Environmental Impacts—Marine Ecosystems

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Abstract

Increase in sea surface temperature is projected to change seasonal succession and induce dominance shifts in phytoplankton in spring and promote the growth of cyanobacteria in summer. In general, climate change is projected to worsen oxygen conditions and eutrophication in the Baltic Proper and the Gulf of Finland. In the Gulf of Bothnia, the increasing freshwater discharge may increase the amount of dissolved organic carbon (DOC) in the water and hence reduce phytoplankton productivity. In winter, reduced duration and spatial extent of sea ice will cause habitat loss for ice-dwelling organisms and probably induce changes in nutrient dynamics within and under the sea ice. The projected salinity decline will probably affect the functional diversity of the benthic communities and induce geographical shifts in the distribution limits of key species such as bladder wrack and blue mussel. In the pelagic ecosystem, the decrease in salinity together with poor oxygen conditions in the deep basins will negatively influence the main Baltic Sea piscivore, cod. This has been suggested to cause cascading effects on clupeids and zooplankton.

Keywords

Baltic Sea • Climate change • Benthic and pelagic communities • Biodiversity • Biogeography • Regime shifts • Cascading effects
19.1 Introduction

The Baltic Sea has undergone rapid post-glacial succession over the past 10,000 years (see Chap. 2). This has meant a succession of different types of communities, resulting in changes in the marine ecosystem. Superimposed on this geological-scale shift, there have also been more rapid changes in the physics, chemistry and biology that can be connected to climate (BACC Author Team 2008). Most importantly, the Baltic Sea system responds to climatological variations in the North Atlantic region, characterised by the North Atlantic Oscillation (NAO, see Chap. 4) and its local counterpart the Baltic Sea Index (BSI) (Matthäus and Schinke 1994; Hänninen et al. 2000; Lehmann et al. 2002). The Baltic Sea ecosystem is also influenced by human-induced global warming, that has been projected to affect various oceanographic parameters in the Baltic Sea in the coming decades (e.g. Meier et al. 2012 and Chap. 13).

The complexity of the interactions and feedbacks between the atmosphere, watershed and marine ecosystem make it difficult to distinguish anthropogenic effects, such as eutrophication, from those caused by changes in climate. This distinction is important to make when designing measures to improve the status of the marine environment by adjusting human actions.

Climate effects may be subdivided into direct and indirect effects. Direct effects influence the individual organisms, their metabolism, growth, survival and productivity, through changes in the properties of the water surrounding them (temperature, salinity, chemical composition and other properties, such as stratification and mixing). Indirect effects influence the structure of communities by changing species interactions, or by shaping temporal and spatial match or mismatch of populations. Such interactions affect the intensity of grazing, predation and competition, and shape the structure of communities and thus affect biodiversity, trophic relationships and ecosystem functioning (Sommer and Lengfellner 2008; Sommer and Lewandowska 2011). Both types of effects may result in changes in species’ ecology and eventually evolution. The responses will together define the realised niches of species in a world affected by changing climate (Lavergne et al. 2010).

Among the climate-driven factors that directly affect individuals, temperature is fundamental. It drives biological processes and ultimately underpins life history traits, population growth and ecosystem processes. Effects range from those directly affecting metabolism of bacteria (e.g. Autio 1998) to those affecting the development of invertebrates (O’Connor et al. 2007) and fish larvae (e.g. Karás and Neuman 1981; Hakala et al. 2003). Temperature may also affect populations indirectly by influencing their food supply (Hoegh-Guldberg and Bruno 2010).

Salinity is also a fundamental factor, because most of the Baltic Sea species are of either marine or freshwater origin and many live at the edge of their salinity tolerance. Other climate-driven environmental factors that have direct effects on individuals include oxygen concentration and the acidity (pH) of the seawater. Climate also indirectly affects species and populations by affecting water stratification, mixing depth and availability of nutrients, thus influencing the primary producers as well the animals feeding on them. For a summary of effects see Table 19.1.

19.2 Community-Level Variations in the Past

19.2.1 Phytoplankton

Evidence for community-level changes in phytoplankton exists for the northern Baltic Sea. For example, a 30-year dataset from the Gulf of Finland showed that the spring bloom (measured as chlorophyll a) declined from 1986 to 2002, while the summer phytoplankton biomass increased from 1990 to 2002 (Raateoja et al. 2005). The decrease in the spring bloom was probably caused by decreased availability of nitrogen in spring, which resulted in less phosphorus consumed, and hence larger phosphorus reserves for the summer. This in turn benefited the nitrogen-fixing summer cyanobacteria.

| Food web component | Higher freshwater discharge | Higher temperature |
|--------------------|-----------------------------|-------------------|
| Phytoplankton      | Reduced productivity        | Lower biomass and size/no consensus |
| Bacterioplankton   | Maintained growth           | Increased growth   |
| Protozooplankton   | Maintained growth           | Increased growth   |
| Sedimentation      | Reduced amount and quality  | Reduced amount and quality |
| Food web efficiency| Reduced efficiency          | No consensus       |

Table 19.1 Summary of short-term effects of freshwater discharge and temperature on the microbial food web and phytoplankton as reported in the current literature.
In a study covering 1979–2008, the summer biomass of cyanobacteria, chrysophytes and chlorophytes increased in the northern Baltic Proper and the Gulf of Finland, while the biomass of cryptophytes decreased (Suikkanen et al. 2007, 2013; Fig. 19.1). Increase in sea surface temperature in summer, decline in salinity and an increase in the winter dissolved inorganic nitrogen to phosphorus ratio (DIN:DIP) were the most important factors explaining the changes observed in the phytoplankton community. Both climate-induced and anthropogenic factors, especially nutrient loading, were concluded to have contributed to the changes.

Further evidence for climate effects on phytoplankton comes from studies of dominance changes between diatoms and dinoflagellates. In the Baltic Sea, the spring bloom is dominated by just a few species of diatoms and cold-water dinoflagellates (Kremp et al. 2008). Their relative proportions depend on temperature and ice conditions, with warm winters favouring dinoflagellates (Wasmund et al. 2011; Klais et al. 2011, 2013). Consequently, it has been suggested that warming promotes a dominance by dinoflagellates over diatoms in the Baltic Sea spring bloom (Kremp et al. 2008; Olli and Trunov 2010). However, although dinoflagellates have increased in the central and northern Baltic Proper (Wasmund and Uhlig 2003; Suikkanen et al. 2007; Klais et al. 2011), the data do not support an increase in spring bloom dinoflagellates for the Baltic Sea as a whole. The response of dinoflagellates to large-scale climate patterns seems to depend on local hydrography and community composition (Klais et al. 2013).

There are only a few studies of the actual mechanisms by which dinoflagellates are favoured in warm conditions. In the northern Baltic Sea, the dinoflagellate Biecheleria baltica has expanded its range in recent decades. This expansion has been linked to the exceptionally efficient benthic cyst production of this species (Olli and Trunov 2010). Given the rise in deep-water temperatures in the Baltic Proper, the benthic cyst germination of B. baltica may have been enhanced and contributed to the spring dominance of this species (Kremp et al. 2008).

19.2.2 Zooplankton

It is well known that oceanic zooplankton respond to variations in climate (e.g. Beaugrand and Reid 2003; Hays et al. 2005). The response has usually been explained as a bottom-up process: the atmospheric forcing influences primary productivity through hydrography and stratification of water, which changes mixing depth, light and availability of nutrients. This in turn affects grazing zooplankton, planktivorous fish and even seabirds (Aebischer et al. 1990; Frederiksen et al. 2006).

Similar responses to climate or weather parameters have also been shown in the Baltic Sea. For instance in the Gulf of Finland, there was a significant positive correlation between westerly winds and the abundance of marine copepods, whereas easterly winds promoted a high abundance of small euryhaline cladocerans (Viitasalo et al. 1995). This could have been caused by westerly winds advecting saline water—and marine species—from the northern Baltic Proper into the Gulf of Finland, and it remained unclear whether any trophic effects were involved. In contrast, rotifers and cladocerans were positively associated with high sea surface temperatures in summer (Viitasalo et al. 1995). In this case, the warm water probably increased growth rates of these surface-dwelling taxa and also increased the availability of suitable small-sized food in the strongly stratified water (Kivi et al. 1993).

In an analysis of open-sea monitoring data for the Gulf of Finland and northern Baltic Proper in 1979–2008, rotifers also increased at the expense of crustacean zooplankton, apparently due to the combined effects of changes in hydrography, eutrophication and top-down pressure (Suikkanen et al. 2013). This resulted in a shift towards a food web structure with smaller sized organisms.
Few studies have investigated the effects of climate-related parameters on shallow-water zooplankton dynamics. Scheinin and Mattila (2010) concluded that temperature and total phosphorus (an indicator of eutrophication) were the most important factors shaping littoral zooplankton communities in the northern Baltic Sea, which suggests that they could be affected by climate-induced warming and eutrophication. Kotta et al. (2009) and Pöllänen et al. (2009) suggested, however, that small-scale environmental variability probably masks the response of shallow pelagic communities to climatic variation.

In addition to trophic effects, climate-related parameters also have direct physiological effects on Baltic Sea zooplankton. For example, *Pseudocalanus acuspes*, a marine species, responded negatively to the 1980s decline in salinity (Lumborg and Ojaveer 1991; Vuorinen et al. 1998; Möllmann et al. 2000), whereas the more euryhaline copepods *Acartia* spp. and *Temora longicornis* increased, apparently due to rising spring temperature in the central Baltic Sea (Möllmann et al. 2000).

Other mechanisms by which climate change may affect zooplankton are life cycle effects. Many Baltic Sea copepod species overwinter as resting eggs in the sediments, and a connection between the timing of spring warming of the water and timing of peak population in spring has been detected (Viitasalo 1992). In many coastal areas, like the Gulf of Riga (Kotta et al. 2009), Darß-Zingst lagoon (Feike et al. 2007), Swedish east coast (Hansson et al. 2010) and Archipelago Sea (Dippner et al. 2001), mesozooplankton has been shown to respond positively to mild winters. This suggests that climate change may influence the benthic germination of copepods in the same way as shown for certain dinoflagellates (Kremp et al. 2008).

### 19.2.3 Open-Sea Benthic Communities

The benthic community of the open Baltic Sea is a mix of species with marine, brackish water and limnic origins. Their latitudinal distribution and species diversity are limited by the gradient of decreasing salinity towards the north (Elmgren 1989; Rumohr et al. 1996; Bonsdorff and Pearson 1999). Spatial studies of species turnover (β-diversity), in the transition zone between the North Sea, Skagerrak, Kattegat and the Belt Sea (Josefson 2009) and along the salinity gradients of the Baltic Sea (Laine et al. 1997; Bleich et al. 2011; Villnäs and Norkko 2011), all demonstrate the key role of salinity in the distribution of macrobenthic animals. The distribution of benthic species is also driven by strong vertical gradients: shallow-water soft bottom communities have higher habitat diversity and thus more species than the sub-halocline communities (e.g. Andersin et al. 1978).

Climate affects both salinity and stratification and consequently the distribution of hypoxia in the Baltic Sea, and it is therefore natural that climatic variation also affects zoobenthos. The earliest evidence for such an interaction comes from reported responses to saline water inflows that enter the Baltic Sea through the Danish Straits (see also Chap. 7). In the mid-1950s, the large saltwater inflow was accompanied by significant range expansions of many benthic marine species into the Baltic Proper (Segerstråle 1969). This process has reversed in the 1980s and 1990s when a decrease in salinity has led to a dominance shift from marine to brackish water taxa in the southern and western parts of the Baltic Sea (Villnäs and Norkko 2011). As the hypoxia is currently the most widespread on record, due both to eutrophication and to climatic conditions favouring stagnation (Conley et al. 2009, see also Chap. 18), benthic communities in the central Baltic Proper are presently in a poor state.

The saline water inflows have different effects in different basins of the Baltic Sea. For example, in the late 1980s and early 1990s, the benthic communities were in a poor state due to long-lasting stagnation. Meanwhile the Gulf of Finland had relatively good oxygen conditions and abundant macrozoobenthos. The major saline water inflow through the Danish Straits in 1993 again improved oxygen conditions in the Baltic Proper, but simultaneously pushed the stagnant oxygen-depleted water from the central Baltic Sea basin into the Gulf of Finland. This water reached the eastern Gulf of Finland by autumn 1995 to spring 1996 and caused a dramatic decrease in the macrozoobenthos (Laine et al. 2007; Savchuk 2010). The situation later reversed: in the Gulf of Finland, the benthic communities recovered, while in the stagnant Baltic Proper, anoxia gradually developed and killed the benthic communities.

Benthic conditions in the Baltic Proper and the shallower Gulf of Finland thus respond to climate-induced oceanographic variations with different time lags.

### 19.2.4 Shallow-Water Benthic Communities

Benthic communities on shallow-water hard and soft bottoms in the Baltic Sea differ from the deeper communities owing to light conditions enabling an abundance of algae and vascular plants. The communities are often based on a few structurally and functionally important species, such as fucoids, seagrasses, blue mussels and a few other habitat-forming species (e.g. Wallentinus 1991; Kautsky and Kautsky 2000). As in the case of deep benthos, the composition and species richness of shallow benthic communities decline from the Kattegat and southern Baltic Sea towards the north and east (Nielsen et al. 1995; Ojaveer et al. 2010).
The spatial distributions of shallow-water benthic species are determined foremost by their ability to adapt to low salinity, but also to variations in sea level, wave exposure, light and oxygen availability, grazing, predation and competition for space (Kautsky and Kautsky 2000 and references therein).

To date, very few studies have explicitly investigated the mechanisms by which climatic variations can affect shallow benthic and algal communities in the Baltic Sea. Mild winters have been shown to result in a denser growth of Fucus near the surface (Kiirikki and Ruuskanen 1996), at the same time promoting a higher production of associated invertebrate fauna (Wikström and Kautsky 2007). This was explained by less ice scraping in milder winters: ice scraping effectively removes key species in the uppermost part of the algal belt and thus delays development of the algae and associated fauna. Also in Haapsalu Bay, eastern Baltic Proper, changes in the macrophyte communities over the past 50 years have been affected by weather-induced changes in salinity and ice conditions (Kovtun et al. 2009).

The reproductive phase of many macroalgae is especially sensitive to seasonal changes in salinity. Laboratory experiments have shown that fertilisation of Baltic Fucus serratus is high at a salinity of 9, but very low at a salinity of 6, typical of the coasts in the northern Baltic Proper (Malm et al. 2001). Also Fucus vesiculosus needs relatively high salinity during its main reproductive periods in May–June and September–October (Serrão et al. 1999; Malm et al. 2001). However, no clear link between climate-induced changes in salinity and long-term changes in Fucus populations has to date been demonstrated.

19.3 System-Level Variations in the Past

19.3.1 Regime Shifts

Theory, experiments and field data all indicate that a gradual change in external drivers can result in an abrupt, nonlinear change in the ecosystem—a regime shift (e.g. Scheffer et al. 2001; Folke et al. 2004; Andersen et al. 2009). In several sea areas of the northern hemisphere, populations of predatory fish have declined, often due to overfishing, causing a large-scale reorganisation of the ecosystem in question (e.g. Myers and Worm 2003; Collie et al. 2004). Similar system-level changes have also taken place in the Baltic Sea during the past century, but these shifts have probably been caused by a combination of climatic and anthropogenic effects, including overfishing and eutrophication.

Around 1935–1955, an ‘oceanisation’ of the Baltic Sea took place: salinity increased and various pelagic and benthic taxa such as marine copepods, the jellyfish Cyanea capillata, the barnacle Balanus improvisus, and cod (Gadus morhua), garfish (Belone belone) and mackerel (Scomber scombrus) spread hundreds of kilometres northwards, while the ranges of species preferring low salinity retreated (Segersrål 1969). The system was characterised by marine species and relatively good oxygen conditions.

In the late 1950s, the oceanisation ended and, as the anthropogenic nutrient load increased, primary production started to increase (Larsson et al. 1985; Elmgren 1989; Stigebrandt 1991). This resulted in increased sedimentation and deep-water oxygen consumption from the early 1960s onwards (Elmgren 1984; Conley et al. 2002). A particularly severe hypoxia of the deep waters developed in the 1980s, during a long ‘stagnation period’ with less inflow of oxygen-rich water from the North Sea (Fonselius and Valderrama 2003). Due to the hypoxia, the macrobenthic bottom fauna below the halocline was eliminated, which caused a major disruption of the benthic food web (Elmgren 1989; Norkko et al. 2010).

The hypoxia also changed the food availability for demersal fishes. While cod in the early twentieth century fed mainly on benthic organisms, once the macrobenthos disappeared the cod switched to pelagic fish, mainly sprat (Sprattus sprattus) and herring (Clupea harengus membras) (Eero et al. 2011). Cod reproduction declined (due to declining egg survival in low oxygen conditions), while cod fisheries remained intense, and cod stocks consequently collapsed. This process fundamentally changed the structure and functioning of the upper pelagic trophic levels of the Baltic Sea in the late twentieth century (see also Sects. 19.3.2 and 19.4.4).

A multivariate time-series analysis suggested that feedback loops were established in the biotic part of the ecosystem, preventing the system from switching back to its previous state (Möllmann et al. 2008, 2009; Casini et al. 2009)—a phenomenon referred to as hysteresis (Scheffer et al. 2001). In the other Baltic Sea areas, the situation may be different. Lindegren et al. (2010a) demonstrated a shift in ecosystem composition in the Sound (the transition area between the western Baltic Sea and the Kattegat). Here, the shift did not show signs of trophic cascade or hysteresis and may therefore be more easily reversible than in areas where the system has entered a new stable state.

19.3.2 Cascading Effects in the Pelagic Ecosystem

In the central and northern Baltic Sea, upper trophic levels of the pelagic ecosystem, including zooplankton, planktivores and piscivores, are all influenced by hydrography. Marine zooplankton typically declines during periods of low salinity, while certain species are favoured by warm water. Temperature
also influences sprat recruitment (e.g. MacKenzie and Köster 2004; Cardinale et al. 2009) because sprat eggs survive better during mild winters (Nissling 2004). Baltic Sea cod reproduction, in turn, is dependent on the volume of sufficiently saline and oxygenated water, termed ‘cod reproductive volume’ (RV) (MacKenzie et al. 2000). After spawning, cod eggs sink to the depth where they are neutrally buoyant, i.e. at a salinity of ~11, and if this water is too low in oxygen, the eggs die (Wieland et al. 1994). The RV is dependent on the water balance as well as density stratification in the Baltic Sea. All these factors are influenced by climatic processes in the Baltic Sea and in the North Atlantic (e.g. Matthäus and Franck 1992).

The climatic and hydrographic control of the upper trophic levels of the pelagic ecosystem is exemplified by the ‘regime shift’ described in the previous section. From the early 1980s to mid-2000s, only one major inflow took place (in 1993), salinity gradually declined, the anoxic layer expanded and cod reproduction collapsed (1986–1993) in the central Baltic Sea (Köster et al. 2005). The sprat stocks expanded sixfold soon after the collapse of cod stocks, during 1988–1995. A simultaneous decrease in zooplankton suggests that the effects of the cod collapse cascaded down from planktivores to zooplankton (Casini et al. 2008; Fig. 19.2). The marine zooplankton also declined because of direct physiological stress caused by declining salinity, and consequently, there was less food available for planktivores. This eventually caused starvation and low growth of clupeids, especially herring, in the late 1980s (Flinkman et al. 1998; Rönkkönen et al. 2003; Möllmann et al. 2005) (Fig. 19.3).

It is notable that the state of the cod stock in the Baltic Sea is not only driven by salinity and oxygen variation. This became clear when the eastern Baltic Sea cod stock started to recover in 2005, after more than two decades of low biomass and productivity, and despite the continuing ‘cod hostile’ (i.e. low oxygen) environment (Cardinale and Svedång 2011). The recovery was mainly driven by a sudden reduction in fishing mortality and occurred in the absence of any exceptionally large year classes. This suggests that effects of fisheries may at times override environmental factors as controllers of cod stocks in the Baltic Sea. The observation launched a vivid debate on the causes and consequences of the variations in the cod stocks in the Baltic Sea (Möllmann et al. 2011).

![Fig. 19.2 Trends in a cod biomass (squares) and sprat biomass (circles); b zooplankton biomass (triangles) and sprat abundance (diamonds) (ind., individuals); and c zooplankton biomass (triangles) and chlorophyll a (squares). The horizontal lines indicate periods of different average levels in the biological time series as detected by the cumulative z-scores. Casini et al. (2008)](image)

### 19.3.3 Microbial Food Web

Enhanced freshwater and nutrient discharge to the central Baltic Sea is usually thought to increase primary production and phytoplankton biomass. This is probably the case in areas where phytoplankton production is limited by the availability of inorganic nutrients. In contrast, the effects of climate change on the dynamics of the microbial food web may be less straightforward.

In the Gulf of Bothnia, increased freshwater runoff may lead to enhanced microbial activity and a decrease in phytoplankton primary production. This is because, in addition to nutrients, river discharge in this area carries a large load of dissolved organic carbon (DOC). The DOC reduces the amount of light reaching the phytoplankton (Pettersson et al. 1997) and also serves as a substrate for bacteria which at carbon substrate sufficiency may outcompete phytoplankton for nutrients (Mindl et al. 2005).

Such an outcome was demonstrated in a field study in the Gulf of Bothnia where the effect of river discharge was investigated for 13 years (1994–2006) (Wikner and Andersson 2012). A marked increase in the ratio of bacterioplankton production to phytoplankton production was observed when river discharge was elevated. This happened despite the increased availability of inorganic nutrients. In addition to lower light availability and competition for
nutrients, this may have been caused by a shortage of the limiting nutrient phosphorus due to chemical binding to iron (Wikner and Andersson 2012). This field observation was supported by mesocosm studies with natural plankton communities, where addition of a DOC source and a corresponding reduction in light resulted in a net heterotrophic food web (Berglund et al. 2007; Dahlgren et al. 2011).

19.4 Potential Future System-Level Responses to Climate Change

19.4.1 Pelagic Dynamics

Biogeochemical models project an increase in freshwater discharge and associated nutrient loads (e.g. Meier et al. 2011). Consequently a 5% increase in total phytoplankton biomass in the Baltic Sea has been projected by one ecosystem model (Neumann 2010). Models suggest that freshwater discharge may increase more in the forested northern catchments, where run-off concentrations of nutrients are low, and may decrease from the agriculture-dominated and nutrient-rich southern rivers (HELCOM 2007). This would suggest that climate change enhances primary production in the northern basin (Gulf of Bothnia) but may alleviate eutrophication in the more southern basins. However, the modelling results of Meier et al. (2012) suggest a larger increase in spring phytoplankton biomass (in ‘business-as-usual’ and ‘reference’ nutrient load scenarios) in the Gulf of Finland and Baltic Proper than in the Gulf of Bothnia.

As explained in the previous section, the Gulf of Bothnia is less prone to discharge driven eutrophication because of the characteristic dynamics of DOC. Future primary production does not depend only on the climate-induced increase in external nutrient loading, but also on the nutrient ratios of the discharge in each catchment, as well as on the internal biogeochemical processes and feedbacks (e.g. internal loading from anoxic sediments) in each basin.

The environmental factor that will change most due to climate change is probably sea surface temperature. Higher surface-water temperatures will favour taxa thriving in warmer stratified water, such as the cyanobacterium Nodularia spumigena (Kononen and Nömm 1992), and prolonged cyanobacterial blooms have been projected (Neumann 2010). Such a shift could change the main productive period from spring to summer.

Changes in zooplankton communities are also expected. Viitasalo et al. (1995) and Suikkanen et al. (2013) suggested that an increase in water temperature will favour the smaller sized ‘surface zooplankton community’, especially rotifers and small cladocerans.

Climate change may also influence zooplankton by affecting the quality of their food. In a mesocosm study simulating effects of climate change, increasing temperature negatively affected food quality, since heterotrophic production increased and zooplankton fed more on items deficient in important fatty acids (Dahlgren et al. 2011). The increase in cyanobacteria may decrease food quality for zooplankton, because cyanobacteria are low-quality food for zooplankton (Karjalainen et al. 2007 and references...
therein). On the other hand, mesocosm studies have shown that copepods can feed and reproduce in a decaying cyanobacteria bloom, apparently by feeding on ciliates and other organisms of the microbial loop thriving in such conditions (Engström-Öst et al. 2002; Koski et al. 2002). The net outcome for zooplankton production in the field is difficult to predict.

In mesocosm experiments simulating climate change effects on light conditions, temperature and grazing pressure on phytoplankton dynamics, a reduced phytoplankton biomass and cell size was observed, partly due to increased activity of overwintering zooplankton (Lewandowska and Sommer 2010; Sommer and Lewandowska 2011). Climate-induced changes in the zooplankton community may thus indirectly shape the future phytoplankton community composition by changing the type of phytoplankton species consumed.

Furthermore, as cyanobacteria are considered poor food for benthic invertebrates (Karlson et al. 2008), an increase in cyanobacteria and changes in the timing and species composition of the spring bloom may influence the quality of the sinking organic matter (Spilling and Lindström 2008) and thus affect the supply of good quality food for the benthic communities.

19.4.2 Benthic Dynamics

The projected decrease in salinity would have a major effect on benthic species distributions. A retreat of marine species from the north towards the south can be expected (Bleich et al. 2011), whereas non-indigenous species with tolerance from the north towards the south can be expected (Bleich et al. 2011). Climate-induced changes in the zooplankton community may thus indirectly shape the future phytoplankton community composition by changing the type of phytoplankton species consumed.

On the other hand, if climate change imposes multiple new stresses on a species, its tolerance limits might be surpassed. For example, shoot densities of eelgrass (Zostera marina) decreased when experimentally subjected to simulated summer heat waves (Ehlers et al. 2008), and if salinity also decreased, this marine species would probably disappear from the margins of its distribution area.

Increased temperature may have important indirect effects in the littoral zone by enhancing the growth of micro- and macroepiphytes on Fucus (Wahl et al. 2010). Grazing by isopods may also intensify during warm summers, because the levels of defence chemicals in macroalgae decrease in high temperatures (Weinberger et al. 2011).

If surface-water salinity declines due to climate change, the geographical distribution limits of all salinity-dependent species will change accordingly. In the littoral environment, this may affect key marine species like fucoids and eelgasses. The distribution limit of the eelgrass Z. marina approximately follows the surface 5 isohaline and will therefore probably disappear from areas with lower future salinity, such as the Gulf of Finland. Salinity decline is also expected to shift the northern distribution limits of the Mytilus community further south (Wikström and Kautsky 2007) and the growth rate also declines with lower salinity (Westerbom et al. 2002). Decline of the mussel beds may affect the associated flora and fauna and may also have an indirect effect on the coastal phytoplankton community, because Mytilus can filter a large fraction of the phytoplankton in the water over the mussel beds (Kautsky 1981; Norén et al. 1999).

Ocean acidification is projected to have severe implications for calcifying organisms such as bivalves and corals (Green et al. 2004; Orr et al. 2005). In addition to calcification, key physiological processes, such as growth, metabolism, reproduction and, hence, diversity and functioning of the benthic communities, could be affected (Widdicombe and Spicer 2008; Widdicombe et al. 2009). Reports from the Swedish Environmental Protection Agency (Naturvårdsverket 2008) and Perttilä (2012) suggest that acidification of the Baltic Sea proceeds at least at the same rate as in the ocean. Between 1993 and 2007, the Baltic Sea declined by 0.06–0.44 pH units, with the greatest changes in the Bothnian Sea and southern Baltic Proper, while globally there has been an estimated decrease of 0.1 pH units since 1750 (Naturvårdsverket 2008 and references therein).

If benthic species are adversely affected by acidification in the Baltic Sea, this would also affect the recovery potential of communities after catastrophic events. This is of concern in the Baltic Sea, where the benthic communities are frequently disturbed by eutrophication-induced hypoxia and anoxia. For further information about acidification of the Baltic Sea and potential impacts, see also Chap. 18 and Havenhand (2012).
19.4.3 Sea-Ice Dynamics

A major feature defining wintertime ecology of the Baltic Sea is the recurring formation and melt of the seasonal sea ice (Chap. 8). The sea ice contains a semi-enclosed brine channel system, comprising small pockets and elongated vertical channels, which is the primary habitat for sea-ice biota such as pennate diatoms, dinoflagellates, flagellated protists, heterotrophic flagellates and ciliates, as well as bacteria (Kaartokallio 2004; Granskog et al. 2006, 2010; Kuparinen et al. 2007).

Both the maximum extent and duration of sea ice in the Baltic Sea are projected to decrease due to climate change (Vihma and Haapala 2009; see also Chap. 8) and consequences for Baltic Sea sea-ice ecosystems are anticipated. The main changes expected are linked to direct habitat loss for ice-dwelling or ice dependent organisms; changes in seasonality (e.g. through light-field changes in spring, or increased wintertime mixing); changes in ice-modulated land-ocean interactions, such as spreading of river water plumes; and changes in nutrient deposition onto and incorporation into the growing ice sheet as well as their release into the water column upon ice melt.

Changes in food web structure and function are also possible. Under-ice phytoplankton blooms, formed by dinoflagellates or haptophytes (Chrysochromulina birgeri) (Larsen et al. 1995; Spilling 2007), contribute to the onset of the phytoplankton spring bloom after ice break-up (Spilling 2007). Thus, changes in sea-ice dynamics could alter the seasonal phytoplankton succession, and hence, also other ecosystem compartments. In polar environments, sea-ice dynamics influence the quality, quantity and timing of the input of organic matter to the benthos (e.g. Norkko et al. 2007; Renaud et al. 2007). These mechanisms and their potential importance to benthos appear completely unexplored in the Baltic Sea.

Reduced ice cover would alter water mixing conditions during winter. Also, because sea ice allows river water plumes to spread long distances underneath the ice, a lack of sea ice could cause the substances carried by rivers to mix into the water column closer to the river mouths. Furthermore, the seasonal sea-ice cover accumulates atmospheric deposition during winter and acts as a significant source of these substances in spring upon ice melt (Granskog and Kaartokallio 2004; Granskog et al. 2006). Sea-ice organisms can also utilise and accumulate inorganic nutrients from under-ice water and thus influence land-ocean transport pathways (Granskog et al. 2005, 2006; Kaartokallio et al. 2007). Such processes would be altered if the ice cover shortens seasonally or disappears altogether.

While there is evidence that the thickness and duration of ice cover influence phytoplankton communities (Kononen and Niemi 1984; Klais et al. 2013), there are to date very few studies attempting to model the effects of climate change on the Baltic sea-ice ecosystem. A sea-ice biogeochemical model (Tedesco et al. 2010, 2012) projected no change in the timing of the spring phytoplankton bloom with nearly ice-free conditions compared to full ice cover, but did project changes in bloom magnitude and phytoplankton community composition.

19.4.4 Regime Shifts and Cascading Effects

Several regime shifts have been identified in the central Baltic Sea during the past three decades, with the most pronounced during the late 1980s to early 1990s (Möllmann et al. 2008, 2009).

It seems clear that cod stocks are influenced by climate, that cod stocks can influence clupeids (herring and sprat) and that clupeids can influence copepod populations in the different basins of the Baltic Sea. At least in late summer and autumn, predation pressure by clupeids and mysids has been calculated to surpass the zooplankton production (Hansson et al. 1990; Rudstam et al. 1992). The effects of cod stocks diminishing may even cascade through planktivores and zooplankton to coastal fish, because in some areas, the open-sea predation by zooplanktivores may also affect the coastal zooplankton (Ljunggren et al. 2010).

Furthermore, it has been suggested that a low summer biomass of zooplankton may increase the probability of cyanobacterial blooms in the Baltic Sea (Casini et al. 2009) and that return of the cod could improve the status of the Baltic Sea through the cod–sprat–copepod–phytoplankton cascade. The key question is whether grazing by zooplankton can control the different phytoplankton and cyanobacteria groups.

In the Baltic Sea, there are several factors that decouple copepods from phytoplankton (see Kierboe 1998). First, the pelagic ecosystem of the Baltic Sea is not based on a simple grazing chain: production is largely based on organisms of the microbial loop (Kuosa and Kivi 1989; Kivi et al. 1993; Sandberg et al. 2004) and many dominant copepods are omnivores that switch opportunistically between phytoplankton and protozoan food (Kierboe et al. 1996). This alleviates both grazing and predation pressure by copepods and reduces the possibility of zooplankton cropping down either group. Second, several studies suggest that in spring, there is a temporal mismatch between phytoplankton and zooplankton and that this mismatch will increase due to climate change (Winder and Schindler 2004; Sommer et al. 2007; Daufresne et al. 2009). Third, in summer a large component of the primary production is produced by toxic filamentous cyanobacteria, which are not preferred food by copepods (e.g. Engström et al. 2000).

Such considerations make it unlikely that the effects of a potential increase in cod stocks would cascade down to
phytoplankton or especially cyanobacteria biomass. This also makes sense because top-down forces are considered most important for the higher trophic levels (piscivores and planktivores), whereas for zooplankton and especially the primary producers, bottom-up forces (light and nutrient availability) are relatively more important (McQueen et al. 1989). Interestingly, Stige et al. (2009) showed in the southwestern Barents Sea that the climatic forcing of zooplankton was stronger when the density of planktivorous fish was low. Whether this is also the case in the Baltic Sea remains to be studied.

It is notable that ecosystem regime shifts took place in both the Baltic Sea and North Sea at approximately the same time (1982–1988) (Beaugrand 2004). This suggests that regime shifts may be induced and driven by large-scale atmospheric variation. At present, there is no evidence that the regime shifts have been caused by the quasi-linear anthropogenic climate change. Rather, the regime shifts in the North Sea have been linked to natural atmospheric variability, such as the NAO (Beaugrand 2004 and references therein). Therefore, Hänninen et al. (2000) suggested that zooplankton and cod stocks, as well as growth rate of herring can be predicted from climatic variation in the North Atlantic (i.e. the NAO).

If the consequences of anthropogenic climate change alter the basic oceanography and biogeochemistry of the Baltic Sea, as suggested by the modelling results of Neumann (2010), Meier et al. (2011, 2012), system-level changes may be expected that can be associated to climate change per se. 19.4.5 Food Web Efficiency

The projected increase in nutrient discharge has been projected to enhance phytoplankton biomass in the Baltic Sea (e.g. Neumann 2010; Meier et al. 2012). In principle, this should also lead to an enhanced secondary production. The consequences of climate change on the productivity and interactions between the trophic levels are, however, difficult to project. As noted in the Gulf of Bothnia (Müren et al. 2005; Wikner and Andersson 2012) and Kiel Fjord (Hoppe et al. 2008), elevated sea surface temperature and increased freshwater and DOC discharge can make the pelagic community net heterotrophic (Fig. 19.4). Similar responses have been reported from the Hudson River estuary, USA (Howarth et al. 2000), and a subtropical estuary in Brazil (Barrera-Alba et al. 2009). Despite the higher resource (nutrient) availability, an increase in heterotrophy can be hypothesised to result in a lower fish production, because a larger proportion of the energy is consumed in the longer food chain of the microbial loop.

The results of Baltic Sea studies are ambiguous. Dahlgren et al. (2011) reported increased food web efficiency due to temperature increase in a mesocosm experiment. Also, results from mesocosms with water from the Gulf of Bothnia (Lefèbure 2012) do not give a clear result. Fish production increased when a pelagic food web including three-spined stickleback (Gasterosteus aculeatus) was subject to realistic climate-induced rises in temperature and DOC. This was explained by higher zooplankton production in warmer conditions.

**Fig. 19.4** Tentative model of food web effects resulting from increased river discharge and higher temperature. Boxes show biomass and arrows show flow of material. Bright colours indicate higher biomass or light irradiance, and fat arrows show higher flow of material. Red star indicates competition of inorganic nutrients between bacterioplankton and phytoplankton. Redrawn from Wikner and Andersson (2012)
water, sustained by an increased production of microzooplankton. Although the number of trophic linkages increased with increasing DOC in the water, the positive effects of increased zooplankton production overrode the negative effects of decreasing food web efficiency (Lefèbure 2012).

19.4.6 Biodiversity

One of the main consequences of global warming in terrestrial and marine ecosystems is a poleward shift in the distribution limits of both southern and Arctic-boreal species. It has been suggested that more species may move in from lower latitudes than will be lost, resulting in a net increase in the species diversity of northern seas (Hiddink and Coleby 2012). However, in poorly connected areas, such as a narrow strait, colonisation by warm-water organisms may slow or be prevented (Jackson and Sax 2010). For the Baltic Sea, the geographical restriction and strong salinity gradient in the Danish Straits could slow dispersion of warm-water species into the Baltic Sea. It has also been suggested that salinity decline could decrease the diversity of the marine community component. What then is the likely net outcome of climate change on Baltic Sea biodiversity?

Hiddink and Coleby (2012) compared trends in fish species richness outside and inside the Danish Straits (i.e. in the Kattegat and southern Baltic Sea), during a warming period in 2001–2008. They expected the warming to result in a greater increase in fish diversity in the better connected Kattegat than in the more isolated southern Baltic Sea. Unexpectedly, fish species richness increased in both the Kattegat and the Baltic Proper, but the effect was probably more connected with salinity change than increasing temperature.

While Remane’s (1934) *arteminiunm* concept (minimum β-diversity at a salinity of 5–8) partly explains why bentthic and fish diversity decreases with a decrease in salinity, the effects of salinity changes on planktonic diversity are less clear. Telesh et al. (2011a, b) challenged Remane’s concept by suggesting that protistan diversity does not decline but peaks at intermediate salinities of the *horohalinicum*. This idea was in turn questioned by Ptacnik et al. (2011), who claimed that Telesh et al. (2011a) derived their diversity patterns largely from coastal bays and lagoons, which are not representative for the Baltic Sea as a whole. The effects of climate-induced salinity shifts on plankton diversity thus remain a matter of debate.

Increasing sea surface temperature and decreasing salinity would make the Baltic Sea a more suitable habitat for species originating from warmer areas with lower salinity. Thus, more non-indigenous species could be expected. The role of non-indigenous species in the Baltic Sea is, however, contentious. Although non-indigenous species are often seen as one of the major threats to marine biodiversity (Costello et al. 2010), the ‘indigenous’ species in the Baltic Sea are of mixed origin and have all invaded since the last glaciation. While the rate at which non-indigenous species have established has increased due to human vectors, it is partly a natural process of post-glacial succession in the Baltic Sea (Bonsdorff 2006) that may be enhanced by climate change.

In addition to species diversity, genetic diversity may also be affected by climate-induced changes in environmental parameters. At the entrance to the Baltic Sea, a steep cline in intra-population genetic diversity has been documented for several marine taxa (Johannesson and André 2006). For instance, diatoms show lower genetic diversity in the Baltic Proper than in the Skagerrak and Kattegat (Härmström et al. 2011) and the brown alga *F. vesiculosus* as well as most marine red algae mainly reproduce asexually in the northern Baltic Sea. In extreme cases, such as the eelgrass *Z. marina*, whole meadows may consist of a few clones only (Reusch et al. 2005; Ehlers et al. 2008); along the Swedish coast of the Bothnian Sea, much of the population of *F. radicans* is a single female clone (Johannesson et al. 2011).

To sum up, the main climate-related threats to Baltic Sea biodiversity include changes in water temperature, salinity and perhaps acidification. In communities with naturally high biodiversity, the large number of species with different functional roles performs a stabilising role and provides resilience against perturbations, while in species-poor communities, genetic diversity is particularly important as a source of variability in functional traits. Low genetic diversity may therefore make the Baltic Sea species vulnerable to external pressures, including climate change.

19.5 Modelling Climate Change—What Can Be Learnt from Simulating Future Ecosystems?

Potential effects of future climate change on species, food webs and ecosystems in the Baltic Sea have been investigated with a range of model types, from conceptual models (MacKenzie et al. 2007), single species population dynamic models (MacKenzie et al. 2011), multispecies models (Heikinheimo 2011), models of simple (Lindegren et al. 2009, 2010b) or complex food webs (Österblom et al. 2007), to coupled physical-biogeochemical models (Meier et al. 2011, 2012). Most studies focussed on the offshore central Baltic Sea (Österblom et al. 2007; Lindegren et al. 2009; Heikinheimo 2011; MacKenzie et al. 2007, 2011; Meier et al. 2011). One reason for this may be that the available physical-biogeochemical models do not seem to work as well in the Bothnian Sea and Bothnian Bay as in the central Baltic Sea (Eilola et al. 2011).
The diversity of ecological models raises the question as to which models are best suited for analysing ecological effects of climate change. Most earlier modelling studies investigated the direct responses of single (often exploited) marine species to climate change, or to general environmental variation (Kuikka et al. 1999; Rahikainen et al. 2003). However, species responses to climate change depend on the interplay between ecological interactions and climate variation, because climate affects species both directly and via their interactions with other species.

Which food web setting should be used for studying climate effects on a particular species? Climate effects on a given species may depend on interactions between species because of the feedbacks these create (Stenseth et al. 2002). Therefore, food web models that consider feedbacks between species, for example by incorporating both predation effects on prey and the energy gained by the predators (Heikinheimo 2011; MacKenzie et al. 2011), probably give more realistic results than models that do not include such feedbacks (Österblom et al. 2007; Lindegren et al. 2009).

Furthermore, it is not known how increasing the complexity of the food webs would affect the simulated responses to climate change. Comparative studies of ecological responses to climate change from models of different complexity, which have been subject to the same forcing scenarios (‘ensemble modelling’), are needed (see Stock et al. 2011). Studies of the responses of species or food webs in the Baltic Sea to climate change rely on models dealing with populations or even species groups (Österblom et al. 2007; Lindegren et al. 2009; Heikinheimo 2011; MacKenzie et al. 2011; Meier et al. 2011), although some ecological processes (especially in the upper trophic levels of the food web) occur between individuals. Similarly, climate forcing on the model species or food webs has often been based on observed correlations of climate and, for example, recruitment of species (Lindegren et al. 2009; Heikinheimo 2011; MacKenzie et al. 2011) rather than on actual mechanisms.

In addition to ecological–climate interactions, marine food web processes are also linked to geochemical cycles through, for example, nitrogen fixation by cyanobacteria and nutrient release during decomposition of organisms. Simulated ecological responses to climate change may again be different if these processes are accounted for, as is done in coupled physical-biogeochemical models (Meier et al. 2011, 2012).

At present, it is not possible to compare the results of biogeochemical models and food web models, because the biogeochemical models developed for the Baltic Sea do not account for the dynamics of trophic levels above phytoplankton (Meier et al. 2011) and the latter rarely extend below zooplankton (Lindegren et al. 2009). To meet this need, so-called end-to-end models have been developed for other marine systems (Fulton and Smith 2004). These are highly detailed biogeochemical ecosystem models that couple physical, biological, social, economic, and management modules. Although it is unclear how underlying climate variation propagates through the coupled modules, inclusion of such models may prove useful in comparative model studies of climate change impacts on marine food webs. The way forward includes scenario analyses with sets of ecological models of varying complexity as well as extending modelling approaches beyond the central Baltic Sea.

Fig. 19.5 A schematic representation of the ecosystem consequences of increasing freshwater discharge into the Baltic Proper and the Gulf of Bothnia

Baltic Proper
More freshwater discharge into the sea
More nutrient input from land
More phytoplankton and Cyanobacteria
More sedimentation
More anoxic sediments
More phosphorus release from sediments

More freshwater discharge
→ more phytoplankton

Gulf of Bothnia
More freshwater discharge into the sea
More DOC from land
More turbidity
More bacteria growth
Less light in water
More competition for nutrients between bacteria and phytoplankton
Lower phytoplankton production

More freshwater discharge
→ less phytoplankton
19.6 Conclusion

Over the past few years, significant steps have been taken in understanding the consequences of climate change on the Baltic Sea ecosystem. Advances have been made in, for example, studies on how climatic variation contributes to regime shifts and cascading trophic effects. Most of the conclusions to date are also based on observations from the open-sea system of the central Baltic Sea, and less is known about regime shifts in coastal and northern systems. Projects the occurrence and pattern of such system-level shifts in the whole Baltic Sea thus remains a challenge.

Increase in sea surface temperature has been suggested to change seasonal succession and induce dominance shifts in primary producers in spring. Shifts in dominant species may affect the biogeochemistry and functioning of the pelagic ecosystem in the following summer (Sommer and Lengström 2008; Spilling and Lindström 2008). As increasing temperature and stratification also favour cyanobacteria, rotifers and small cladocerans, the plankton community is projected to shift towards smaller sized organisms.

Mesocosm studies also suggest that climate change may influence the seasonal succession of phytoplankton and zooplankton, potentially increasing the temporal mismatch between these groups in spring. Such changes may have negative consequences on zooplankton production and thus food conditions of planktivorous fish. A climate-induced decrease in salinity together with poor oxygen conditions in the deep basins would negatively influence the main Baltic Sea piscivore, cod. Several studies have confirmed that this causes cascading effects on clupeids and zooplankton. It is less clear whether the effects cascade from zooplankton to phytoplankton.

Reduced duration and spatial extent of sea ice would cause habitat loss for ice-dwelling organisms, affect the ice-modulated land–ocean interactions and probably induce changes in nutrient dynamics within and under the sea ice. There are, however, no estimates of the effects of declining sea ice on the overall productivity and pelagic-benthic coupling of the Baltic Sea ecosystem.

Modelling efforts suggest that climate change could worsen eutrophication by increasing freshwater discharge and thereby nutrient loads from land. An increase in sea surface temperature would probably also favour cyanobacteria that bind nitrogen from the atmosphere and increase the supply of nitrogen to the nitrogen-limited phytoplankton. Summer primary production and sedimentation would then increase, worsening oxygen conditions and inducing the release of phosphorus from sediments. On the other hand, increasing the supply of freshwater and associated DOC may also reduce phytoplankton productivity, at least in the Gulf of Bothnia (Fig. 19.5). Thus, it is clear that the effects of climate change on the productivity of the marine ecosystem vary from basin to basin.

Some of the most profound effects of the projected salinity decline involve losses in functional diversity that would accompany the loss of marine elements in the fauna. Also, the potential increase in primary production and sedimentation of organic matter in the northern Baltic Proper, as well the climate-driven decrease in trophic efficiency, as suggested for the Gulf of Bothnia, are potentially important factors for benthic communities.

Human-induced pressures, such as overfishing and eutrophication, may erode the resilience of the Baltic Sea ecosystem, thereby making it more vulnerable to climatic variations. The Baltic Sea communities, that are poor in both species and genetic diversity, may therefore be particularly vulnerable to external forcing factors caused by the climate change.

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