic transitions, because the abrupt detachment of the nutrient-rich hypolimnion from the euphotic layer is likely to trigger stronger competition between autotrophic species resulting in changes in phytoplankton species composition and ecosystem functionality (Wilhelm and Adrian 2008; Wagner and Adrian 2009a, b, 2011).

10.7 Modelling

Predicting the fate of freshwater ecosystem processes under climate change is non-trivial, because many physical, chemical and biological processes interact, and may be affected on different spatial and temporal scales by climate forcing. In attempting to account for these complex interactions, mechanistic numerical models continue to play a greater role in hypothesis testing (system understanding) and for predicting the future state of ecosystems given the projections of future climatic forcing according to climate models (Trolle et al. 2012). Thus, the ability to link—and equally importantly to quantify—complex interactions between physical, chemical and biological processes makes models one of the most important tools of modern science, and for the past decade, models have been used extensively, aiming to establish the potential effects of future climate on freshwater ecosystems (Mooij et al. 2007; Trolle et al. 2011; Elliott 2012).

10.7.1 Linking Physical and Ecological Dynamics

A widely accepted effect of increased climate warming on lakes is increased stability of the water column, which is readily quantified by hydrodynamic models (see Fig. 10.8). Increased stability can cause prolonged periods of stratification, with subsequent effects on biogeochemical cycling, for example by increasing the duration of anoxia in bottom waters and thereby the potential for release of iron-bound phosphorus.

Climate warming is also expected to result in decreased duration and thickness of ice cover on lakes, and models such as MyLake have recently been applied to provide quantitative estimates of such decreases.

Models with a strong focus on food-web dynamics, such as PCLake (Janse 1997) have also been used to quantify the effects of warming in facilitating lake ecosystems to shift from a clear, macrophyte-dominated state to a turbid, phytoplankton-dominated state, under different combinations of warming scenarios and external nutrient load scenarios (Fig. 10.9). Modelling exercises of this type are readily undertaken using a standard desktop computer, in contrast to testing such scenarios in experimental mesocosm studies, for example, which is extremely time consuming and expensive.

One of the key messages from the model study by Mooij et al. (2007) shown in Fig. 10.9 was that the critical loading of phosphorus to a lake, at which a shift from a clear to a turbid state occurs, is likely to decrease as warming continues. This effectively means, that according to the model, external loading will need to be reduced in the future, if lakes are to retain the ecological quality of present day.

10.7.2 Predictions Versus Observations

Modelling studies of the long-term effects of climate change on northern hemisphere temperate lakes (e.g. Elliott et al. 2005; Mooij et al. 2007; Trolle et al. 2011) generally imply that overall phytoplankton biomass is likely to increase, and that cyanobacteria will become a more dominant feature of the phytoplankton species composition. This is in line with empirical observations from time series (Jöhnk et al. 2008; Wagner and Adrian 2009a, b; Posch et al. 2012) and with cross-system analyses (Jeppesen et al. 2009; Kosten et al. 2012). However, the effects may be even more severe than suggested by models, as current models do not fully account for structural changes in the lake ecosystems that could occur due to warming. As stated in Sect. 10.4.1 the composition of fish stocks could change towards smaller and faster reproducing fish, implying more predation on zooplankton and so less grazing on phytoplankton (Jeppesen et al. 2010a; Meerhoff et al. 2012). Such changes have yet to be included in dynamic models.

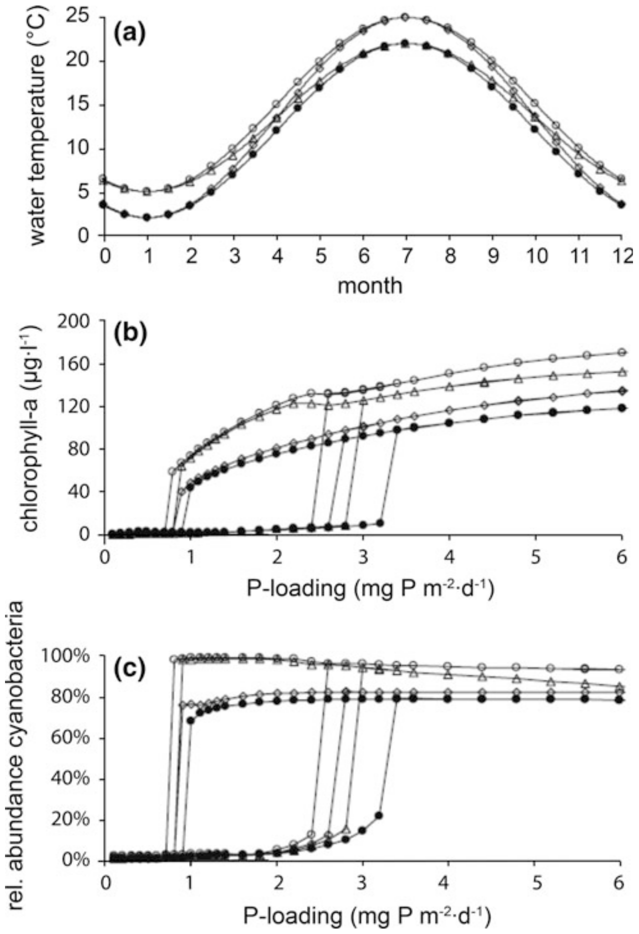


Fig. 10.9 Three scenarios with elevated temperatures (**a**) simulated using PCLake adapted for shallow Dutch lakes, and evaluated for average summer chlorophyll-a concentration (**b**) and the percentage of cyanobacteria relative to total phytoplankton biomass (**c**). The simulations include four scenarios: a control (*closed circles*), an all year round temperature increase of 3 °C (*open circles*), an increase in summer maximum temperature of 3 °C but no change in the winter minimum (*open diamonds*), and an increase in winter minimum temperature of 3 °C, but no change in the summer maximum (*open triangles*) (adapted from Mooij et al. 2007)

Table 10.1 Level of certainty for key climatic impacts on freshwater ecosystems

Parameter	Comment
High certainty	
Lake temperature	Several time series, strong modelling tools
Ice development	Several time series, strong modelling tools, satellite data
Phenology	Several time series, modelling tools for autotrophs
Water level, runoff, retention	Strong hydrological modelling tools
Thermal regime	Extension of stable stratification periods, good modelling tools
Oxygen depletion	Several time series, linked with hydrology and trophic state
Medium certainty	
DOC concentration	Long-term data, good modelling tools
Concentrations of key elements	Some data, closely linked with hydrology
Primary production	Contrasting effects of DOC and nutrient inputs. Local differences
Autotroph community composition	Prevalence of cyanobacteria. Local differences
Deterioration of trophic state	Warming acts like eutrophication; linked with hydrology and trophic state
Range expansion of invasive species	Northwards distribution of species
Loss of cold cold-stenothermic fish species	Several time series; results from fish harvest
Low certainty	
Secondary production	Hard to arrive at general conclusions. Taxon- and locality-specific differences
Heterotroph community composition	Taxon- and locality-specific differences. Secondary impacts of autotrophs
Diversity	Limited data availability, taxon- and locality-specific differences; changes in ecosystem function
Food-web responses	Accumulated uncertainty from all other responses
Greenhouse gases (carbon dioxide, methane, nitrous oxide)	Lakes as carbon sink or source, large-scale enclosure experiments
Water clarity	Progress expected with new satellite data

10.7.3 Linking Landscape Activities and Nutrient Losses

A recent trend is to assemble multidisciplinary modelling teams with expertise both in hydrological and ecological modelling. Coupling hydrological and ecological models (Norton et al. 2012; Nielsen et al. 2013) enables a direct and quantitative link between land use activities and surface water quality. For example, Norton et al. (2012) used a farm-scale nutrient budget model (PLANET; Planning Land Applications of Nutrients for Efficiency) combined with a generic nutrient runoff model (GWLF; Generalized Watershed Loading Function) to estimate nutrient losses to Loweswater, a small lake in northwest England. The simulated nutrient losses were subsequently used as input to an ecological model for the lake, PROTECH (Phytoplankton RespOnses To Environmental CHange). This model-chain has been used to forecast the abundance of different phytoplankton types within the lake in response to a range of catchment management measures. Ongoing research projects are currently expanding such model chains to include the effects of future climate on both hydrology and aquatic ecosystems.

10.8 Conclusion

Freshwater systems, and notably lakes, are well suited to trace climate-induced effects both directly via changes in ice cover, hydrology and temperature, but also indirectly via biotic communities since they represent closed bodies (aquatic islands in the landscape). Moreover, they also offer strong tools as ‘sentinels’ by integrating changes at the catchment scale that elsewhere would be hard to detect (Adrian et al. 2009). The North Sea region has a wide range of freshwaters that reflect changes related directly and indirectly to climate forcing. This includes a number of long-term monitoring sites, and experimental studies offer insights into climate change in freshwaters—and subsequent impacts on downstream coastal recipients. The major impacts on lakes, both those known to date and those predicted to occur, can be addressed with different levels of certainty (tentatively summarised in Table 10.1). The level of certainty falls substantially, once higher trophic levels and the complexity of trophic interactions are included. Nevertheless, this summary may be used to identify systems and parameters that are already well suited for addressing climate responses, those that need further attention, and those that are likely to need addressing at local scales and where general statements and predictions are hard to achieve.

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11 Environmental Impacts—Terrestrial Ecosystems

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Abstract

The chapter starts with a discussion of general patterns and processes in terrestrial ecosystems, including the impacts of climate change in relation to productivity, phenology, trophic matches and mismatches, range shifts and biodiversity. Climate impacts on specific ecosystem types—forests, grasslands, heathlands, and mires and peatlands—are then discussed in detail. The chapter concludes by discussing links between changes in inland ecosystems and the wider North Sea system. Future climate change is likely to increase net primary productivity in the North Sea region due to warmer conditions and longer growing seasons, at least if summer precipitation does not decrease as strongly as projected in some of the more extreme climate scenarios. The effects of total carbon storage in terrestrial ecosystems are highly uncertain, due to the inherent complexity of the processes involved. For moderate climate change, land use effects are often more important drivers of total ecosystem carbon accumulation than climate change. Across a wide range of organism groups, range expansions to higher latitudes and altitudes and changes in phenology have occurred in response to recent climate change. For the range expansions, some studies suggest substantial differences between organism groups. Habitat specialists with restricted ranges have generally responded very little or even shown range contractions. Many of already threatened species could be particularly vulnerable to climate change. Overall, effects of recent climate change on terrestrial ecosystems within the North Sea region are still limited.

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11.1 Introduction

The chapter starts with a discussion of general patterns and processes (Sect. 11.2), such as impacts of climate change on productivity, phenology and biodiversity. Climate impacts on specific ecosystem types, such as forests, grasslands and mires are discussed in more detail in subsequent sections (Sects. 11.3–11.6). The chapter concludes by discussing links between changes in inland ecosystems and the wider North Sea system (Sect. 11.7) and then summarises the main findings of this assessment in the form of a table (Sect. 11.8). The chapter focuses on the direct impacts of climate change; the potential impacts of indirect drivers are beyond the scope of this chapter.

11.2 General Patterns and Processes

11.2.1 Vegetation Zone Shifts, Productivity and Carbon Cycling

The terrestrial part of the North Sea region lies mainly in the temperate forest zone, with some boreal elements and treeless tundra at higher altitudes in Scandinavia and Scotland (Fig. 11.1). Below the tree line, significant areas of treeless vegetation would naturally occur only in wetlands (marshes, river floodplains and mires), where soil saturation precludes tree growth.

Deforestation and land degradation as a result of grazing and other anthropogenic activities have decreased the natural forest cover over thousands of years (e.g. Simmons 2003; Kaplan et al. 2009; Gaillard et al. 2010). Most of the lowland forests in England, for example, had already been cleared 1000 years ago (Ruddiman 2003). Forest cover over large parts of the UK, the Netherlands, north-western Germany and Denmark is currently less than 15 % (Eurostat 2015; Fig. 11.2).

The current distribution of zonal vegetation types in the North Sea region is influenced climatically mainly by temperature because terrestrial net primary productivity (NPP) is less limited by water supply, which is relatively high during the growing season because this is when most rainfall occurs (see Sect. 1.5). In terms of future changes in climate and weather (see Chap. 5), the warming expected by the end of the century can be expected to lead to a northward shift in zonal vegetation types or up in altitude (Hickler et al. 2012), and an increase in NPP where the warming is not accompanied by substantially drier conditions. Most climate change scenarios project an increase in annual precipitation across the North Sea region by the end of the century, although substantially drier conditions have been projected for summer and in particular for the southern part of the

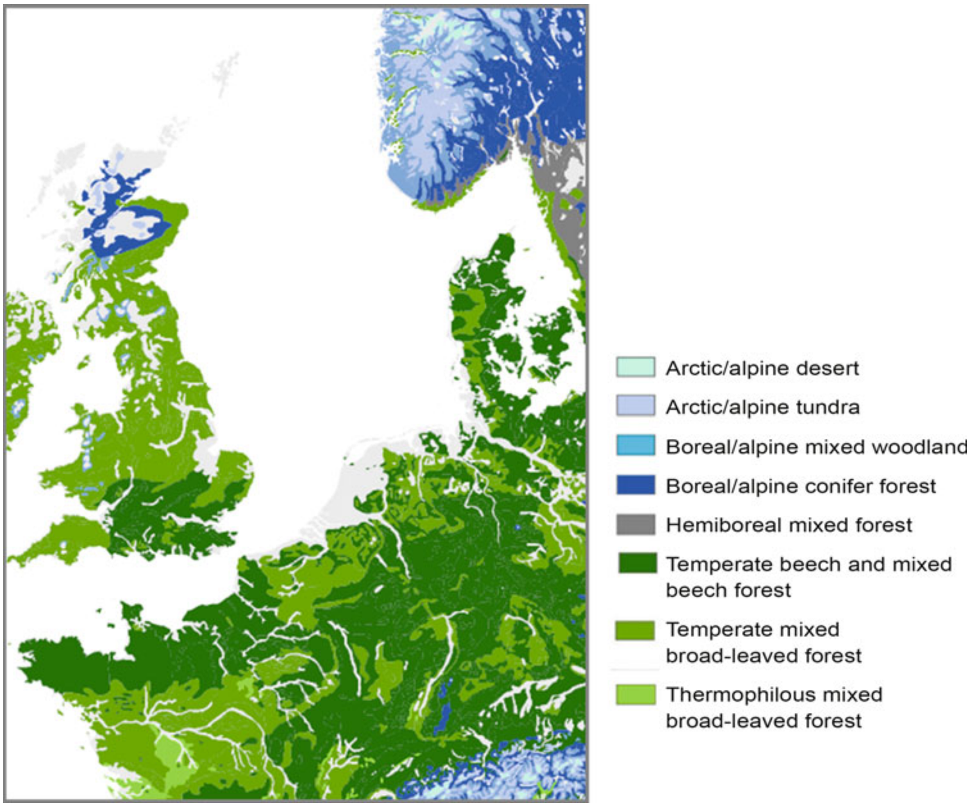

Fig. 11.1 Potential natural zonal (determined by macro-climate) vegetation types in the North Sea region. *Grey areas* were not classified (Bohn et al. 2003; simplified by Hickler et al. 2012)

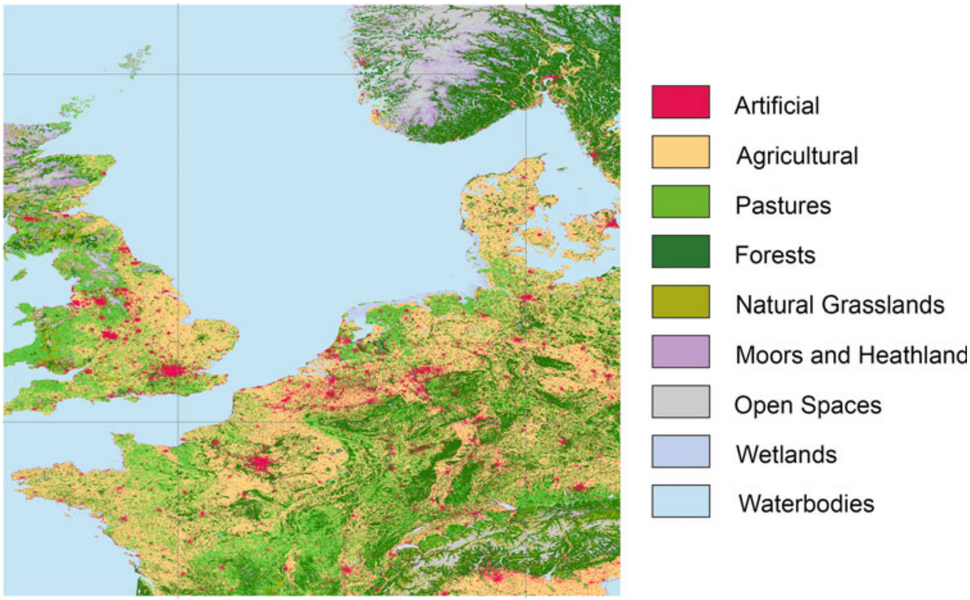

Fig. 11.2 Current land cover in the North Sea region according to CORINE Land Cover (EUROSTAT 2014)

region, where water availability already constrains vegetation productivity (see Chap. 5). Together with the slight projected increase in dry spell length (see Chap. 5 and Jacob et al. 2014), vegetation productivity might, therefore, decrease in the southern North Sea region. However, these projections are based on average results from a number of regional and global climate models (RCMs and GCMs) and because not all models agree in terms of the sign of the change in summer precipitation for different parts of the North Sea region, these projections of future water availability during the main growing season contain uncertainties (see Chap. 5 and Jacob et al. 2014). Furthermore, water availability also controls forest productivity strongly in the south-eastern UK (Broadmeadow et al. 2005), not strictly the southern part of the study region. Here too, increasing drought stress in summer would probably negatively impact NPP. Nevertheless, it should be noted that unchanged precipitation implies less water availability because evapotranspiration will increase with rising temperature. According to the multi-model mean of the CMIP5 models (see Chap. 5), the net outcome of changes in precipitation and evapotranspiration is projected to be an increase in annual run-off in the northern part of the region and a decrease in the south (Collins et al. 2013). These changes in the water balance are particularly important for wetlands (see Sect. 11.6).

The uncertainties in projections of future summer moisture (see Chap. 5) make it difficult to predict the impacts of climate change on terrestrial ecosystems. Morales et al. (2007) simulated the combined effects of climate change and increasing atmospheric carbon dioxide (CO_2) levels on European ecosystems with a dynamic vegetation model, using projections from a variety of combinations of RCMs, bounding GCMs and emission scenarios (Christensen et al. 2007, not accounting for changes in land use). With the exception of north-western France, all simulations indicated increasing NPP in the North Sea region by the end of the century. According to these simulations, the northern part of the study region remains a carbon sink, and the southern part continues to be a small source. However, different climate impact models can yield different results even when driven by the same climate scenario data. Using the SRES high A1Fi scenario (Nakićenović and Swart 2000), a number of dynamic global vegetation models (DGVMs) simulated increasing NPP over most of the North Sea region by the end of the century (Sitch et al. 2008), whereas the Lund-Potsdam-Jena (LPJ) DGVM showed decreased vegetation carbon storage especially in the southern part (Sitch et al. 2008). Most of the models in this study, as well as the model used by Morales et al. (2007), included the potential beneficial plant-physiological effects of increasing atmospheric CO_2 concentrations, but not the constraints on this effect through nutrient limitation.

Increasing levels of atmospheric CO_2 will increase NPP (sometimes referred to as the CO_2 fertilisation effect), and most plants reduce stomatal opening in response to higher CO_2 concentrations (e.g. Ainsworth and Long 2005; Hickler et al. 2015). Reduced stomatal opening leads to lower plant transpiration rates, commonly increasing soil water content and thereby counterbalancing potentially increasing drought stress under climate warming (Arp et al. 1998; Morgan et al. 2004; Körner et al. 2007). Increasing leaf area as a result of higher NPP can counteract this water saving effect (e.g. Gerten et al. 2004), but mostly under conditions of ambient nutrient supply, which enables plants to take advantage of increasing CO_2 and to increase their leaf area (Arp et al. 1998; McCarthy et al. 2006; Norby et al. 2010). According to future simulations with a GCM that includes dynamic vegetation changes, the net outcome of the two effects will be a substantial increase in global run-off (Betts et al. 2007). However, CO_2 enhancement experiments with conifer trees have shown hardly any reduction in stomatal conductance (Körner et al. 2007), implying that the vegetation models probably overestimate the reduction in stomatal conductance and transpiration in conifer forests (Leuzinger and Bader 2012). The magnitude of the CO_2 fertilisation effect on NPP and carbon storage is highly debated (e.g. Körner et al. 2007; Thornton et al. 2007). Although photosynthesis increases under elevated CO_2, this enhancement of carbon assimilation often does not lead to increased biomass as the extra carbon is mainly allocated to below-ground carbon pools with fast turnover (fine roots, root exudates, transfer to mycorrhiza) (Körner et al. 2005; Finzi et al. 2007; Norby et al. 2010; Walker et al. 2014). Nitrogen (N) deposition can also increase NPP, but in the southern North Sea region, N-deposition is already so high that nitrogen is not limiting terrestrial productivity directly (but may decrease productivity through negative side effects such as soil acidification; Bowman et al. 2008; Horswill et al. 2008). N-deposition across the study region is expected to remain at similar levels as today (2014) or to decrease slightly (Tørseth et al. 2012), but N-mineralisation in the soil will probably increase in the northern North Sea region due to warming (Lükewille and Wright 1997; Melillo et al. 2011), which would increase terrestrial productivity particularly in N-limited vegetation on acidic soils (see also Sects. 1.7 and 11.6).

Net primary productivity is an important driver of many ecosystem services, including total carbon storage, but in the North Sea region its dynamics are determined largely by land use, which has not been accounted for in the DGVM study mentioned previously (Sitch et al. 2008). Over most parts of Europe, including the North Sea region, forest carbon stocks, for example, are currently increasing as forests grow older and less timber is harvested than a few decades ago (Janssens et al. 2003; Nabuurs et al. 2003; Ciais et al. 2008).

Total ecosystem carbon storage is further influenced by soil carbon dynamics. Soil respiration, and thereby carbon losses from the soil, is expected to increase under global warming, but the sensitivity of the soil carbon pool remains uncertain (Davidson and Janssens 2006; Luyssaert et al. 2010), and combined effects of potentially increasing NPP (and carbon inputs into the soil) and increasing soil respiration rates (reducing carbon storage) on total ecosystem carbon storage are very difficult to estimate.

11.2.2 Changes in Phenology

Changes in the phenology of biota currently provide the most sensitive and compelling evidence of climate warming impacts in the North Sea region and elsewhere in the middle and higher latitudes. At the same time these changes are particularly well documented due to a pan-European network of phenological data collections that has been run continuously since the mid-20th century (e.g. Menzel 2000) as well as long-term data from bird-ringing stations (e.g. Sparks et al. 2005) and butterfly monitoring programmes (Roy and Sparks 2000). Phenological changes that can be attributed to climate change include leaf unfolding, flowering and leaf colouring as well as the arrival dates of migrant birds, dates of egg laying of birds or the timing of the first appearance of butterflies (Parmesan and Yohe 2003; Parmesan 2006).

An analysis of observational data from the International Phenological Gardens in Europe for the 1959–1996 period (Menzel and Fabian 1999; Menzel 2000) revealed that spring events such as leaf unfolding have advanced on average by 6.3 days (-0.21 days year^{-1}), whereas autumn events such as leaf colouring have been delayed on average by 4.5 days ($+0.15$ days year^{-1}). This trend has resulted in an average extension of the annual growing season by 10.8 days since the early 1960s. This trend is of particular significance for regions bordering the North Sea Basin such as Denmark and northern Germany. Similar results were obtained in a more regional study analysing data from the phenological network of the German Weather Service for the period 1951–1996. In this study, Menzel et al. (2001) found the strongest phenological advances in key indicators of earliest and early spring (-0.18 to -0.23 days year^{-1}) whereas changes in autumn were less pronounced (delay of $+0.03$ to $+0.10$ days year^{-1}). Overall, the mean growing season for the period 1974–1996 was up to 5 days longer than for the period 1951–1973. Similar findings were made by van Vliet et al. (2014) in the Netherlands. Using data from the Dutch phenological observation network they found that significant changes in life cycle events started only in the early 1990s. In a large-scale meta-analysis using data from 21 European countries for the period 1971–2000 (Fig. 11.3), Menzel et al. (2006) showed that 78 % of all bud break, flowering and fruiting records advanced, and only 3 % were delayed.

This study clearly demonstrated that phenology is directly linked to the temperature of preceding months with a mean advance of spring/summer by 2.5 days per °C and a mean delay of leaf colouring and leaf fall by 1.0 days per °C. So far, phenological changes of this type are reversible and depend on weather conditions in the year of observation.

In the UK, mean laying dates for the first clutches of 20 bird species advanced on average by 8.8 days between 1971 and 1992 (Crick et al. 1997). Similarly, spawning of two amphibian species (toads) in England advanced by two to three weeks between 1978 and 1994, and the arrival of three newt species in breeding pools advanced by as much as five

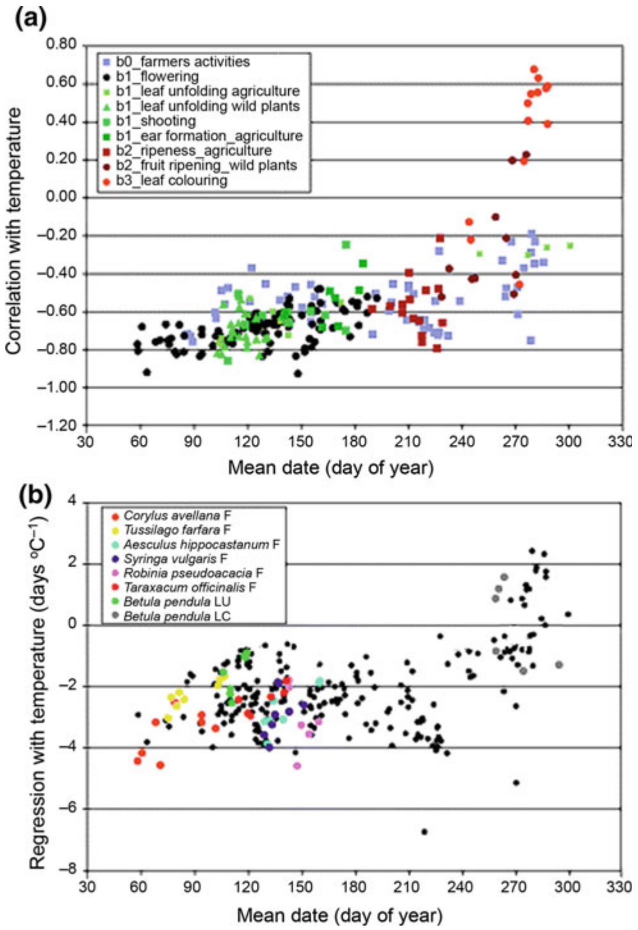

Fig. 11.3 Temperature sensitivity and response across the year. **a** Maximum correlation coefficients for 254 mean national time series of phenophases in nine European countries with mean temperatures of the previous months. **b** Regression coefficients against mean temperature of the previous month. *F* flowering; *LU* leaf unfolding; *LC* leaf colouring. The overall dependence of temperature sensitivity and response on mean date is high **a** $R^2 = 0.59$, $p < 0.001$; **b** $R^2 = 0.47$, $p < 0.001$) (Menzel et al. 2006)

to seven weeks (Beebee 1995). Based on a composite map of 70,000 records for 1998–2007 for the common frog *Rana temporaria*, Carroll et al. (2009) found an average advance of first spawning of about 10 days in the UK compared to map-based data 60 years before.

On the island of Heligoland in the south-eastern corner of the North Sea, mean spring passage times for 24 species of migratory birds advanced by 0.05–0.28 days year^{-1}, which in most species correlated strongly with warmer local temperature during the migration period as well as with the strength of the North Atlantic Oscillation (NAO; Hüppop and Hüppop 2003). Almost identical findings were made at a larger spatial scale from several ringing stations by Sparks et al. (2005). At the continental scale, Both et al. (2004) analysed 23 European populations of pied flycatcher *Ficedula hypoleuca* and found that nine showed an advanced laying date, which were all from those areas with the strongest warming trend and mostly situated at the southern fringe of the North Sea basin. In an area of southern England (Oxfordshire), Cotton (2003) demonstrated that earlier arrival of 20 species of long-distance migratory birds was positively correlated with enhanced air temperatures at wintering grounds in Sub-Saharan Africa.

Climate change also has significant impacts on the winter distribution of migratory birds that fly south to avoid the northern winter. Based on ringing data from the Netherlands, Visser et al. (2009) found that 12 of 24 species studied showed a significant reduction in their migration distance to the south, and that this was strongly correlated with the Dutch winter temperature in the year of recovery. For three common waterfowl species, Lehikoinen et al. (2013) demonstrated that shifts in wintering areas to the northeast correlated with an increase of 3.8 °C in early winter temperature in the north-eastern part of the wintering areas, where bird abundance increased exponentially, corresponding with decreases in abundance at the south-western margin of the wintering ranges. In line with these findings, Maclean et al. (2008) showed that the centres of wintering distribution for five species of wading birds along the north-western European coast flyway shifted 95 km north-eastwards within the period 1981–2000.

For the UK, Roy and Sparks (2000) showed that 26 of 35 species of butterfly exhibited an earlier appearance over the relatively short period 1976–1998 (statistically significant for 13 species). The authors estimated that a warming of 1 °C might advance first and peak appearances of most butterfly species by 2–10 days.

11.2.3 Matches and Mismatches Across Trophic Levels

Shifts in phenology as a response to climate change differ among species and populations. This has been shown for a range of taxonomic groups (Parmesan and Yohe 2003; Parmesan 2006). If climate responses differ between strongly-interacting species, such differences can have immediate impact on key ecological interactions, such as plant–pollinator, herbivore–plant, host–parasite/parasitoid and predator–prey (Visser and Both 2005; Thackeray et al. 2010). This may lead to a phenological mismatch of evolutionary-synchronised species but also to a phenological match of formerly asynchronised species resulting in so far avoided competition, parasitism or predation (Parmesan 2006).

For the Netherlands (Fig. 11.4), it was demonstrated that earlier bud break in sessile oak *Quercus petraea* due to climate warming leads to an earlier appearance of caterpillars, thus disrupting food supply during the main hatching period of the migratory pied flycatcher, which did not keep pace in its arrival at breeding grounds with the advance in peak food supply (Both and Visser 2001; Both et al. 2006). As a consequence of this mismatch in timing, pied flycatcher populations breeding in oak forest declined by 90 % between 1987 and 2003 (Both et al. 2006).

Such phenological mismatches may show effects across four trophic levels leading to deterioration in the timing of food demand and availability for passerines and their avian predators (Both et al. 2009). Biotic mismatches are also considered a major cause of the disproportionate decline in long-distance migratory bird species compared to short-distance migrants that are able to react more flexibly to phenological changes in their breeding areas (Møller et al. 2008; Both et al. 2010; Saino et al. 2011). Evidence for this phenomenon is, however, so far mostly correlative. The genetic basis of mechanisms of adaptation to phenological change is still poorly understood. Although the actual consequences of phenological changes on ecosystem functioning are not clear, several studies highlight the potential risk of desynchronising trophic linkages between primary and secondary consumers (Thackeray et al. 2010). This includes, for example, the distortion of entire food webs, in which top predators moving to cooler regions may trigger trophic cascades that lead to local extinctions and altered ecosystem processes (Montoya and Raffaelli 2010). To date, most of these assumptions are theoretical and more or less unsupported by experiments or empirical data.

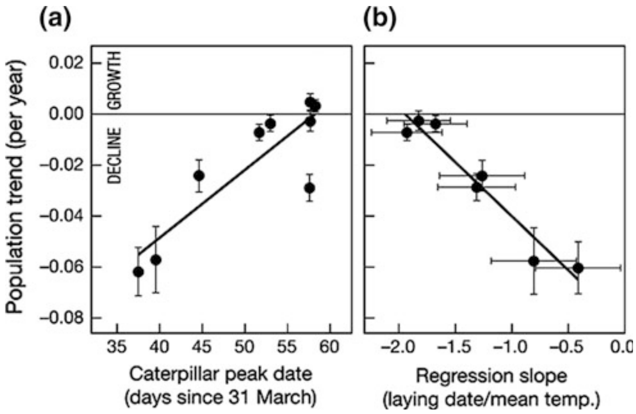

Fig. 11.4 Trends in pied flycatcher populations in response to the local date of peak caterpillar abundance (Spearman rank correlation: $r_s = 0.80$, $n = 9$, $p = 0.013$) (**a**), and the slope of annual median egg laying date on spring (16 April–15 May) temperature ($r_s = -0.86$, $n = 7$, $p = 0.03$) (**b**). Populations of pied flycatchers with an early food peak and a weak response declined most strongly. Population trend is the slope of the regression of the log number of breeding pairs against year. In '**b**', the *x* axis shows the slope of a linear regression of median laying date against mean temperature from 16 April to 15 May. *Error bars* represent the standard errors of the slopes of the regression lines. All points in '**b**' are also in '**a**', except for one point, for which no data regarding the caterpillar peak were available (Both et al. 2006)

Differences in response to climate change among species may also lead to a matching of originally asynchronous species, also with considerable ecological implications (Visser and Both 2005; Parmesan 2006). Case studies documenting this process are rare. Van Nouhuys and Lei (2004) showed that warmer, early spring-temperatures favoured the parasitoid wasp *Cotesia melitaearum* disproportionally, bringing it into closer synchrony with its host the butterfly *Melitaea cinxia*. Although the authors found no direct effect of the phenological matching on local host population size, the synchrony is likely to be important for overall host meta-population dynamics via variation in the rate of colonisation by the parasitoid.

In addition to phenological mismatches, trophic interactions can also become disrupted if host plants and species feeding on these host plants shift their ranges asynchronously. For the monophagous butterfly *Boloria titania* and its larval host plant *Polygonum bistorta*, Schweiger et al. (2008) showed that climate change may lead to a spatial mismatch of trophically interacting species due to asynchronous range shifts. Schweiger et al. (2012) analysed the potential for such mismatches in the future for 36 European butterfly species by simulating the potential range shifts for butterflies and host plants separately with bioclimatic envelope models, also taking into account land use. They found that those butterflies that are already limited in their distribution by their host plants could suffer most from global climate change, particularly if the host plants have restricted ranges.

11.2.4 Range Shifts and Biodiversity

Recent climate change has already influenced the distribution of species and their abundance (Walther et al. 2002; Parmesan and Yohe 2003; Parmesan 2006; Lenoir et al. 2008; Chen et al. 2011). According to a recent meta-analysis covering a range of taxonomic groups across the globe, species have on average shifted their ranges 16.9 km to higher latitudes and 11 m up in altitude per decade, more than estimates from earlier studies. The average shifts have been larger in those areas that have experienced the strongest warming and have, on average, been sufficient to track temperature changes, but with large variation between species, and most observations are from the temperate zone and tropical mountains (Chen et al. 2011). More than 20 % of species actually shifted in the opposite direction (in latitude and altitude) to the one expected based on temperature changes over the last few decades. Such changes can be explained by drivers other than temperature, such as habitat destruction and water availability, together with biotic interactions such as dependency on certain host plants and special physiological constraints (e.g. minimum or maximum temperatures during crucial phases of the life cycle) (Chen et al. 2011; Crimmins et al. 2011; Tingley et al. 2012). The differences between species reported here were only poorly related to broad taxonomic groups, such as birds and butterflies; rather the differences within such groups were larger than the differences between groups. In all taxonomic groups, habitat specialists and those with a low dispersal and colonisation capability show the lowest or even negative range shifts towards higher latitudes or altitudes (Warren et al. 2001; Chen et al. 2011). However, a recent global analysis of projected rates of temperature shift across landscapes compared to maximum projected speeds at which species can move across landscapes (from observations and modelling studies) showed that many species will probably be unable to track climate change, particularly for the warmer scenarios, which imply faster warming than in the recent past (Settele et al. 2014). Furthermore, this analysis also suggested large differences between organism groups in terms of their dispersal capacity. Herbaceous plants and trees seem to have particularly low dispersal capacity (Settele et al. 2014). An analysis for the British Isles (Fig. 11.5) also showed substantial differences in range expansion for different taxonomic groups (Hickling et al. 2006).

In the North Sea region, substantial average northward shifts have been well-documented for birds, butterflies, moths, dragonflies and damselflies, but mostly with large numbers of species also showing no shift or even retreating northern range boundaries (Parmesan 2006). Among the well-studied groups, plant ranges show the smallest responses to recent climate change, at least in lowland areas, probably because of their limited capacity to disperse and colonise new habitats in highly-fragmented landscapes (Honnay et al. 2002; Bertrand et al. 2011; Doxford and Freckleton 2012). Analyses of community composition, however, show substantial increases in warm-adapted vascular plants and epiphytic lichens across the Netherlands, which have probably been partly driven by climate change (van Herk et al. 2002; Tamis et al. 2005). Also, as these changes have clearly been driven by other factors (such as changes in land use, eutrophication and, in the case of lichens, decreasing sulphur emissions) attributing them to climate change is challenging. Seventy-seven new epiphytic lichen species colonised the area between 1979 and 2001, nearly doubling the total number of species (van Herk et al. 2002) and overall vascular plant richness also increased (Tamis et al. 2005).

Average model projections for the migration rates that would be necessary to track climate change in Europe are substantially larger than those historically observed, but the magnitude of the mismatch depends heavily on the climate change scenario (Skov and Svenning 2004; Huntley et al. 2008; Doswald et al. 2009). Simulations with bioclimate envelope models suggest large local (per grid cell) species losses and turnover rates, assuming that species fully track climate change by migration (Thuiller et al. 2005; Pompe et al. 2008). For the SRES A1 scenario (Nakićenović and Swart 2000) and the HadCM3 climate model, for example, Thuiller et al. (2005) estimated an average turnover of 48 % per grid cell for the European plants considered (1350 for all of Europe) in the European Atlantic region by 2080. However, results from bioclimate envelope models should be

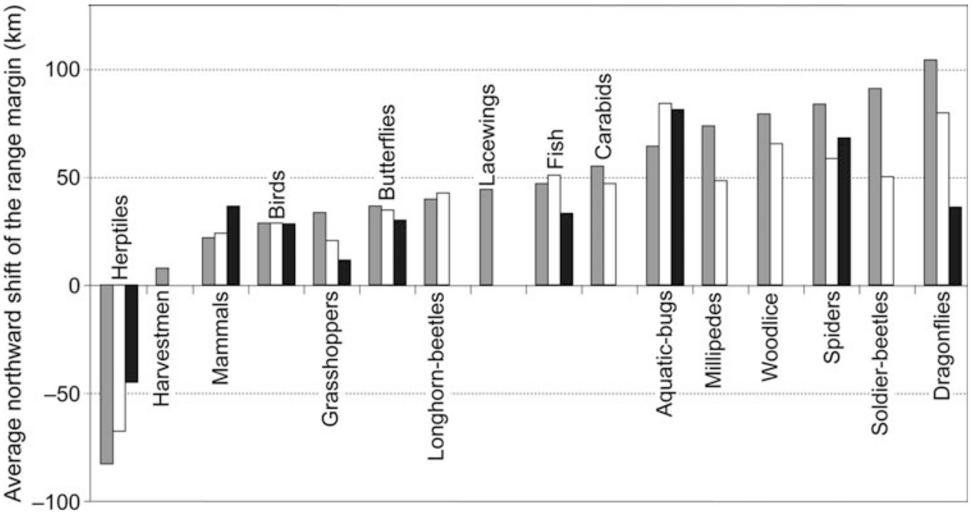

Fig. 11.5 Latitudinal shifts in northern range margins for 16 taxonomic groups in the British Isles during recent climate warming. Results are given for three levels of data subsampling (*grey* recorded; *white* well-recorded; *black* heavily recorded). Only species occupying more than twenty 10 km grid squares across two time periods (between 1960 and 2000, depending on organism group) are included in the analyses; for several of the species-poor groups, these criteria excluded all species from the analysis of 'heavily recorded' squares (Hickling et al. 2006)

interpreted more as potential shifts in the climatic window in which species can thrive rather than projections in range shifts. Furthermore, such models may overestimate change because they are developed based on correlations between species ranges and environmental factors. They do not capture the fundamental niche of species and so underestimate the climatic niche when species have not yet reached their distribution in equilibrium with the climate, which appears to be common, at least for trees (Svenning and Skov 2004; Normand et al. 2011). Furthermore, dispersal is rarely simulated explicitly, and dispersal projections are uncertain, for example, because of large uncertainties in projected wind speeds (Bullock et al. 2012). Nevertheless, it could be expected that many mobile, generalist species will continue to shift their distributions northward and up in altitude in response to climate change, although many habitat specialists (often those that are rare and already endangered) will not, and that many cold-adapted species will probably experience range losses at their southern distribution limit or at lower elevations (Hill et al. 2002; Chen et al. 2011; Sandel et al. 2011; Schweiger et al. 2012). As the area south of the North Sea region is generally more species-rich (e.g. Thuiller et al. 2005), biodiversity in the North Sea region could even increase. Negative impacts on cold-adapted species are expected to be most severe in mountain regions, where species have limited possibilities to migrate upwards or northwards, such as on mountains in the British Isles (Berry et al. 2002; Hill et al. 2002). Recent climate change has also affected the community compositions of birds and butterflies in Europe. Analyses of 9490 bird and 2130 butterfly communities in Europe show large changes, equivalent to a 37 and 114 km northward shift in bird and butterfly communities, respectively. However, these analyses suggest an even larger 'climatic debt', corresponding with a migration lag of 212 and 135 km for birds and butterflies (Devictor et al. 2012).

Intensification of agricultural activities and increasing anthropogenic nitrogen inputs since the 1950s and 1960s have been major drivers of biodiversity changes in the North Sea region (e.g. Ellenberg and Leuschner 2010). Wesche et al. (2012) found large changes in grassland community composition in five floodplain regions in northern Germany between the 1950s and 2008 and a decline in species richness at the plot level of 30–50 %. The decline was particularly strong among nectar-producing herbs, which is likely to have had negative effects on pollinators (Wesche et al. 2012). An analysis of Ellenberg indicator values for nutrient availability and a qualitative comparison with a protected area in the same region suggests that these changes were largely driven by increased nutrient inputs. Also, for a number of insect groups, a decline in species preferring low-productivity habitats and dry grassland specialists has been recorded in northern Germany (Schuch et al. 2012a, b). Pollinators are generally declining in Europe, and this has been particularly well documented for the Netherlands and the UK (Biesmeijer et al. 2006; Potts et al. 2010). However, the reasons for the decline are unclear. Potential drivers include habitat loss and fragmentation, agrochemicals, pathogens, invasion of non-native species, climate change and the interactions between them (Potts et al. 2010). These changes show the significant role of land use practice for biodiversity in north-western Europe. Further intensification of agricultural practices, possibly driven by an increasing demand for biofuels, is likely to have negative effects on biodiversity even if atmospheric N-deposition does not increase.

11.3 Forests

Forests are currently considered the most important carbon sink in Europe (Janssens et al. 2003). Due to the relatively low proportion of forests in the present land cover for countries bordering the North Sea—except Norway—the regional significance of this area as a carbon sink is relatively small or even negative compared to other European regions with higher forest cover (Janssens et al. 2005).

11.3.1 Climate Impacts on Productivity and Carbon Stocks

Although estimates of the mean long-term carbon forest sink (net biome production, NBP) are more reliable than those from grasslands (Janssens et al. 2003), the role of wood harvests, forest fires, losses to lakes and rivers and heterotrophic respiration remains uncertain and difficult to predict. Almost one third of the NBP is sequestered in the forest soil, but large uncertainty remains concerning the drivers and future of the soil organic carbon pool under climate change (Luyssaert et al. 2010). Nevertheless, increasing temperatures, longer growing seasons, higher atmospheric CO_2 concentrations, and in the north, increasing N-mineralisation, are likely to increase the potential forest productivity where summer precipitation does not decline (Lindner et al. 2010). Moreover, it is uncertain to what extent this potential can be realised as forests will increasingly face a climate to which the planted species or provenances are not adapted, which might increase their susceptibility to pests and pathogens, such as bark beetle (Scolytinae) outbreaks, which can lead to major forest die-back events particularly in Norway spruce *Picea abies* stands (Schlyter et al. 2006; Bolte et al. 2010). Furthermore, warmer and longer vegetation periods will accelerate the development of bark beetles, in some regions allowing for additional generations within a growing season (Jönsson et al. 2009). Other insect herbivores will also benefit from warmer conditions (Lindner et al. 2010). In a climate manipulation experiment in a Norwegian boreal forest, raised temperature and CO_2-level stimulated the outbreak of heather beetle *Lochmaea suturalis* and led to a shift in the ground vegetation from common heather *Calluna vulgaris* to blueberry *Vaccinium myrtillus* and cowberry *Vaccinium vitis-idaea* (van Breemen et al. 1998).

The complex interplay between climatic stress, pests and pathogens, and further disturbance such as windfall is hardly captured in the forest models used to project potential future impacts of climate change (e.g. Kirilenko and Sedjo 2007). As a result, it is highly uncertain whether climate change will lead to higher standing biomass in forests.

11.3.2 Shifts in Communities and Species Distribution

Projections of potential climate-driven transient shifts in broadly-defined forest types suggest only moderate changes in the North Sea region by 2100 (Hickler et al. 2012). The most significant changes projected are the spread of broadleaved and hemi-boreal mixed forests northward in southern Sweden and Norway as well as an upwards shift of the tree-line in the southern Scandes, which is already taking place (Kullman 2002).

Long-term equilibrium of shifts in forest type could be much more substantial, with thermophilous forests dominating in the south-western UK and temperate broadleaved forest along most of the Norwegian coast (Hickler et al. 2012). Recent range shifts northward (Fig. 11.6) have already been observed for cold-hardy, broadleaved, evergreen species such as holly *Ilex aquifolium* at their northern distributional limit in Europe (Walther et al. 2005; Berger et al. 2007).

Many European tree species have not yet filled their potential climatic niche in Europe because of dispersal limitations (Svenning and Skov 2004; Normand et al. 2011). Thus dispersal-limited species may be unable to track future climate change, unless foresters assist migration.

In contrast, there is almost no evidence of range shifts in herbaceous forest plants. Unlike mountain forest with short migration distances, there is some evidence that in lowland forests plant distribution changes will lag behind climate warming (Bertrand et al. 2011). Observational (Honnay et al. 2002) and modelling studies (Skov and Svenning 2004) suggest that this is probably due to dispersal limitation resulting from forest habitat fragmentation in lowlands. Where significant range shifts of forest herbs northward and eastward have been documented, such as for the oceanic annual woodland herb climbing corydalis *Ceratocapnos claviculata*, it is questionable whether this is due to climate change or to other drivers such as eutrophication or assisted migration through the international timber trade (Voss et al. 2012).

Among the major forest tree species, beech *Fagus sylvatica* is expected to extend its range northward in Britain and southern Scandinavia (Kramer et al. 2010; Hickler et al. 2012), whereas environmental conditions for the commercially-important Norway spruce will become less favourable (Pretzsch and Dursky 2002; Schlyter et al. 2006; Hanewinkel et al. 2013). Although beech is often considered to be very sensitive to drought, several studies (Lebourgeois et al. 2005; Meier and Leuschner 2008; Mölder et al. 2011) showed considerable phenotypic plasticity in response to drought stress (e.g. Bolte et al. 2007). The same is true for sessile oak, which proved to be highly resilient even to extreme drought (Leuschner et al. 2001; Lebourgeois et al. 2004; Friedrichs et al. 2009; Merian et al. 2011; Härdtle et al. 2013). Given the generally damp climatic conditions of north-western Europe, major broadleaved forest trees such as beech and sessile oak are probably not constrained by the projected climate change, which is in line with predictions of vegetation models (Kramer et al. 2010; Hickler et al. 2012). However, using older climate projections with lower projected rainfall than the latest average projections (see Chap. 5), simulations with a forest tree suitability model based on climatic and edaphic factors suggested that the majority of native broadleaved species would become unsuitable for commercial timber production in southern England due to increasing drought severity (Broadmeadow et al. 2005).

Forest management includes a wide range of measures to mitigate climate change effects, such as the selection and planting of species and provenances adapted to future climate (Isaac-Renton et al. 2014); a reduction in rotation cycles to accelerate the evolution and establishment of better adapted genotypes (Alberto et al. 2013); and the use of mixtures of high genetic variation across an array of environmental conditions (Hemery 2008; Köhl et al. 2010). Scientifically-sound implementation of such adaptation measures requires a wide range of research and monitoring activities such as testing of the suitability of new tree species and provenances, a regional risk analysis based on retrospective performance as well as the analysis of climate envelope and climate matching under potential future climates (Hulme 2005; Bolte et al. 2009; Hemery et al. 2010).

11.4 Grasslands

After cropland, grasslands are the dominant land use type in the North Sea catchment area. In the UK, grasslands comprise more than 40 % of land cover (EUROSTAT 2015).

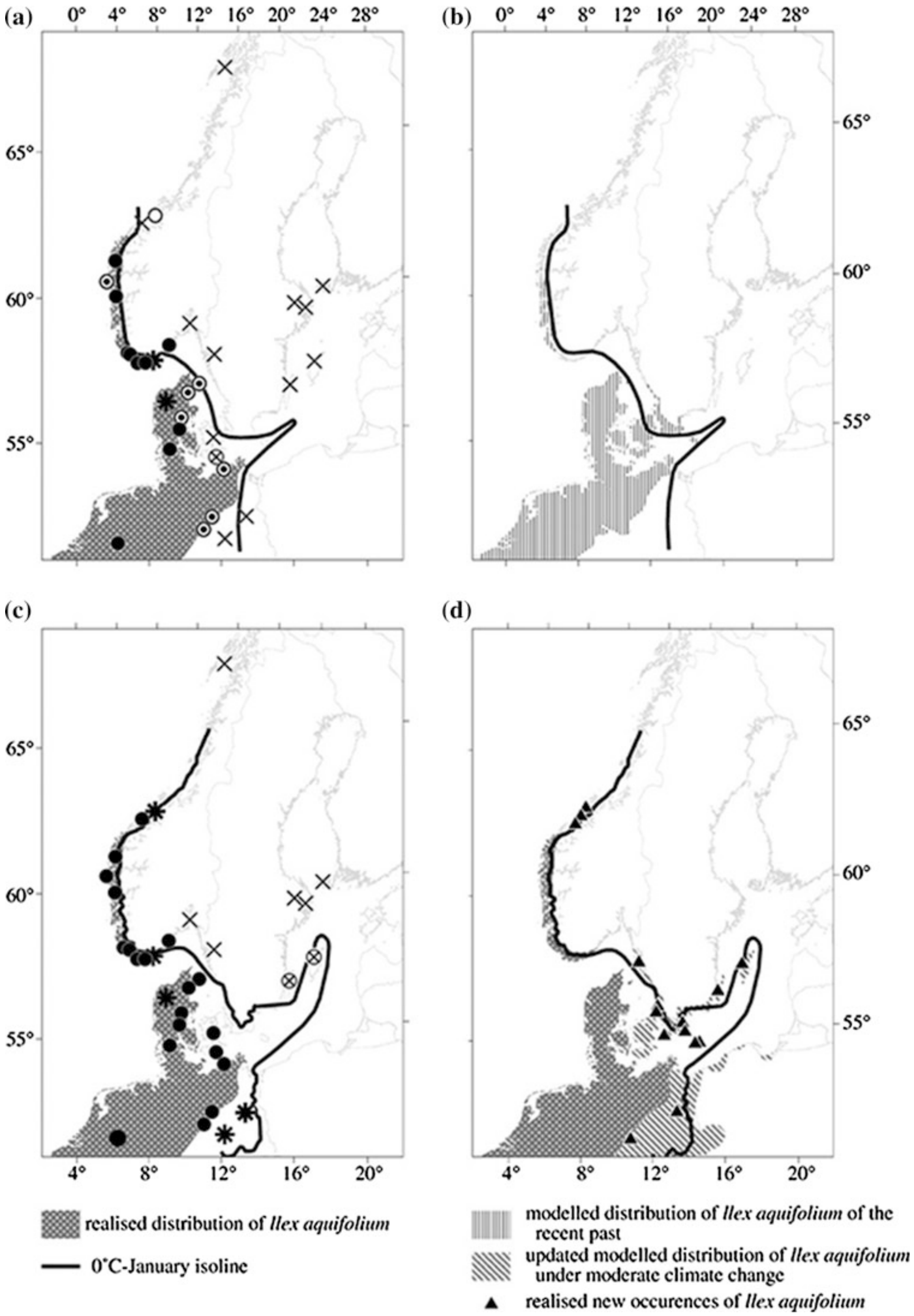

Fig. 11.6 Distribution of holly *Ilex aquifolium* and the 0 °C-January isoline at different times. **a** Former range of *I. aquifolium* based on Enquist (1924) and Meusel et al. (1965), isoline based on Walter and Straka (1970), symbols based on Iversen (1944); *circles*: *I. aquifolium* within or at the border of the station area; *circles*: *with cross I. aquifolium* strayed into woods from gardens; *stars*: *Ilex* area lies immediately outside the station area; *crosses*: *I. aquifolium* missing in the station area. **b** Modelled range of *I. aquifolium* in the recent past (1931–1960), isoline as in '**a**'. **c** Former range of *I. aquifolium* as in '**a**'; isoline updated for 1981–2000 based on Mitchell et al. (2004), symbols as for '**a**'. **d** Former range of *I. aquifolium* complemented by the simulated species distribution under a moderate climate change based on 1981–2000 climate data, isoline as in '**c**'; *triangles* represent locations with new observations of *I. aquifolium* (Walther et al. 2005)

Due to conversion into cropland, and the cessation and intensification of agricultural practices, grasslands underwent fundamental change during the 20th century (Bullock et al. 2011). Changes in management practice and eutrophication are currently the major drivers of ecological change in grasslands. At the same time, grasslands are of major significance for biodiversity and nature conservation in north-western Europe.

11.4.1 Climate Impacts on Carbon Stocks and Cycling

Unlike forests, carbon accumulation in grassland ecosystems occurs mostly below ground. As fluxes of greenhouse gases in grasslands are intimately linked to management and site conditions, grasslands can be either a sink or a source of greenhouse gases. Although many studies consider temperate grassland to be a carbon sink (Soussana et al. 2004), there is still high uncertainty about their current and future net global warming potential (in terms of CO_2 equivalents) at both a regional and continental scale (Janssens et al. 2003, 2005; Smith et al. 2005).

For Britain and Wales, both dominated by grasslands, Bellamy et al. (2005) suggested that significant losses of soil organic carbon (SOC) between 1978 and 2003 must be attributed to climate change because they occurred across all types of land use. However, as shown by Smith et al. (2007), this assumption was precarious and lacked clear empirical evidence. At a global scale (Guo and Gifford 2002), current SOC losses and gains in grasslands can be predominantly attributed to changes in land cover and management, whereas the role of climate change remains uncertain but is predicted to increase over the coming century (Smith et al. 2005). These considerable uncertainties are because grassland ecosystems are particularly complex and difficult to study owing to the wide range in management and environmental conditions to which they are exposed. As a result, studies on the effects of climate change on grasslands are often affected by this variability as well as by other confounding effects such as eutrophication and changes in management practice, which cause difficulties for observational studies and modelling (Soussana et al. 2004).

11.4.2 Climate Impacts on Plant Communities

Few experimental studies attempt to isolate the effects of climate change from other confounding effects. A study simulating warming and extended summer drought in calcareous grasslands at Buxton and Wytham in northern England (Grime et al. 2000) covered two different types of grassland with contrasting effects: after five years of climate manipulation, the more fertile, early successional grassland at Wytham showed significant changes in species composition and aboveground productivity especially for the combination of winter warming and summer drought. In contrast, an oligotrophic and more traditional calcareous grassland at Buxton exhibited almost no response to warming and drought treatments. This was still true even after 13 years of climate modification (Fig. 11.7; Grime et al. 2008). One reason for the high resistance of this infertile grassland may be the small-scale spatial heterogeneity in soil depth allowing the coexistence of

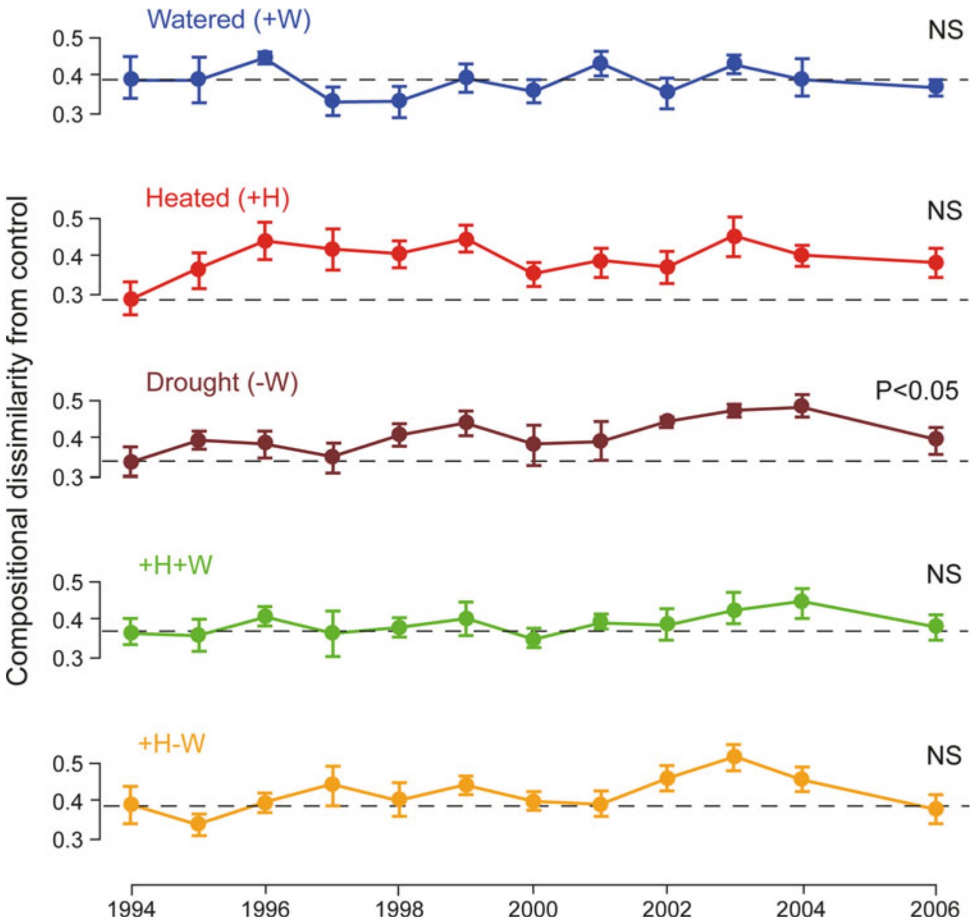

Fig. 11.7 Mean dissimilarity of treatment and control species composition for each year of the Buxton climate change experiment conducted in a nutrient-poor calcareous grassland. Dissimilarity was measured by Sørensen distance estimated separately within each replicate (n = 5 per treatment year). *Dashed lines* indicate mean dissimilarity in year 1 of the experiment. *Error bars* indicate one standard error of the mean. Statistics indicate whether treatment dissimilarity progressively increased over time based on linear autoregressive models (Grime et al. 2008)

drought-tolerant and more mesic species at small spatial scales (Fridley et al. 2011). As indicated by seed addition experiments, the minor changes in species composition, even after long-term climate treatments, are significantly affected by dispersal limitation rather than just biotic resistance (Moser et al. 2011). The prominent role of dispersal limitation as a cause of delayed response to climate effects has also been highlighted in several other studies (Buckland et al. 2001; Stampfli and Zeiter 2004; Zeiter et al. 2006).

Overall, the results of the Wytham and Buxton experiments suggest that more productive grasslands, strongly altered by human activities, might respond more to effects of climate change than infertile and more traditionally managed grasslands with rich species pools that can buffer climate effects (Grime et al. 2000, 2008). However, infertile traditional grasslands show low resilience towards eutrophication and changes in land management, which are currently more important drivers of ecological change in grasslands than climate change. Conversely, future warming potentially in association with increased drought risk could supersede eutrophication as the main driver of change, and in so doing potentially favour the persistence or even spread of dry and infertile grassland types (Buckland et al. 1997).

Observational studies also suggest that changes in the grasslands of north-western Europe can be attributed to recent regional climate change (e.g. Gaudnik et al. 2011), but these are mostly of high uncertainty due to strong confounding effects (McGovern et al. 2011). However, flowering phenology of many typical grassland plants in the UK does reveal significant effects of climate warming. Of 385 plant species, 16 % flowered significantly earlier in the early 1990s compared to previous decades, and earlier onset of flowering was most significant in annual species (Fitter and Fitter 2002). Williams and Abberton (2004) confirmed a significant trend of earlier flowering within different agricultural varieties of the common grassland legume white clover *Trifolium repens*.

11.4.3 Climate Impacts on Animal Communities

More convincing evidence of climate change effects in grasslands comes from animal groups typical of grassland habitats such as butterflies and grasshoppers; several have extended their range northwards significantly over past decades (Parmesan et al. 1999; Hill et al. 2002; Hickling et al. 2006). Unlike most vascular plants, which are often chronically persistent and immobile, highly-mobile animal species can often quickly respond to changing climate by significant range extensions. In north-western Germany, for example, the Roesel's busch-cricket *Metrioptera roeselii*, a typical grassland species, has been rapidly extending its range northward since the early 1990s, which was probably helped by increased rates of macroptery in this normally short-winged species, as a sign of density stress at the range margin (Hochkirch and Damerau 2009; Poniatowski and Fartmann 2011; Poniatowski et al. 2012).

Significant northward range expansions have also been documented for many typical grassland butterflies in the UK (Hill et al. 1999, 2002). However, only particularly mobile habitat generalists can fully exploit the emerging potential offered by climate warming (Fig. 11.8), whereas less mobile species and habitat specialists still suffer from habitat fragmentation and deterioration of habitat quality (Hill et al. 1999; Warren et al. 2001). Thus, range expansion is in many cases significantly lagging behind the current climate and can be reduced or even reversed by non-climatic drivers (Hulme 2005; Oliver et al. 2012).

11.5 Heathlands

In countries bordering the North Sea basin, heathlands dominated by shrubs of the ericaceous family still cover extensive areas especially in highlands of the UK and the southern Scandes (Webb 1998; van der Wal et al. 2011). Due to conversion into cropland and afforestation, heathlands have declined dramatically in the UK-lowlands and in the southern part of the North Sea region (Denmark, Germany, Netherlands). In these regions, they are at the edge of extinction in many sites and have become a major object of biodiversity and nature conservation efforts. Eutrophication and acidification through atmospheric inputs and changes in land management are currently the major drivers of change in these ecosystems (Härdtle et al. 2006), which makes the identification of climate change impacts difficult.

11.5.1 Climate Impacts on Ecosystem Processes

Effects of climate change on ecosystem processes in European heathlands were specifically addressed within the framework of two EU-projects simulating raised temperatures and drought (Wessel et al. 2004). These studies included sites in the UK, Denmark and the Netherlands. Experimental warming of 1 °C induced a significant increase in total above-ground plant biomass growth of 15 % in the most temperature-limited site in the UK, whereas drought treatments led only to a slight decline (Peñuelas et al. 2004). Drought decreased flowering (by up to 24 % in the UK). Warming and drought decreased litterfall in the Netherlands (by 33 and 37 %, respectively). Tissue concentrations of phosphorus (P) generally decreased and the N:P ratio increased with warming and drought except at the UK site,

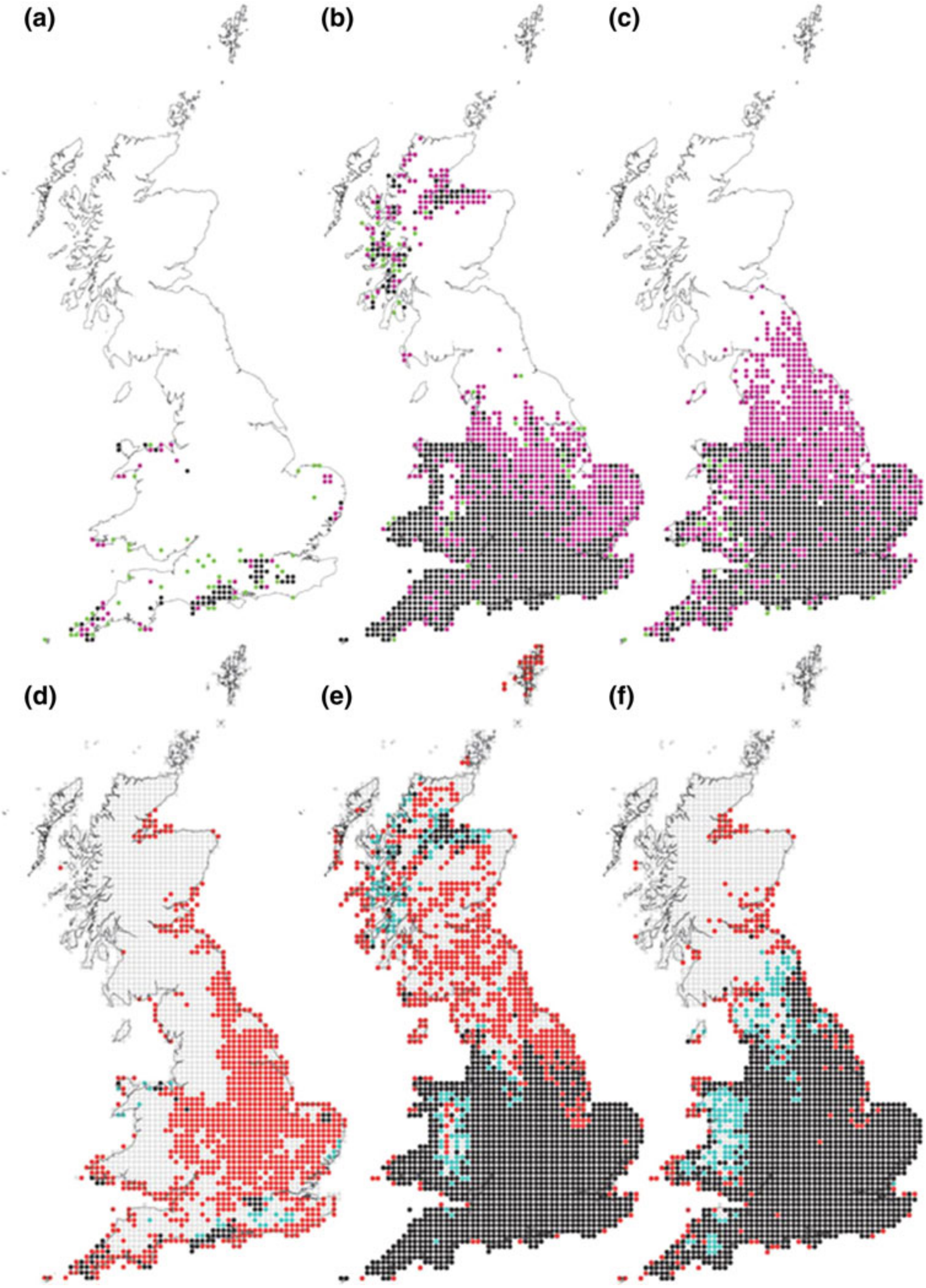

Fig. 11.8 The degree to which three butterfly species have changed their ranges (**a–c**, without subsampling) and are lagging behind current climate in Britain (**d–f**; 10-km grid resolution). **a+d**, silver-studded blue *Plebejus argus*; **b+e**, speckled wood *Pararge aegeria*; **c+f**, comma *Polygonia c-album*. For maps **a–c**, *black circles* show butterfly records for both 1970–1982 and 1995–1999; *green circles* show apparent extinction (recorded 1970–1982; not 1995–1999); *pink circles* show apparent colonisation (no record 1970–1982; record 1995–1999). For maps **d–f**, *black circles* (climate suitable, butterfly recorded) and *grey circles* (climate unsuitable, butterfly not recorded) show where observed 1995–1999 and simulated distributions agree; *red circles* (climate predicted suitable, butterfly not recorded) and *blue circles* (climate deemed unsuitable, butterfly recorded) show mismatches (Warren et al. 2001)

indicating the progressive importance of P-limitation as a consequence of warming and drought.

Owing to their richness in soil organic matter, mature heathlands may become important sources of C and N-release triggered by increasing temperatures and more frequent periods of drought. For the same experiments as above, Schmidt et al. (2004) found mostly weak and insignificant effects of warming and drought treatments on nitrogen and carbon budgets in the soil solution. Only at a strongly N-saturated site with high atmospheric N-deposition in the Netherlands, did warming trigger a significant increase in N-leaching. Similarly, in the same warming and drought experiments, Jensen et al. (2003) and Emmett et al. (2004) found largely weak or inconsistent responses in major soil processes such as decomposition, respiration and N-mineralisation. The latter turned out to be predominantly controlled by soil moisture. The response of soil-related processes to warming and drought treatments was generally found to be strongly dependent on local site conditions (Emmett et al. 2004). At mesic sites in the Netherlands and Denmark, soil respiration decreased in response to drought but recovered quickly to pre-drought levels after re-wetting in the following winter. In contrast, repeated drought treatments at a particularly damp site in the UK, which was particularly rich in organic matter, caused a disturbance in soil structure and a persistent reduction in soil moisture, which induced increased and continuing carbon losses through soil respiration (Sowerby et al. 2008).

The heathland studies conducted within the framework of the CLIMOOR and VULCAN projects (Peñuelas et al. 2007) show that the magnitude of the response to warming and drought was dependent on differences between sites, years, and plant species. Thus there are complex interactions between other environmental factors that condition plant and ecosystem performance, which makes it extremely difficult to predict net responses.

11.5.2 Climate Impacts on Plant Communities

Observational and experimental evidence for floristic changes in heathlands that can be clearly attributed to climate change is weak; for example, Werkman et al. (1996) found some indications that climate warming in combination with N-deposition might enhance the spread of the noxious weed bracken *Pteridium aquilinum* into heathlands in the UK. However, declines in arctic-alpine and boreal-montane lichen species in the heathlands of north-western Europe can be attributed to changes in traditional management practices and acidification, and are probably not directly connected to climate change (Hauck 2009).

11.5.3 Climate Impacts on Animal Communities

A significant decline has been observed over recent decades in artic-alpine bird species inhabiting mountain heathlands in the north of the UK such as ptarmigan *Lagopus mutus*, dotterel *Charadrius morinellus* and snow bunting *Plectrophenax nivalis.* In contrast the thermophilous, submediterranean Dartford warbler *Sylvia undata* has increased its population and spread into southern England, probably due to warmer winters (van der Wal et al. 2011). There is currently almost no empirical evidence of climate change impacts in other heathland-specific animal groups. However, modelling approaches suggest (Thomas et al. 1999; Berry et al. 2002) that eco-thermic animal species in heathlands may benefit from climate warming at their northern range margin.

11.6 Mires and Peatlands

Peatlands store significant quantities of carbon, nitrogen and other elements in their soils (e.g. Limpens et al. 2008; Yu et al. 2010) and are widespread in the North Sea region (Montanarella et al. 2006, Fig. 11.9). According to Joosten and Clarke (2002), peatlands are areas with a naturally accumulated peat layer at the surface, whereas mires are peatlands where peat is currently being formed. While about 80 % of the peatlands in Sweden and Norway are still mires,

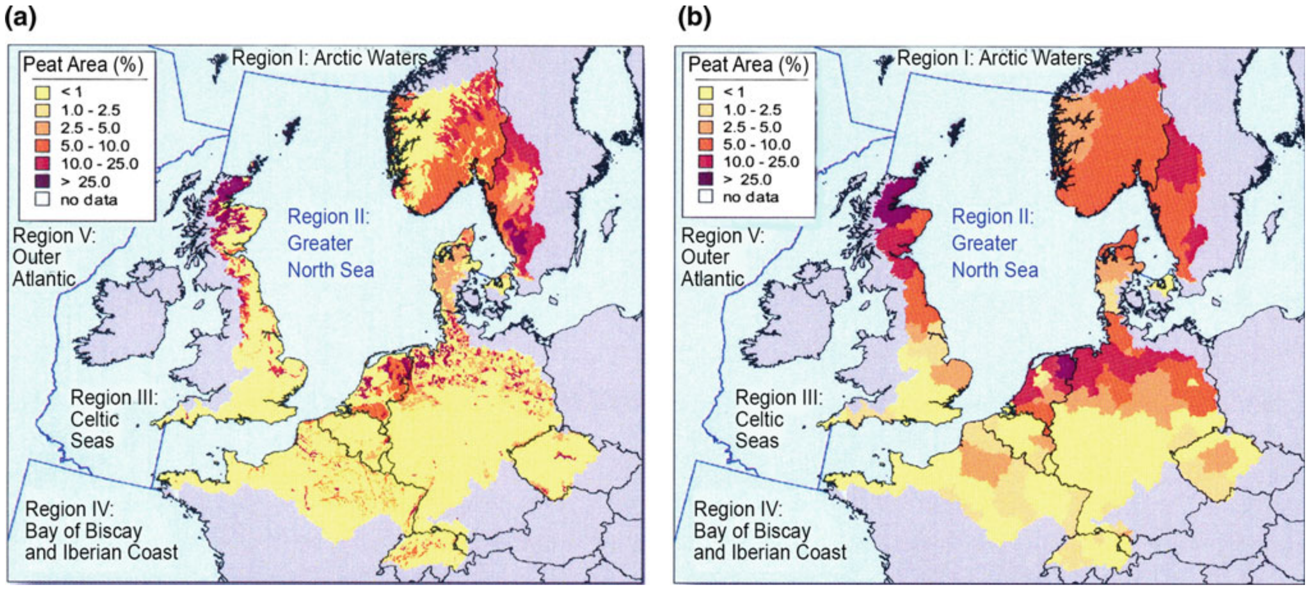

Fig. 11.9 Relative cover of peatlands and peat-topped soils in the North Sea catchment area. Maps based on **a** the soil mapping units of the European Soil Database (King et al. 1994, 1995) and **b** the NUTS (Nomenclature of Territorial Units for Statistics) level 2 administrative regions (R. Hiederer non-published data)

the contribution of mires to the total peatland area in the other, more southern North Sea-bordering states is only 1–7 % due to widespread drainage and intensive land use (Joosten and Clarke 2002).

Peatlands exchange C- and N-containing gases with the atmosphere, particularly the greenhouse gases CO_2, methane (CH_4) and nitrous oxide (N_2O) and thus influence climate (Blodau 2002; Frolking and Roulet 2007; Limpens et al. 2008; Finkelstein and Cowling 2011). Peatlands also exert strong influences on aquatic ecosystems by lateral waterborne export fluxes of elements, especially as particulate and dissolved organic matter (Urban et al. 1989; Freeman et al. 2001; Worrall et al. 2002; Billett et al. 2004; Dinsmore et al. 2010). Importantly, carbon accumulation, and vertical land-atmosphere and lateral waterborne bio-geochemical fluxes of peatlands are affected by climate change, and at the same time by changes in atmospheric chemistry and land use (e.g. Bragg 2002; Belyea and Malmer 2004; Dise 2009; Billett et al. 2010; Charman et al. 2013).

11.6.1 Climatic Impacts on Abiotic Conditions

Climatic change will have direct effects on the energy and water budgets of peatlands. Changing quantities and temporal patterns of precipitation will affect the water table in peatlands; with drought lowering and increased precipitation raising peatland water levels (e.g. Sottocornola and Kiely 2010). Higher temperatures, which are projected for the North Sea region in the future (Chap. 5) will increase evapotranspiration through a larger atmospheric water demand (Kellner 2001; Wu et al. 2010; Peichl et al. 2013). Other important variables influencing the energy and water budget of peatlands are net radiation and incoming short-wave radiation (Moore et al. 2013; Runkle et al. 2014). A continuation of the ‘brightening period’ through reduced aerosol loading (Wild et al. 2005) in Europe could increase evapotranspiration (Oliveira et al. 2011) leading to lower peatland water tables. However, most atmospheric models simulate a future decrease in shortwave radiation in the northern North Sea region and an increase in short-wave radiation in the south (Chap. 5). A long-term lowering of the water table due to increased evapotranspiration is expected to be modulated by changes in leaf area and the distribution of plant functional groups leading to increased surface resistance, reduced evapotranspiration and an attenuated fall in water tables (Bridgham et al. 1999; Moore et al. 2013). Desiccation of the moss layer during summer droughts can also lead to reduced evapotranspiration (Sottocornola and Kiely 2010). Higher winter precipitation as projected for the North Sea region (Chap. 5) would lead to larger winter discharge from peatlands and probably to a larger lateral export of dissolved organic matter and nutrients (e.g. Tranvik and Jansson 2002; Worrall et al. 2002, 2003; Pastor et al. 2003; Holden 2005). Increasing summer drought and winter rainfall would enhance peatland erosion and export of dissolved organic carbon (DOC) and particulate organic carbon (POC) in susceptible areas, particularly in the upland blanket bogs of the UK and Norway (e.g. Bower 1960, 1961; Francis 1990; Evans et al. 2006b; Evans and Warburton 2010). Drier mire surfaces in summer would enhance the risk of peatland fires, which lead to strong local emissions of CO_2 (Davies et al. 2013) and waterborne DOC (Holden et al. 2007; Clutterbuck and Yallop 2010). At bare peat sites (under peat extraction or crop cultivation), higher wind speeds and rainfall intensities can lead to strong aeolian or water erosion of peat (Warburton 2003).

11.6.2 Climatic Impacts on Biotic Interactions

Climate change is expected to have large impacts on biotic processes in peatlands (e.g. Heijmans et al. 2008; Charman et al. 2013). Higher temperatures will generally increase microbial peat decomposition and carbon mobilisation (Ise et al. 2008), leading to greater concentrations of DOC in peatland surface and soil pore waters (Freeman et al. 2001, Fig. 11.10). The mobilised DOC can be mineralised and released to the atmosphere as CO_2 (e.g. Silvola et al. 1996; Lafleur et al. 2005) or CH_4 (e.g. Dunfield et al. 1993; Moore and Dalva 1993; Daulat and Clymo 1998; Hargreaves and Fowler 1998; Fig. 11.11) depending on the reduction-oxidation status of the organic soils. It can also be laterally exported with the peatland discharge into limnic systems (Tipping et al. 1999; Worrall et al. 2003). Warming-induced increases in soil carbon emissions result partly from the direct temperature effect on soil microbial physiological processes and growth and partly from better substrate availability in the soil pore water caused by higher plant productivity (Mikkelä et al. 1995; Joabsson et al. 1999; Van den Pol-van Dasselaar et al. 1999).

These findings from field and laboratory studies have been incorporated in local, regional and global soil process models (e.g. Walter et al. 2001; van Huissteden and van den Bos 2006; Bohn et al. 2007; Meng et al. 2012). The models predict considerable increases in CH_4 emissions from peatlands over the coming century due to warming as long as wetland area and soil moisture conditions remain unchanged. However, several global models tested within the Wetland and Wetland CH_4 Intercomparison of Models Project (WETCHIMP) predict a decrease in wetland area in the North Sea region in response to higher temperatures, which is likely to lead to lower CH_4 emissions (Melton et al.

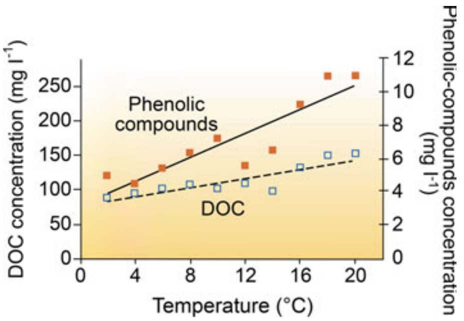

Fig. 11.10 Laboratory observations of increased concentrations of dissolved organic carbon (DOC) and phenolic compounds in peat soil in response to rising temperature (Freeman et al. 2001)

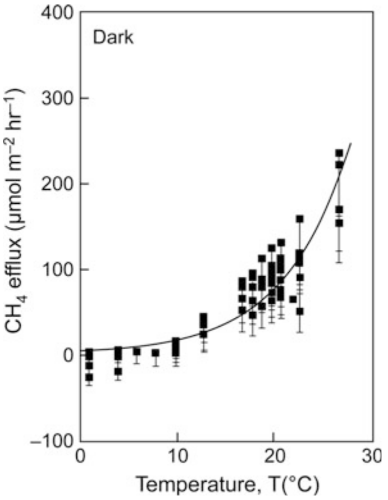

Fig. 11.11 Effects of temperature on methane (CH_4) efflux from 30 cm diameter *Sphagnum papillosum* mire cores. Flux measurements were performed in dark conditions (after Daulat and Clymo 1998)

2013); however, it should be noted that these models show a very wide range of responses.

Whether increased peat decomposition and carbon mobilisation due to higher temperatures leads to lower net ecosystem productivity and to higher net carbon emissions, will depend on the land use of peatlands. For the period 1978–2003, Bellamy et al. (2005) reported carbon losses from all soil types across England and Wales, with particularly strong losses from peat soils. However, it is not clear from such data whether carbon was lost due to climate change or to concomitant changes in atmospheric chemistry and land use (see Sect. 11.4.1 and 11.6.3). Likewise, mapping of peat soils in the Dutch province of Drenthe showed that 42 % of the area of peat soils was converted to mineral soils in the last 30–40 years by carbon loss due to drainage and agricultural management; on average 1 cm peat thickness was lost per year (De Vries et al. 2008). In near-natural peatlands with typical mire vegetation, peat accumulation is expected to increase in response to higher mean annual temperatures because the benefit to primary productivity will be higher than for ecosystem respiration (Loisel et al. 2012; Charman et al. 2013). Longer growing seasons (higher winter temperatures, shorter snow-cover duration) allows the vegetation to take up more photons over the year leading to higher plant productivity and peat accumulation. This increase in net carbon uptake under a warming climate—a negative feedback on climate warming—will be modulated by cloud cover and levels of photosynthetically active radiation (Yu et al. 2010; Loisel et al. 2012; Charman et al. 2013).

If peatland water tables become significantly lower due to increased evapotranspiration and/or decreased summer precipitation, peat decomposition and the release of CO_2 will be enhanced (e.g. Silvola et al. 1996; Laine et al. 2009). Higher N_2O emissions can also be expected with lower peatland water levels (Martikainen et al. 1993; Regina et al. 1996; Goldberg et al. 2010). On the other hand, CH_4 production and emission will decrease, while CH_4 oxidation will be enhanced (e.g. Daulat and Clymo 1998; Hargreaves and Fowler 1998; Nykänen et al. 1998; Le Mer and Roger 2001; Laine et al. 2007, 2009).

The impact of water table drawdown on net ecosystem productivity depends on the response of peatland vegetation, which is difficult to predict and can vary strongly with the micro-topography of mires (Malmer et al. 1994; Strack and Waddington 2007; Lindsay 2010). Since *Sphagnum* mosses have neither roots nor vessels to transport water from deeper soil layers, they rely on high water tables. Water that is lost at the soil surface through evaporation can be replaced by precipitation and capillary rise in *Sphagnum* peat and vegetation. But—depending on the *Sphagnum* species present and the degree of peat decomposition—capillary rise is only efficient in this regard if water tables are not lower than 0.5 m below the land surface (Clymo 1984). Thus, long-lasting drought may damage the vitality of *Sphagnum* mosses (Gerdol et al. 1996; Bragazza 2008; Breeuwer et al. 2009; Robroek et al. 2009).

Medium- to long-term changes in climatic variables such as temperature and precipitation have complex effects on mire vegetation composition that interact with changes in CO_2 concentration and nutrient availability (e.g. Heijmans et al. 2008; Breeuwer et al. 2010, see also Sect. 11.6.3). In a *Sphagnum*-dominated bog in southern Sweden, significant shifts in vegetation composition since the 1950s indicate higher nutrient availability, higher productivity, and drier and shadier conditions due to enhanced tree and shrub growth, which have probably all been triggered by warming (Kapfer et al. 2011). Projected climate change, particularly higher summer temperatures and lower summer precipitation may reduce the bio-climatologically suitable space for blanket

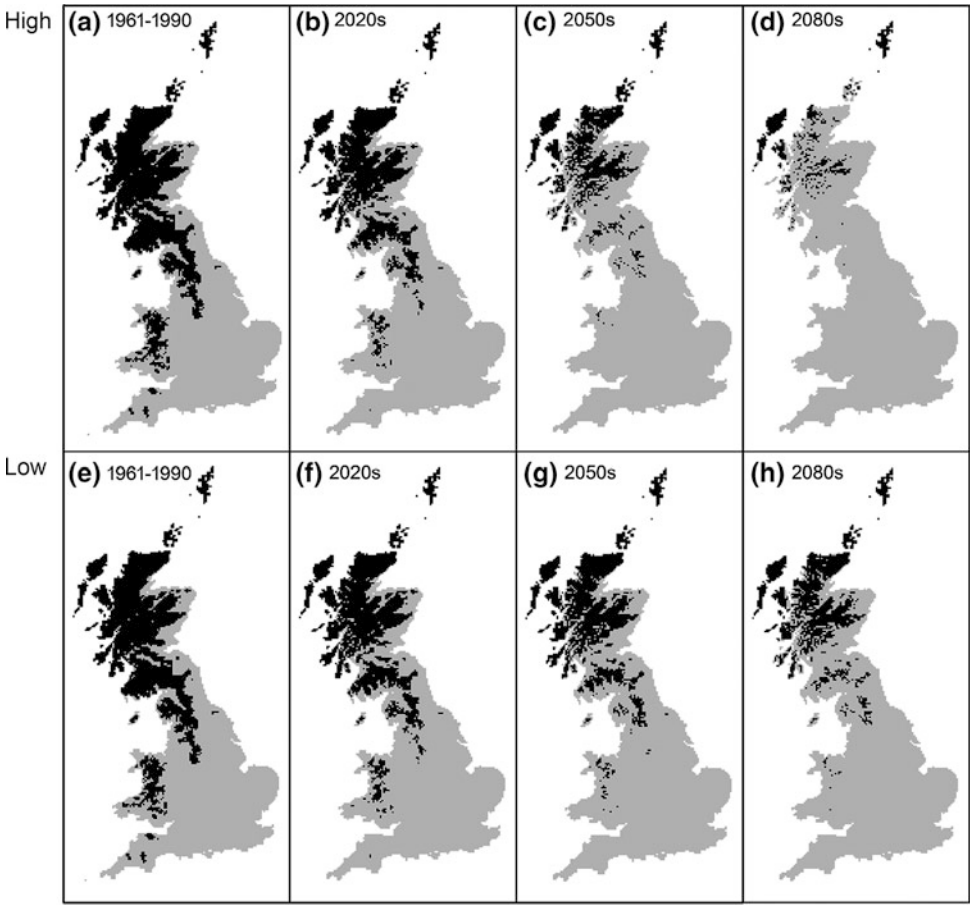

Fig. 11.12 Area covered by the bioclimatic envelope of blanket peatlands as predicted by the model PeatStash using the bioclimatic thresholds associated with the 1961–1990 baseline climate for the UKCIP02 high and low emissions scenarios ('High' and 'Low', respectively) for three time periods: 2020s, 2050s and 2080s. An Ordnance Survey/EDINA supplied service (© Crown Copyright/database 2009) and Met Office/UKCIP gridded climate data (UKCIP02 © Crown Copyright 2002) (Gallego-Sala et al. 2010)

bogs in the UK (Clark et al. 2010; Gallego-Sala et al. 2010; Gallego-Sala and Prentice 2013, Fig. 11.12). Berry and Butt (2002) suggested that the dominant species in lowland raised bogs of Scotland would find suitable conditions, but that some rare species will probably lose suitable climate space under the expected future climatic conditions. Since lower summer precipitation and higher summer temperatures are projected for the entire North Sea region (Chap. 5), mires on the European continent—especially ombrogenous mires—are likely to experience falling summer water levels with negative impacts on typical mire plant communities. However, Lindsay (2010) cautioned that the climate envelope approaches applied might underestimate the importance of local atmospheric humidity, cloud cover and mist frequency for mire occurrence. Other studies even propose—on the basis of biogeographical, bioclimatological and ecophysiological reasoning—that northern oceanic peatlands will expand owing to the increased oceanicity of the future climate (Crawford 2000; Crawford et al. 2003). Lindsay (2010) also stated that mires with a well-developed acrotelm and microtopography might be able to react to climate change without losing their ability to grow and sequester carbon. Mires that are already degraded will have much less resilience to the projected changes in climate (Lindsay 2010).

11.6.3 Competing Effects of Climate Change and Other Influences

In addition to the changes in climate, there have also been changes in the intensity of land use and atmospheric chemistry (such as CO_2 concentration, and atmospheric deposition of nitrogen and sulphur) over recent decades, with strong impacts on near-natural and degraded peatlands. These may intensify, mask or reverse the effects of climate change on peatlands.

11.6.3.1 Atmospheric Chemistry

Research in *Sphagnum* bogs found that elevated atmospheric CO_2 concentrations did not affect NPP due to the strong N-limitation of these ecosystems (Berendse et al. 2001). However, CH_4 emission (Dacey et al. 1994; Hutchin et al. 1995) and DOC export (Freeman et al. 2004; Van Groenigen et al. 2011) from peatlands were enhanced under elevated CO_2 concentrations. Increased N-deposition promotes microbial peat decomposition and thus CO_2 and CH_4 emissions (Aerts et al. 1992; Aerts and de Caluwe 1999) and DOC export fluxes (Bragazza et al. 2006). Large shifts in mire vegetation composition may also occur in response to elevated CO_2 concentrations and increased N-deposition

(Van der Heijden et al. 2000; Berendse et al. 2001; Fenner et al. 2007; Heijmans et al. 2008). Deposition of nitrogen and sulphur leads to acidification of top soils and thus changes the solubility and mobilisation of dissolved organic matter. The rise in DOC concentrations in limnic water bodies observed in the latter half of the 20th century in Great Britain and Sweden seems to have been mainly driven by decreasing S-deposition with the warming effect of minor importance (Freeman et al. 2001; Worrall et al. 2002; Evans et al. 2005, 2006a, 2007; Monteith et al. 2007; Erlandsson et al. 2008). However, S-deposition has also been shown to suppress CH_4 emissions because sulphate reduction is energetically favourable compared to methanogenesis (Dise and Verry 2001). Heavy air pollution can even lead to die-off of *Sphagnum* mosses, triggering for example peat erosion in blanket mires (e.g. Tallis 1985).

11.6.3.2 Land Use

Drained and degraded peatlands are hotspots of greenhouse gas emissions (e.g. Oleszczuk et al. 2008; Couwenberg 2011; Joosten et al. 2012). Mineralisation of peat organic matter and the respective CO_2 emissions are strongly related to drainage depth and management intensity (Aerts and Ludwig 1997; Dirks et al. 2000; Beetz et al. 2013; Leiber-Sauheitl et al. 2013; Schrier-Uijl et al. 2014). A project on peatlands in Germany has shown that the annual greenhouse gas balance of managed peatland areas can be estimated well from two predictor variables—mean annual water level and carbon exported by harvest—which together can be used as a proxy for management intensity (Drösler et al. 2011, 2012). Within the set of managed peatlands, greenhouse gas emissions from deeply-drained peatlands such as cropland or intensively-used pastureland are especially large (Veenendaal et al. 2007; Drösler et al. 2011; Elsgaard et al. 2012; Leiber-Sauheitl et al. 2013). Greenhouse gas emissions can stay high at such sites even when management intensity is moderated by nature conservancy measures (Best and Jacobs 1997; Schrier-Uijl et al. 2010; Hahn-Schöfl et al. 2011). Intensively-used peatlands are more common in lowlands than in uplands due to better accessibility and suitability for high-intensity agriculture. Burning peatland vegetation as a management practice in the UK may strongly affect carbon sequestration and dissolved organic matter export (Garnett et al. 2000; Clutterbuck and Yallop 2010; Yallop et al. 2010) although the evidence is not conclusive (cf. Worrall et al. 2007; Clay et al. 2009; Allen et al. 2013). It should be stressed that change in land use is the primary driver of changes in peatland hydrology and biogeochemistry, and probably has a stronger impact than climate change. However, some climate change effects will exacerbate the impact of human activities such as drainage, grazing, burning and peat mining (e.g. Petrescu et al. 2009). On the other hand, land use-related effects on peatlands often make them more vulnerable to climate change impacts (e.g. Parish et al. 2008).

11.7 Inland Ecosystems and the Wider North Sea System

Inland ecosystems have important functions within the coupled land-ocean-atmosphere system of the North Sea region. Major functions of inland ecosystems are freshwater storage and transmission, carbon storage, carbon sequestration, greenhouse gas emission and the export of dissolved and particulate organic matter to aquatic systems. While forests in the North Sea region currently sequester carbon and act as greenhouse gas sinks (Ciais et al. 2008; Luyssaert et al. 2010), agricultural systems are greenhouse gas sources through CO_2 and N_2O emissions from soils and CH_4 emissions from enteric fermentation of livestock and manure management (Schulze et al. 2009). Greenhouse gas emissions from degraded and agriculturally-used peatlands are significant in several countries of the North Sea region when compared to their total national greenhouse gas emissions, with contributions of about 5 % in Germany and Denmark, 2–3 % in the Netherlands and about 1 % in the UK (Cannell et al. 1999; Van den Bos 2003; Drösler et al. 2008, 2011; Verhagen et al. 2009; Joosten 2010; Worrall et al. 2011; Nielsen et al. 2013). On the other hand, CO_2 uptake by the few remaining near-natural peatlands in the North Sea region is negligible compared to CO_2 release by degraded peatlands or CO_2 uptake by forests. This means that reducing emissions from reclaimed peatlands is more important than the possible contribution of natural peatland to carbon sequestration.

The export of dissolved and particulate organic matter from inland ecosystems has important effects on the biogeochemistry and ecology of the receiving aquatic systems (i.e. lakes, rivers, estuaries and the North Sea) and supplies them with inputs of carbon, nitrogen, phosphorus and other important nutrient elements (e.g. Evans et al. 2005). Because export of DOC and POC is controlled by many interacting factors (e.g. temperature, nutrient supply, precipitation, evapotranspiration, run-off), its future behaviour is difficult to predict. Run-off is projected to increase in the northern part of the North Sea region and to decrease in the south (Alcamo et al. 2007). However, due to the projected warming and higher frequency of heavy rain events in the North Sea region (Chap. 5), enhanced mobilisation of soil organic matter and transport of terrestrial DOC to the limnic ecosystems and the North Sea are likely. Dissolved organic matter affects ecosystem nutrient availability (Carpenter et al. 2005), acidification of limnic systems (Oliver et al.

1983) and solubility, transport and toxicity of heavy metals and organic pollutants (Carter and Suffet 1982; Pokrovsky et al. 2005). It also regulates the photochemistry of natural waters (Zafiriou et al. 1984) and influences aquatic production of algae and bacteria (Wetzel 1992; Carpenter and Pace 1997). The export of organic matter into limnic systems can affect human health adversely since these organic substances support bacterial proliferation and lead to the formation of carcinogens when they react with disinfectants (such as chlorine) during water treatment (Nokes et al. 1999; Sadiq and Rodriguez 2004). The magnitude of DOC fluxes in rivers correlates with organic matter storage in the soils of their catchments (e.g. Hope et al. 1997). Riverine organic matter is modified strongly and largely removed through mineralisation and sedimentation during transport in rivers and estuaries (e.g. Raymond and Bauer 2000; Wiegner and Seitzinger 2001; Abril et al. 2002; Raymond et al. 2013). Thomas et al. (2005) estimated that about one million tons of DOC and POC are transported into the North Sea by rivers each year. Only 10 % of the riverine input of organic carbon is probably buried in the shelf sediments (Hedges et al. 1997; Schlünz and Schneider 2000), with the rest incorporated in the food webs of coastal seas.

Flood risk mitigation is an important issue in coastal and fluvial lowlands bordering the North Sea, especially given the projected acceleration in sea-level rise in the future due to climate change (Chap. 5). Peat soil degradation causes land subsidence by a combination of peat oxidation and compaction after drainage (Schothorst 1977). Historical subsidence—caused by drainage since medieval times—often combined with peat extraction for fuel, in coastal peatlands of the Netherlands, Germany and eastern Britain may have resulted in up to several metres of subsidence (Godwin 1978; Borger 1992; Verhoeven 1992; Hoogland et al. 2012). In the eastern British fenlands, compaction and peat oxidation has resulted in up to 4 m of subsidence in 150 years (Godwin 1978). In Dutch managed peatlands, subsidence is ongoing at up to one centimetre per year (Hoogland et al. 2012, and references therein). Under a warmer climate, peat decomposition would be even faster, particularly in drained peatlands. This would increase flood risk, induce costs for creating and managing flood protection systems and ever deeper drainage, and threaten the economic viability of agriculture. Subsidence also influences peatland hydrology and hydrochemistry. The need for increasingly deeper drainage enhances the upwelling of sulphate-rich brackish or salt water (Hoogland et al. 2012). This in turn may enhance peat decomposition by sulphate reduction, with adverse impacts on water quality by increasing dissolved and particulate organic matter and nutrient mobilisation (Smolders et al. 2006). Replenishing surface water with alkaline river water in agriculturally managed peatlands in dry periods may have a similar effect on peat decomposition.

11.8 Summary

The expected future impacts of climate change on terrestrial ecosystems are summarised in Table 11.1.

Future climate change is likely to increase NPP in the North Sea region due to warmer conditions and longer growing seasons, at least if future climate change is moderate and summer precipitation does not decrease as strongly as projected in some of the more extreme climate scenarios. The physiological effects of increasing atmospheric CO_2 levels and increasing N-mineralisation in the soil may also play a significant role, but to an as yet uncertain extent.

The effects of total carbon storage in terrestrial ecosystems are highly uncertain, due to the inherent complexity of the processes involved. For example, water table effects in mires, large uncertainties in soil carbon modelling, the unknown fate of additional carbon taken up through CO_2 fertilisation, and other important drivers, such as changes in land use (e.g. forest harvest and wetland drainage). For moderate climate change, land use effects are often more important drivers of total ecosystem carbon accumulation than climate change.

Across a wide range of organism groups, range expansions to higher latitudes and altitudes, changes in phenology, and in the case of butterflies and birds, population increases in warm-adapted species and decreases in cold-adapted species have occurred in response to recent climate change. Regarding range expansions, some studies suggest substantial differences between organism groups; for example, herbaceous plants show only small or no responses while variability within other groups is large. Habitat specialists with restricted ranges have generally responded very little or even shown range contractions. Many of these often already threatened species could therefore be particularly vulnerable to climate change. Cold-adapted mountain top species are at particular risk because they have very limited habitat space in which to track climate change.

Overall effects of recent climate change on forest ecosystems within the region are limited, and major impacts on forest type distribution and forest functioning are unlikely if future warming is moderate and summer precipitation does not decrease as much as is projected in some of the more extreme climate scenarios. However, current models simulating potential impacts of climate change on forests rarely include a number of drivers of potentially rapid changes in forest functioning, such as forest pests and diseases (e.g. Kirilenko and Sedjo 2007; Jönsson et al. 2009). As a result, projections of climate-driven changes in future forest productivity, biomass and carbon storage are highly uncertain.

For grasslands, significant range expansion of thermophilous animal species (e.g. Parmesan et al. 1999), changes in flowering phenology (e.g. Fitter and Fitter 2002), and population increases (e.g. Poniatowski et al. 2012) are

Table 11.1 Climate change impacts on terrestrial ecosystems of the North Sea region

Class of impact	Impact of recent climate change	Projected impact of future climate change	Uncertainties
Phenology			
Shift towards earlier spring and summer phases in plants	Spring events advanced on average by 6.3 days ✓✓✓	Further advancement depending on temperature increase ✓✓	Modified responses due to non-linear effects of further increasing temperatures early in the year
Shift towards later autumn phases in plants	Autumn events delayed by on average 4.5 days ✓✓	Further delay depending on temperature increase ✓	Limited data quality
Extension of growing period	Extension of growing season by about 20 days ✓✓	Further extension depending on temperature increase	Limited data quality
Earlier onset of reproduction in animals	Earlier onset of first spawning in amphibians by 10–20 days ✓✓✓	No studies	
	Advances of dates of first clutches in bird species by on average 8.8 days ✓✓✓		
Changed migratory patterns and behaviour	Advances in the arrival of migratory birds ✓✓✓	No studies	
	Shift in winter distribution of waterfowl and waders to the North-East ✓✓✓		
Biogeography and community structure			
Range shifts in vascular plants and cryptogams	Plants: range extensions lagging warming due to dispersal and/or habitat limitation ✓✓	Strongly limited range filling due to dispersal limitation in fragmented landscapes ✓✓	Impact of other abiotic factors (e.g. nutrients)
			Dispersal and recruitment limitation
			Habitat limitation and landscape fragmentation
			Changed biotic interactions (e.g. competition, herbivory, pathogens)
			Changing land-use and disturbance regimes
			Impact of climate extremes
	Lichens: cold-adapted species declining and warm-adapted expanding their ranges northwards	Decline of cold-adapted species at the rear edge and at lower mountain elevations ✓	Poorly known phenotypic plasticity and evolutionary capacity
Range shifts in animals	Substantial range extension to the north in many mobile, generalist animal species ✓✓✓	Continuing range expansion to the north in mobile, generalist species ✓✓	Impact of other abiotic factors (e.g. nutrients)
			Dispersal and recruitment limitation
			Habitat limitation and landscape fragmentation
			Changed biotic interactions (e.g. competition, herbivory, pathogens)
			Changing land-use and disturbance regimes
	No or minor range extension or range contraction in many habitat specialists		Impact of climate extremes
	Decline in some northern species in the south	Decline of cold-adapted species at the rear edge ✓	Poorly known phenotypic plasticity and evolutionary capacity

(continued)

Table 11.1 (continued)

Class of impact	Impact of recent climate change	Projected impact of future climate change	Uncertainties
Changed composition in plant communities	Limited evidence for primarily climate-induced changes so far ✓	Relatively slow shifts in species composition	Impact of other abiotic factors (e.g. nutrients)
			Dispersal and recruitment limitation
			Habitat limitation and landscape fragmentation
			Changed biotic interactions (e.g. competition, herbivory, pathogens)
			Changing land-use and disturbance regimes
			Impact of climate extremes
			Poorly known phenotypic plasticity and evolutionary capacity
			Few studies, 'new' biotic interactions
Changed biome distribution	Upward shift of tree-line in the southern Scandes into arctic-alpine Tundra ecosystems ✓✓	Moderate shifts mostly in the northern part of the region between nemoral and boreal forests (spread of broadleaved trees) and boreal forests and arctic-alpine tundra (spread of shrubs and trees) ✓✓	Impact of other abiotic factors (e.g. nutrients)
			Dispersal and recruitment limitation
			Habitat limitation and landscape fragmentation
			Changed biotic interactions (e.g. competition, herbivory, pathogens)
			Changing land-use and disturbance regimes
			Impact of climate extremes
		Reduction of bioclimatologically suitable space for blanket bogs ✓	Poorly known phenotypic plasticity and evolutionary capacity
Biotic mismatch	Few well documented examples for birds and insects ✓	Increasing spatial mismatches between butterflies and host plants, particularly for those butterflies that are already constrained by specific host plants ✓	
Physiological tolerance and stress			
Tree stress and forest dieback	Limited evidence for drought stress in southern part of the region ✓	Increasing drought risk especially in the southern part of the region ✓	Ecological complexity and lack of process understanding
			Other abiotic factors
	Role of pests and pathogens still rather uncertain. ✓	Increasing risk of pathogens and pests ✓	Species-specific reactions and genetic variability within species

(continued)

Table 11.1 (continued)

Class of impact	Impact of recent climate change	Projected impact of future climate change	Uncertainties
Ecosystem functioning			
Net primary productivity and forest growth	Increased growing season length and NPP ✓✓✓	Further increase of NPP especially in the north of the region ✓✓	Impact of other drivers such as N-deposition and enhanced mineralisation, acidification and potential CO_2 'fertilisation'
		Mixed effects on NPP in the southern part of the region, depending on water supply ✓	Impacts of drought stress and disturbance events poorly captured in vegetation
	Increasing forest growth especially in northern regions and at sites without moisture limitation ✓✓✓	Increased NPP in mires and drained peatlands ✓	Tree species selection and forest management practices
Carbon sequestration capacity	Enhanced vegetation carbon fixation due to increased forest growth ✓✓	Northern areas remain net carbon sinks, southern areas may eventually turn into small to moderate sources ✓	Relative importance and interplay of raised soil respiration and NPP
			Feedbacks of changed hydrology on carbon exchange in wetlands
			Human alterations in land cover and land use
		Increased peat accumulation in mires, accelerated peat decay in drained peatlands✓	Only one regional modelling study included total terrestrial carbon cycle
Greenhouse gas release from mineral and organic soils	Increased soil respiration and CH_4 release from hydrologically intact peatlands. ✓✓	Enhanced carbon release especially from desiccated peat soils and other humus-rich soils ✓✓	Unpredictable hydrological changes associated with climate warming
			Competing effects of climate change and other influences (atmospheric chemistry, land use)
	Increased C-release from desiccated and degraded peat soils, especially in the south ✓✓		Large uncertainties in soil carbon modelling
Lateral waterborne export fluxes of elements	Increased run-off in northern part, decreased run-off in the southern North Sea region ✓✓	Further enhanced mobilisation of DOC, especially from drained peatlands ✓✓	Unpredictable hydrological changes associated with climate warming
			Competing effects of climate change and other influences (atmospheric chemistry, land use)
	Increased export of DOC ✓		Large uncertainties in soil carbon modelling

✓✓✓ strong evidence; ✓✓ moderate evidence; ✓ minor evidence currently more obvious signs of climate change, than changes in plant community composition and ecosystem processes. Even in experimental studies simulating drought and warming, responses to treatments were modest (Bates et al. 2005; Grime et al. 2008; Kreyling 2010). Evidence from observational and correlative studies is weak and speculative due to many confounding effects such as eutrophication and changes in management practice (e.g. Gaudnik et al. 2011; McGovern et al. 2011).

For heathlands, overall evidence for effects of recent climate change from experimental warming and drought treatments is also weak, variable and inconsistent, suggesting that now and in the near future, climate warming is of low significance compared to other predominant drivers of ecological change in heathland ecosystems such as eutrophication, acidification and altered management practices (e.g. Härdtle et al. 2006). For more extreme climate scenarios, however, substantial effects could be expected in heathlands. Projections of the exact nature of these future effects are highly uncertain.

The projected climatic changes for the North Sea region are likely to have significant impacts on abiotic and biotic processes in mires and drained peatlands. However, the consequences will vary widely between mires and drained peatlands. Higher temperatures and longer growing seasons will increase NPP, but also ecosystem respiration, CH_4 emission and DOC export in mires and drained peatlands. The net effect is expected to result in increased peat accumulation in mires but accelerating peat decay in drained peatlands. In mires, lower water tables due to less summer precipitation and/or higher evapotranspiration will enhance NPP but also—and to a much greater degree—ecosystem respiration, leading to a net loss of peat organic matter and the release of CO_2. On the other hand, CH_4 emission will also be reduced, while effects on DOC export are less clear. In drained peatlands, climatic changes will have less effect on the water budget and biogeochemical fluxes since water tables are regulated.

Low summer precipitation and/or high evapotranspiration can make conditions unsuitable for some mire types. However, well-developed natural mires may have considerable resilience to climate change. The status of peatlands, namely the level of drainage and soil degradation will determine whether peatlands mitigate or exacerbate climate change.

Besides their function as a sink for atmospheric carbon, the export of dissolved and particulate organic carbon and nutrients from terrestrial ecosystems is probably the most significant process directly affecting the North Sea system. Because this export is controlled by many interrelating factors (temperature, precipitation, evapotranspiration, run-off, human impact), its future development is very uncertain and therefore difficult to predict.

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