5.2.5 Marine Ecosystem

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Contents

5.2.5.1 Classification of climatic effects

(Viitasalo)

The structure and functioning of the ecosystem of the Baltic Sea is influenced by various external forcing factors, natural and anthropogenic. Many of the Baltic Sea species are in various ways affected by water salinity, temperature and stratification, which in turn are affected by climatic factors, such as precipitation and wind directions. It is therefore plausible that the ecosystem has shown fluctuations that can be connected with climatic variations.

The complexity of the interactions and feedbacks between climate and the responses of the ecosystem make it difficult to distinguish the anthropogenic effects (such as eutrophication) from those caused by climatic variations. This distinction is important to make when one wants to design measures to improve the state of the marine environment, as in HELCOM Baltic Sea Action Plan and the Marine Strategy Framework Directive of EU. Therefore the causal relationships between variations in environmental parameters affected by climate and the responses in individuals, communities and ecosystems need to be identified.

Climate change will affect species ranges, biodiversity and ecosystem functioning. The effects radiate to changes in (1) *species ecology* (climatic niche requirements, dispersal capacities), (2) *species interactions* (including changes in competition, facilitation and trophic relationships), and (3) *species evolution* (involving contemporary micro-evolution and macro-evolutionary trends).The responses will together define the realized niches of species in a world affected by changing climate (Lavergne et al. 2010).

We may divide the climate effects to those that (*i*) directly affect species through physiology and biochemistry of individuals, (*ii*) indirectly affect the productivity of populations, e.g. via changes in physics and chemistry of water and sediments, and (*iii*) indirectly affect the structure of communities through interspecific interactions.

Changes in physical and chemical characteristics of water directly affect the *metabolism and biochemistry* of organisms. They affect the *production capacity* of individuals and hence influence the *population size*. First, temperature is a fundamental driver of biological processes which affects metabolic rates and ultimately underpins life-history traits, population growth and ecosystem processes. E.g. the metabolism and productivity of heterotrophic bacteria in the Baltic Sea are directly affected by temperature (Autio 1998); the uptake of harmful substances increases with temperature (Dippner et al., and references therein); the development of invertebrate (REF.) and fish larvae (Karås and Neuman 1981, Hakala et al. 2003) speeds up at high temperatures. Too high water temperature can also be harmful to certain cold water taxa, such as the

glacial relicts. In the benthic system, temperature affects the food supply, respiration and growth of populations, as well as the recruitment dynamics of species (O'Connor et al. 2007, Hoegh-Guldberg & Bruno 2010). Increased temperatures may result in mismatches between developing larvae and availability of food, and may reduce larval dispersal and thus limit connectivity and between populations (O'Connor et al. 2007). Second, as most of the Baltic Sea species have either marine or freshwater origins, a decline in salinity induces osmotic stress in marine species and benefits freshwater species. Other direct salinity effects include increased uptake of metals at reduced salinities (Lee et al. 1998).

In addition to direct effects on the metabolism, growth and reproduction of organisms, climate also induces various *indirect effects* that influence species and populations via their effects on hydrographical or biogeochemical processes. Changes in population sizes then affect the intensity and type of *intra- and interspecific interactions*, such as grazing, predation and competition, which shape the *composition and functioning of communities*.

5.2.5.2 System-level variations in the past

(Blenckner)

During the last century several system-level changes took place due to climate related factors, eutrophication, fishing and hunting. The important predatory fish, cod, increased in abundance during the 1920s, probably due to good spawning conditions, i.e. high oxygen and salinity levels in the deep basins (Thurow 1999), and low predation pressure by seals (due to seal hunting activities; Österblom et al. 2007). After the Second World War an increase in the nutrient load from the surrounding countries caused the eutrophication of the Baltic Sea (Larsson et al. 1985), which caused an increase in primary production (Stigebrandt 1991). This resulted in increased sedimentation and increased deep water oxygen consumption. As a long 'stagnation period' without inflows of salinity-rich water from the North Sea prevailed, large hypoxic bottom areas were observed (Fonselius and Valderrama 2003).

Due to the hypoxia, the bottom fauna below the halocline was eliminated, causing a major disruption of the benthic food web (Elmgren 1989, Norkko et al. 2010). The decrease in benthic conditions also induced a major switch in the diet of demersal fishes, especially cod. While in the early twentieth century, benthic organisms were the main food of cod, these were in the second half of the century replaced by fish, mainly sprat and herring (Eero et al. 2011). A major reorganization of the ecosystem took place, from a more benthos driven food-web to a more pelagial-driven food-web.

Another example of climate induced system level variations is the change of geographical limits of salinity-

dependent species. During the 'oceanization' of the Baltic Sea, that took place in 1936-1954, various pelagic taxa such as marine copepods, jellyfish *Cyanea capillata*, barnacle *Balanus improvisus*, as well as cod, garfish and mackerel spread hundreds of kilometres northwards, while species preferring low saline waters retreated (Segerstråle 1969).

The above examples illustrate the sensitivity of the Baltic Sea ecosystem to climatic variations. Further examples of such processes and other demonstrated and potential effects of climate are given in chapters below.

5.2.5.2.1 Primary producers and the phytoplankton community

(Lindegren, Blenckner & Olli)

Climate change and biogeochemical models project that the increasing run-off and nutrient loads may enhance the total phytoplankton biomass by about 5% in the Baltic Sea (Neumann 2010). Effects on phytoplankton biomass are also expected due to changes in land use, which impact the nutrient flux between the land and the Baltic Sea (REFERENCE). Community changes are expected both in the spring as well as summer.

The Baltic Sea spring bloom is dominated by a few species of diatoms and cold-water dinoflagellates (Kremp et al. 2008). The relative proportion of diatoms and dinoflagellates depends on temperature and ice conditions, with warm winters generally favouring the dominance of dinoflagellates (Klais et al. 2011, Wasmund et al. 2011). The fate of the spring bloom, which dominates the seasonal productivity cycle, is either disintegration in the water column (e.g. dinflagellates), or rapid sinking to the seabed (e.g. diatoms). Hence, climate induced shifts in the spring bloom community composition control the quantity and degradability of sinking organic matter (e.g., Spilling & Lindström 2008).

Several authors have also suggested that, potentially associated with the climate change, the role of dinoflagellates in the Baltic Sea spring bloom has increased over the last decades Sea (Kremp et al. 2008; Olli and Trunov 2010) (Wasmund et al. 2011). Although certainly true for some basins, the overall increase of spring bloom dinoflagellates is not supported by data for the Baltic Sea as a whole. The response of dinoflagellates to large-scale climate patterns is highly basin specific, depending on local hydrography and community composition (Klais et al. 2011).

To understand how climate change can affect phytoplankton communities, it is important to identify the processes influencing the autecology of individual species. For instance, in the northern Baltic Sea the dinoflagellate *Biecheleria baltica* has been expanding in recent decades. This expansion has been linked to

the extraordinarily efficient benthic cyst production of this species (Olli and Trunov 2010). Given the rise of deep water temperatures in the Baltic Sea (Klais et al. 2011), the benthic cyst germination of *B. baltica* may have been enhanced, which has contributed to the dominance of this species in spring (Kremp et al. 2008).

These shifts in the group and species level dominance in spring have consequences on the food web (Sommer 2009), biogeochemistry (Spilling and Lindström 2008), and thereafter to the pelagic diversity and ecosystem functioning during the following summer. Increase of sea surface temperature is predicted to prolong cyanobacterial bloom season in the Baltic Sea, shifting its beginning ahead by about 1 month. The annual nitrogen fixation potential will not change, however (Neumann 2010).

5.2.5.2.2 Zooplankton dynamics

(Lindegren, Blenckner & Olli)

It is well known from oceans that zooplankton respond to variations in climatic parameters (e.g., Beaugrand and Reid 2003, REF.). The response is usually assumed to take place through a bottom-up process: the atmospheric forcing influences the hydrography and stratification of water, which change light and nutrient conditions and hence primary productivity, which in turn affects predominantly herbivorous zooplankton. In the Baltic Sea, the reasons for these changes may however be different, because in the Baltic there is a temporal mismatch between the phytoplankton spring bloom and the zooplankton peak in summer, and most of the summer production in the Baltic Sea is based on recycling within the microbial loop (REF.). Most probably some Baltic zooplankton species respond directly to changes in salinity, some to temperature, some species may be affected by availability of food, and some by predation by planktivorous fish. Thus direct physiological and indirect bottom-up and top-down effects are probably at work at the same time. Some examples of such interactions are given below.

Salinity plays an important role in the Baltic Sea by limiting the spatial distribution of key zooplankton species (Vuorinen et al. 1998, Möllmann et al. 2000). For example, *Pseudocalanus acuspes*, an important food source for cod larvae and planktivorous fish, is a marine species and therefore responds strongly to salinity changes (Möllmann et al 2009). In the Central Baltic Sea, the copepod species *Acartia* spp. and *Temora longicornis* are positively related to the spring temperature (Möllmann et al. 2000) and, in the Gulf of Riga, a strong response to climatic variation (mild winters) was found for zooplankton dynamics (Kotta et al. 2009). Similar results were found for coastal areas (Feike et al. 2007, Hansson et al. 2010), as well as the Archipelago Sea (Dippner et al. 2001). In the Gulf of Finland, rotifers and cladocerans increased with long-term increase in sea surface temperature (Viitasalo et al. 1995, Rönkkönen et al. 2003). This may have been caused by increased growth rates of these rapidly reproducing taxa, and by the increased availability of suitable food in the warmer water. Zooplankton dynamics may also depend on the timing of the spring

phytoplankton bloom and post-bloom food availability (Dutz et al. 2010). Temperature may indirectly affect food quality (through reduced fatty acid content), thereby causing changes in the nutritional value of zooplankton prey for higher trophic levels (Dahlgren et al. 2011).

It is also worth noting that zooplankton also exists in the littoral. In these shallow water ecosystems small-scale environmental variability in various factors, such as nutrient load, significantly modifies the response of communities to large-scale pressures such as climatic variation (Kotta et al. 2009, Põllumäe et al. 2009). Temperature and total phosphorus appear to be the most important regulating factors for shaping the littoral zooplankton communities in the Northern Baltic Sea (Scheinin et al. 2010).

5.2.5.2.3 Open sea benthos

(Norkko)

Benthic communities in the Baltic Sea comprise species with marine, brackishwater and limnic origin (Remane 1934, Bonsdorff 2006). Their distribution and diversity are constrained by the distinctive salinity and oxygen gradients present (Segerstråle 1957, Rumohr et al. 1996, Villnäs & Norkko 2011). Their latitudinal distribution is limited by the gradient of decreasing salinity towards the north: the decreasing salinity reduces macrozoobenthic diversity, affecting both the structure and function of benthic communities (Elmgren, 1989, Ruhmohr et al., 1996, Bonsdorff & Pearson, 1999). In addition, the distribution of benthic communities is driven by strong vertical gradients. Generally, the more species-rich communities in shallow-water habitats (with higher habitat diversity) differ from the sub-halocline communities, which are dominated by only a few species (Andersin et al. 1978).

It is well established that inter-decadal changes in climate and oceanography can affect benthic species distributions and interactions (e.g. Dayton et al. 1992). In the Baltic Sea, climatic variation, that strongly affects the long-term dynamics of temperature, salinity and oxygen conditions in the Baltic Sea, can have a large influence on the deep benthic communities. Already Segerstråle (1965) suggested that changes in benthic communities may be linked to climate variability. Despite this, there are very few published studies that explicitly address climate change effects on macrobenthic communities of the sub-halocline waters of the Baltic.

In the southern and western parts of the Baltic Sea, temporal variations in salinity are common and associated with the magnitude of salt-water inflows (REFERENCE). E.g., the large saltwater inflow in the mid 1950's was accompanied accompanied by significant range expansions of many marine species into the Baltic Proper. The phenomenon was accordingly termed "oceanization" of the Baltic Sea (Segerstråle 19xx;

Leppäkoski 1975). During the past few decades salinity has gradually decreased again, resulting in a shift from a dominance of marine to brackish-water taxa (WHERE?) (Villnäs & Norkko 2011).

In the 1990s, a major change took place in the ecosystem of the Gulf of Finland. It was most probably caused by the major Baltic Sea salinity inflow in 1993. Before the inflow, the shallow Gulf of Finland was well mixed, leading to good oxygen conditions and high benthos abundances. The inflow probably pushed forward saline, oxygen depleted water from the Central Baltic Sea. This water reached the Eastern Gulf of Finland by autumn 1995 - spring 1996, where it sharpened the vertical stratification and reduced deep-water oxygen concentrations (Savchuk 2010 and references therein). This stratification induced hypoxia caused a large decrease in the macrozoobenthos (Laine et al. 2007). Also, spatial studies examining species turnover (beta-diversity), in the transition zone between the North Sea, the Skagerrak and Kattegat, and the Belt Sea (Josefson 2009) and along the salinity gradients of the Baltic Sea (Bleich et al. 2011, Villnäs & Norkko 2011), all demonstrate the key role of salinity for the distribution of macrobenthic animals.

Also, the timing and extent of the sea ice influences the benthic communities through its effect on the pelagic-benthic coupling. Our knowledge from polar environments suggest that sea-ice has a profound influence on primary productivity and benthic secondary production by affecting the quality, quantity and timing of the input of both phytoplankton and ice algae to the benthos (e.g. Dayton & Oliver 1977, Renaud et al. 2007, Norkko et al. 2007). These mechanisms and their potential importance appear completely unexplored in the Baltic Sea.

5.2.5.2.4 Sublittoral ecosystem

(Kautsky)

The shallow communities on hard and soft bottoms in the Baltic Sea are based on a few structurally and functionally important species, such as fucoids, blue mussels, and a few other habitat forming species (Voipio 1981, Wallentinus 1991, Kautsky and Kautsky 2000). Composition and species richness of these communities decline from Kattegat, via the Baltic Proper into the Bothnian Bay and the innermost part of the Gulf of Finland (Nielsen et al. 1995, Ojaveer et al. 2010). Their distribution patterns are set foremost by their ability to adapt to low salinity, in combination with factors such as wave exposure, light and oxygen availability, competition for space and predation. Also, fresh water species inhabiting low salinity waters in coastal bays or in the northern part of the Baltic Sea are stressed by salinity (Kautsky and Kautsky 2000 and refs. therein).

Influence of the climatic variations on marine environment – increase of temperature, decrease of salinity and changes in water level and wind waves are first seen in shallow water. This, together with the marine and

freshwater origins makes the sublittoral environment especially prone to climatic influences. On the other hand, due to the high variability of these environments, littoral organisms are usually also well adapted to extreme variations. They are seasonally and even daily subjected to large variations in temperature, pH and nutrient availability. Therefore climate induced changes in temperature and pH have been suggested to have less impact in structuring coastal marine communities than for some other more stable communities (Thomsen and Melzner, 2010).

Few studies have investigated the possible effects of climatic variations on sublittoral species in the Baltic Sea. In a mesocosm study, the shoot densities of eelgrass (*Zostera marina*) declined when it was subjected to simulated summertime heat waves in a mesocosm study (Ehlers et al. 2008). Also, mild winters may affect macroalgae through their effects on ice cover. Ice scraping affects key algal species in the uppermost part of the algal belt, and mild winters have been shown to result in a denser growth of *Fucus* close to the surface (Kiriiki and Ruskanen 1996) and thereby contribute to a higher production of associated invertebrate fauna (Wikström and Kautsky 2007). In the eastern Baltic Proper, long-term changes in the macrophyte communities during the past 45 years were associated with weather induced large scale changes in salinity and ice conditions (Kovtun et al. 2009).

Changes in river runoff may also influence the reproductive success of macroalgae. E.g. fucoids have a species specific window for reproductive success (Malm et al. 2001, Serrão et al. 1999), and a mismatch in timing may result in a recruitment failure of these habitat forming species and result in cascading effects on their associated flora and fauna.

These examples indicate the importance of multiple environmental factors which may function as additive or synergetic stressors for the sublittoral communities (Wahl et al. 2011). It is also notable that in the Baltic Sea the genetic diversity in macroalgal and seagrass species is reduced compared to their oceanic counterparts (Johannesson and André 2006). E.g. the eelgrass *Zostera marina* rarely flowers and sets seeds in the Baltic Proper and, thus, whole meadows may consist of only few clones (Reusch et al. 2005, Ehlers et al. 2008). *F. vesiculosus* and most marine red algae also mainly reproduce asexually in tyhe northern Baltic Sea, resulting in low genetic variation. An exceptionally highly clonal species is *Fucus radicans* (Tatarenkov et al. 2005): along the Swedish coast of the Bothnian Sea a large part of the population consists of only one female clone (Johannesson et al. 2011). This may make these populations more sensitive to effects of climate change.

Suggested scenario: Map showing the existing and new distribution patterns of structurally and functionally dominating benthic communities at reduced salinity.

5.2.5.2.5 Winter ecosystems

(Kuosa)

STILL MISSING!

5.2.5.2.6 The case of cod, sprat and herring: a regime shift

(Blenckner & Lindegren)

Cod reproduction is dependent on the amount of sufficiently saline oxic water, termed 'reproductive volume' (RV) (MacKenzie et al. 2000). After spawning, cod eggs sink down to a depth level where they have neutral buoyancy, i.e. ca. 11 psu (Wieland et al. 1994). This water exists at a depth of ca. 150 m and is nowadays largely anoxic. The RV is thus a product of hydrographic processes (frequency of inflow events from the North Sea; e.g. Matthäus & Franck 1992) and anthropogenic impact, affecting the oxygen conditions of the Baltic Sea. In addition, retention-dispersal processes, influenced by wind and current conditions during the planktonic (pre-settlement) phase, have shown to impact growth and survival of juvenile cod in the coastal nursery areas (Hinrichsen et al. 2002).

As for sprat and herring, temperature seems the dominant direct factor regulating recruitment (e.g., MacKenzie & Köster 2004; Cardinale et al. 2009). Sprat year classes have been larger during mild winters compared to hard ones, due to better survival of sprat eggs in warmer water (Nissling 2004). Also, bottom-up effects may limit recruitment, through availability of key zooplankton prey during early life-stages (e.g. MacKenzie and Köster 2004; Lindegren et al. 2011).

It has been shown by theory, experiments and field data that a gradual change in external drivers can cause an abrupt, non-linear change in the ecosystem (May 1973, Scheffer et al. 2001, Scheffer and Carpenter 2003, Folke et al. 2004). After the system has crossed a threshold, the ecosystem fluctuates around a new dynamic average: a 'regime shift' has taken place (Scheffer et al. 2001). These shifts may be smooth, abrupt, or discontinuous (Collie et al. 2004). The first two represent reversible transitions between alternative ecosystem states, whereas a discontinuous shift involves feedbacks that prevent the system from switching back to the previous state even if external conditions are restored – a phenomenon called hysteresis (Scheffer et al. 2001).

In several sea areas of the northern hemisphere populations of predatory fish have declined, which has caused large-scale reorganizations of the ecosystems in question (Collie et al. 2004; deYoung et al. 2004;

Drinkwater et al. 2009; Myers). A similar shift occurred during the late 1980s/early 1990s in the central Baltic Sea. This restructuring was probably induced by the additive effects of eutrophication, overfishing and atmospheric forcing. It had the characteristic of a discontinuous regime shift: the collapse of the cod stock resulted in a marked increase in sprat stocks and a decrease in the weight at age of both sprat and herring (Österblom et al. 2007) (Fig. 1). A multivariate time-series analysis indicates that feedback loops were established in the biotic part of the ecosystem, suggesting hysteresis (Casini et al. 2009, Möllmann et al. 2008, 2009).

Lindegren et al. (2010) also demonstrated a regime shift in the Sound (southern Baltic Sea). Here, the regime shift however does not show signs of trophic cascade or hysteresis and may therefore be of the reversible kind. Evidence for this is provided by recent observations on the cod populations in the southern Baltic. In 20xx the cod fishing was strongly regulated and a few years later cod started to return to the southern Baltic Sea. This suggests that, for cod populations of the southern Baltic, overfishing had a major impact, and the population may come back despite suboptimal environmental conditions.

In the Gulf of Finland, an alternative explanation was given to explain the decline of weight-at-age of herring (Rönkkönen et al. 200X): in the 1980s the abundance of larger marine copepods declined due to desalination of the Baltic Sea, to a state where the amount and quality of food was not high enough to support rapid growth of herring (Rönkkönen et al. 2003). This hypothesis is supported by the fact that herring weight-at-age started to decline already before the increase of sprat populations. On the other hand, a time series analysis shows a negative correlation between long-term changes in sprat biomass and herring weight-at-age. Most probably both bottom-up and top-down forces were at work at the same time, albeit at different times and with different strengths at different trophic levels (Flinkman et al. 1998).

The observed changes in the Baltic Sea indicate that local, mainly human-induced pressures, such as overfishing and eutrophication, may erode the resilience of the ecosystem, thereby making it vulnerable to large-scale changes in the climate.
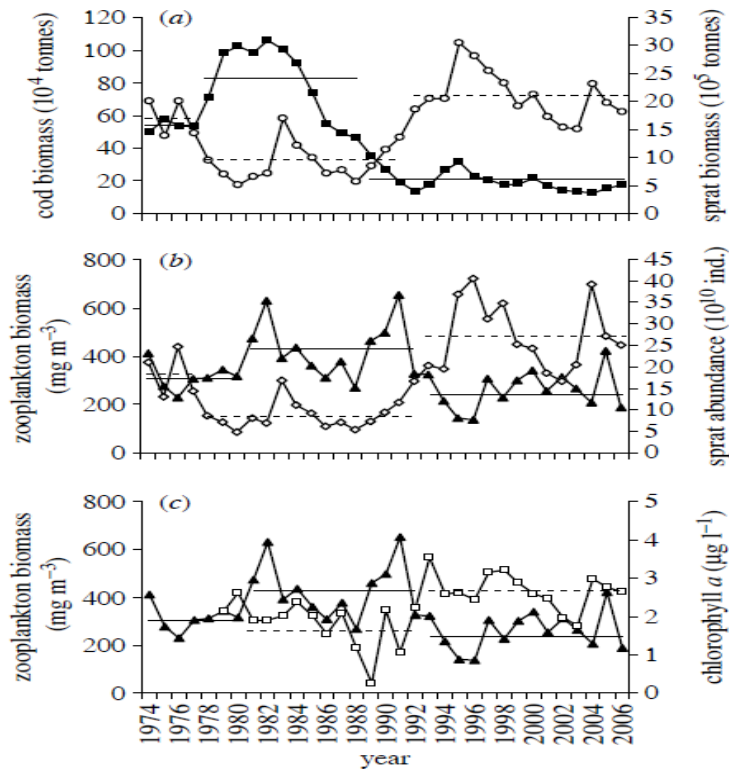
Figure X. Trends of (a) cod biomass (squares) and sprat biomass (circles); (b) sprat abundance (diamonds) and zooplankton biomass (triangles) (ind., individuals); and (c) zooplankton biomass (triangles) and chlorophyll a (squares). (From Casini et al. 2008)

5.2.5.3 Future system-level responses to climate change

5.2.5.3.1 Nutrient and carbon dynamics

Climate change will increase precipitation in the Baltic Sea catchment (REF.), which will result in increased nutrient run-off from land (REF.). The magnitude of this nutrient load increase depends on the land use properties and terrestrial and aquatic nutrient dynamics of each watershed. E.g. the discharges of nitrogen and phosphorus from Finnish rivers to the Baltic Sea have been projected (with a XXXX model) to increase by x and x %, respectively, in xx years. Instead, the annual dynamics of this loading will be completely changed: the main nutrient load will take place in November-March, instead of May (Vehviläinen et al. xxxx). Consequently the seasonal dynamics of primary producers will also change, in a way that is currently difficult to foresee. Some probable scenarios for system-level changes can however be given.

If the spring bloom will decline, a relatively larger fraction of the annual primary production will take place in summer. The summer community, largely consisting of flagellates and cyanobacteria, is more dependent on internal dynamics and recycled nutrients than the spring bloom community (REF.). Higher sea surface temperatures will enhance temperature stratification, which would also favour these communities, especially thermophilic species, such as the cyanobacterium *Nodularia spumigena*. Actually, biomass of cyanobacteria and chlorophytes in summer have been reported to increase (e.g. Suikkanen et al. 2007). This is probably is due to increasing temperature, and associated changes in water stratification and nutrient availability.

Furthermore, the predicted decreasing of surface salinity potentially favors cladocerans with freshwater origins (Viitasalo et al. 1995). The exceptionally P rich cladocerans (Sterner and Elser 2002) will drive the system more towards P limitation, and favour phytoplankton species that are characteristic to limnic systems (cf. Kangro et al. 2007). Freshwater cladocerans also have different feeding mechanisms and food preferences than the more marine zooplankton species, which may influence the composition of the phytoplankton communities. In this way the climate change may have indirect effects on phytoplankton community through selective feeding of the mesozooplankton groups and through different stoichiometric retention and recycling of major nutrients.

The increasing discharge of freshwater and associated DOC may increase bacterial production and decrease primary production and push the system towards net hetrotrophy (see XXX below). The enhanced importance of the microbial food web has many consequences to the dynamics of both pelagic and benthic systems. Increased pelagic consumption and degradation of sedimenting matter in the pelagic zone reduces sedimentation (Sandberg et al. 2004 (Muren et al. 2005); (Maar and Hansen 2011)) and may influence the benthic system (a mesocosm study; (Wiklund et al. 2009).

5.2.5.3.2 Benthic dynamics

(Norkko, Kautsky)

The projected continued decrease in salinity will have a major influence on benthic species distribution. We may expect a geographical shift of the salinity regime and a decrease in marine species richness from the north to the south (Bleich et al. 2011). The amphipod *Pontoporeia femorata* with a minimum salinity tolerance of 6 is an example of a species shift southward from the northern Baltic. However, the interaction between salinity level and development of vertical density stratification will be crucial. Even in areas where surface salinity will decline, bottom-water salinity may approach 9-10, and here oxygen conditions, rather than salinity, limit the distribution of species.

Because oxygen and salinity are such strong drivers for the diversity of benthic communities, they can mask the potentially more subtle effects of climate change, such as temperature and acidification. If the climate change will enhance eutrophication, increased deposition of organic material will increase hypoxia in areas with limited water exchange, further limiting macrobenthos. However, it is possible that the total amount of sedimented material will not increase. A recent model projection up to year 2100 does not predict an increase in the anoxic areas, and the area covered by hypoxic water is actually predicted to decrease (Neumann 2010). Therefore other factors than the quantity of the sedimenting material need to be considered.

However, of critical importance to benthic consumers is food quality (Elmgren 1978; Cederwall & Elmgren 1980). In the Baltic Sea, the spring bloom is considered to be the most important input of high-quality organic matter to the sub-halocline macrobenthic community. The possible decrease of the spring bloom will give relatively more importance to the summer dynamics. It is notable that cyanobacteria are poor food for invertebrates because of their toxin content, low nutritional value, and morphology (Karlson et al. 2008). If the climate change will change the annual dynamics of primary producers, benthic communities may receive less and poorer quality food. *(Norkko)*

As for the shallow water ecosystems, the climate induced salinity decline is expected to move the northern distribution limits of the structurally dominating species such as fucoids, eel grass (*Zostera marina*) and perennial red algae, as well as the *Mytilus* community, further south together with their associated fauna and flora (REF.). This may have an indirect impact on the phytoplankton communities in coastal areas, because blue mussel populations in the Baltic proper are able to annually filter the water total volume of the Baltic Proper (Kautsky 1981, Kautsky and Kautsky 2000). *(Kautsky*

In contrast, the direct impact of temperature and pH may be smaller: the predicted temperature increase, 3–6 ^{o}C, and acidification, 0.5 pH units, (IPCC 2007) are small relative to the natural daily fluctuations in the shallow water habitats. In contrast, indirect effects of temperature increase may be important also in the littoral: temperature increase will enhance the growth of micro- and macroepiphytes on *Fucus* (Wahl et al. 2010) and increase and prolong the effect of the major grazers (such as *Idothea baltica*) during the summer period, because the levels of defense chemicals has been shown to decrease under high temperatures (Weinberger et al. 2011). *(Kautsky)*

Acidification of the oceans and decreasing levels of carbonate ions (CO32-) has been projected to have severe implications for calcifying organisms such as bivalves and corals (Orr et al. 2005). In addition to calcification, key physiological processes, such as growth, metabolic rate, reproduction and activity, are likely to be affected. Acidification may thus affect abundance, diversity and functioning of benthic communities (Widdicombe & Spicer 2008, Widdicombe et al. 2009). Reports from the Swedish Environmental Protection Agency (Naturvårdsverket 2008) and Perttilä (2012) suggest that acidification

proceeds at a slightly faster rate in the Baltic Sea than in the ocean. Very few studies on the subject exist. According to Greeen et al. (2004), calcification of bivalve shells is expected to slow down especially in juvenile stages. If benthic species are adversely affected by acidification, this will also affect the recovery potential of the community. This is especially of concern in the Baltic Sea, where the benthic communities are frequently disturbed by eutrophication-induced hypoxia and anoxia.

5.2.5.3.3 Microbial food web and plankton dynamics

(Wikner)

It has been projected that the timing and magnitude of freshwater discharge into the Baltic Sea will increase. This has been suggested to increase the amount of nutrients entering the Baltic Sea, and hence, speed up eutrophication (e.g. HELCOM XXXX, Neumann 2010). On the other hand, nutrient dynamics vary in different Baltic Sea basins. For instance the Gulf of Bothnia differs from the main basin of the Baltic Sea in its lack of density stratification. This secures oxygenation of the deep water and limits internal loading of phosphorus. This also makes the Gulf of Bothnia more dependent on external loading of nutrients than, e.g. Gulf of Finland, where a large fraction of phosphorus derives from the sediment (REF.). Increasing runoff of river-borne nutrients could therefore be expected to speed up eutrophication in the Gulf of Bothnia. Recent studies have however shown that this may not be the case. In addition to nutrients, the rivers running to the Gulf of Bothnia carry a large load of dissolved organic carbon (DOC). DOC changes the light regime of the area, and serves as a substrate for bacteria which, in this relatively oligotrophic environment, compete for nutrients with phytoplankton (REF.). The river supply of total organic carbon thus provides a synergistic effect by reducing light irradiance to phytoplankton and provides an alternative carbon source for bacterioplankton.

This was demonstrated in a field study where the effect of increased freshwater discharge was investigated during a 13 year period (19xx-xxxx) in the Gulf of Bothnia. A marked increase in the ratio between bacterioplankton production and phytoplankton production was observed, correlating with the discharge of total organic carbon (Wikner and Andersson, submitted). The main cause to the changed trophic balance was a reduced phytoplankton production, despite the increased availability of inorganic nutrients. A similar result was obtained in a 400 L mesocosm study with a natural plankton community, where addition of a dissolved carbon source and a corresponding reduction of light resulted in a net heterotrophic food web (Berglund et al. 2007; Dahlgren et al. 2011). The mechanisms behind this may include reduced light irradiance to phytoplankton, by both higher light extinction and deeper mixed layer. A shortage of the limiting nutrient phosphorus may arise both due to chemical binding to metals like iron and competition with now carbon sufficient bacterioplankton, further enhancing the negative effect on phytoplankton and macroalgal production.

An increase in temperature also promotes a net heterotrophic system, as found in mesocosm studies in the Bothnian Sea (Muren et al. 2005) and the Kiel Fjord (Hoppe et al. 2008). This was shown to be an indirect effect due to increased activity of overwintering zooplankton in mesocosm experiments with water from the Kiel fjord, which resulted in reduced phytoplankton biomass and cell size (Lewandowska and Sommer 2010; Sommer and Lewandowska 2011). Similar results are reported from the Bothnian Sea (Muren et al. 2005). Thus temperature may indirectly contribute to a reduced phytoplankton production.

This effect obviously varies from basin to basin. As for the Bothnian Bay, allochthonous carbon input is as large as the phytoplankton production (model study; Stigebrandt 1991) and 36 % of the carbon in copepods is of terrigenous origin (stable isotope analysis; Rolff and Elmgren 2000), whereas in the Bothnian Sea only 10 % of the carbon is estimated to originate from land. Studies from the Baltic Proper are scarce, but effects of allochthonous carbon on the coastal sea in the Gulf of Gdansk have been reported (Witek et al. 1999).

Taken together, the outcome of the increased temperature and freshwater discharge is a net heterotrophic food web with low transfer efficiency of biomass to fish (Fig. X). A low trophic efficiency can be hypothesized to support a low fish production. Parallel processes have been discovered from a few other sites in the world, such as Hudson River estuary, USA (Howarth et al. 2000).

Interestingly, during the period of low salinity (and high freshwater runoff), several planktivores and predators of the northern Baltic have suffered from growth anomalies. The case of cod, sprat and herring was explained earlier, but also the survival of salmon smolts has decreased (ICES xxxx), and the chicks of sprat-eating guillemots lost weight during almost the same period (Österblom et al. xxxx). Furthermore, the fat layer of female grey seals has started to get thinner in the 1990s (Karlsson & Bäcklin 2009). The ultimate reasons for these phenomena are not known, but it is tempting to speculate that they have been caused by the same factors as the thinning of clupeids, i.e. climate-induced decrease in the availability and/or quality of resources (Viitasalo 2012).
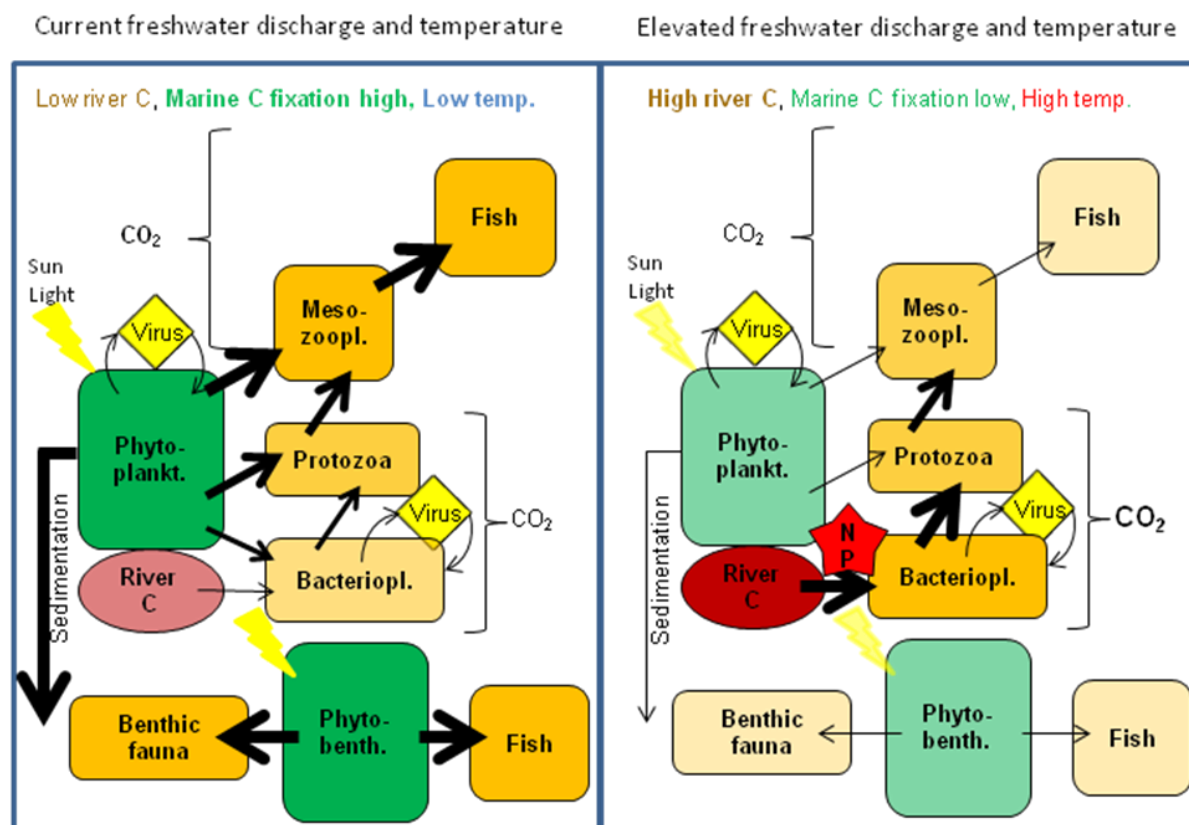
Fig. 1 Tentative model of food web effects by increased river discharge and temperature. Boxes show biomasses and arrows flow of materials. Bright colors indicate higher biomasses or light irradiance, and fat arrows higher flow of materials. Red star indicate competition of inorganic nutrients between bacterio- and phytoplankton.

Table 1. Summary of short-term effects of freshwater discharge and temperature on the microbial food web and phytoplankton as reported in the current literature. Where effects are similar for the climate drivers synergistic consequences for the food web is expected.

Food web component	Higher freshwater discharge	Higher temperature
Phytoplankton	Reduced growth	Lower biomass and size
Bacterioplankton	Maintained growth	Increased growth
Protozooplankton	Maintained growth	Increased growth
Sedimentation	Reduced amount and quality	Reduced amount and quality
Food web efficiency	Reduced efficiency	Increased efficiency

5.2.5.4   Biodiversity in the Baltic Sea – how does the climate change affect it?

(Olli)

One of the main consequences of global climatic warming in both terrestrial and marine ecosystems is the poleward shift of the distribution limits of both southern and arctic-boreal species. A recent study considering fish diversity in the Baltic Sea suggests that, with increasing water temperature, more species could be gained from low latitudes than will be lost poleward, resulting in net increase of species diversity in the Baltic Sea (Hiddink and Coleby 2011). However, the colonization by warm water organisms may lag behind the retreat of cold water species if the newly available habitats are geographically or environmentally poorly connected (Jackson and Sax 2010). Even when the temperature is suitable, the restricted geography and strong salinity gradient at the Kattegat/Danish Straits area may slow down dispersion of warm water species into the Baltic Sea (Hiddink and Coleby 2011).

For species strongly affected by hydrographical parameters, especially salinity and temperature, effects may be more obvious. E.g., fish species richness has increased both in Kattegat and the Baltic Proper after temperature increase (Hiddink and Coleby 2011). Also, the inflow of North Sea water in 1993 contributed to an abrupt salinity driven increase of fish species richness. Species appearing or increasing in the central Baltic were poor cod, *Trisopterus minutus* mackerel, *Scomber scombrus*, anchovy, *Engraulis encrasicolus* and horse mackerel, *Trachurus trachurus*. While this event was obviously reversible, it shows how sensitive the Baltic biodiversity is to the water exchange with the North Sea.

Overall the climate models predict higher precipitation and lower salinity in the Baltic Sea area (Mackenzie et al. 2007), which suggests decreased species richness of fish in the future. This is true for other groups as well, such as the benthic macrofauna. The α-, β-, and γ-diversity of benthic macrofauna decline along the north south salinity gradient in the Baltic Sea (Villnäs and Norkko 2011). The projected salinity decrease will probably decrease benthic invertebrate diversity firstly in the northern Baltic Sea, and a retreat of less tolerant benthic fauna towards the south (Bleich et al. 2011).

The composition and biodiversity of planktonic assemblages in the Baltic Sea are foremost influenced by the physiological constraints imposed by the water salinity. The relationship of planktonic diversity to salinity along the Baltic Sea salinity gradient is a matter of current debate (Ptacnik et al. 2011). A re-analysis of a multi-decadal phytoplankton monitoring data set suggested a phytoplankton diversity - salinity relationship similar to the classical 'Remane curve' (Remane 1934; Bleich et al. 2011), with the 'Arteminimum' (minimum alpha diversity) at slightly higher salinities (8-9 psu) compared to the benthic invertebrates (5-7 psu) (Ptacknik et al. , submitted, Fig. 1). The diversity minimum at 8-9 psu coincided with a sudden transition in

phytoplankton species composition and concomitant high beta-diversity (Ptacknik et al. submitted). With the climate change projected freshening of the surface water (Mackenzie et al. 2007; Neumann 2010), we could expect a gain of fresh-water species number to exceed the loss of marine species, and a net increase in total phytoplankton species richness in large areas of the Baltic Sea with salinity < 8 psu.

In addition to species diversity, genetic diversity may be affected by climate induced changes in environmental parameters. At the entrance to the Baltic a steep cline in intra-population genetic diversity has been documented for several marine multicellular organisms (Johannesson and André 2006). Also micro-organisms from the Skagerrak and Kattegat reveal highly structured and great genetic diversity, whereas the Baltic populations display reduced ditto, irrespective of taxa studied (Godhe and Härnström 2010; Härnström et al. 2011). In species-poor communities, genetic diversity of dominant species may replace the stabilizing and functional role of species diversity as it may represent phenotypic variability, i.e. variability in functional traits such as photosynthetic capacity, growth or nutrient uptake efficiency. The strongly reduced genetic diversity of populations make the Baltic Sea assemblages particularly vulnerable to climate changes due to the reduced 'biodiversity insurance'.
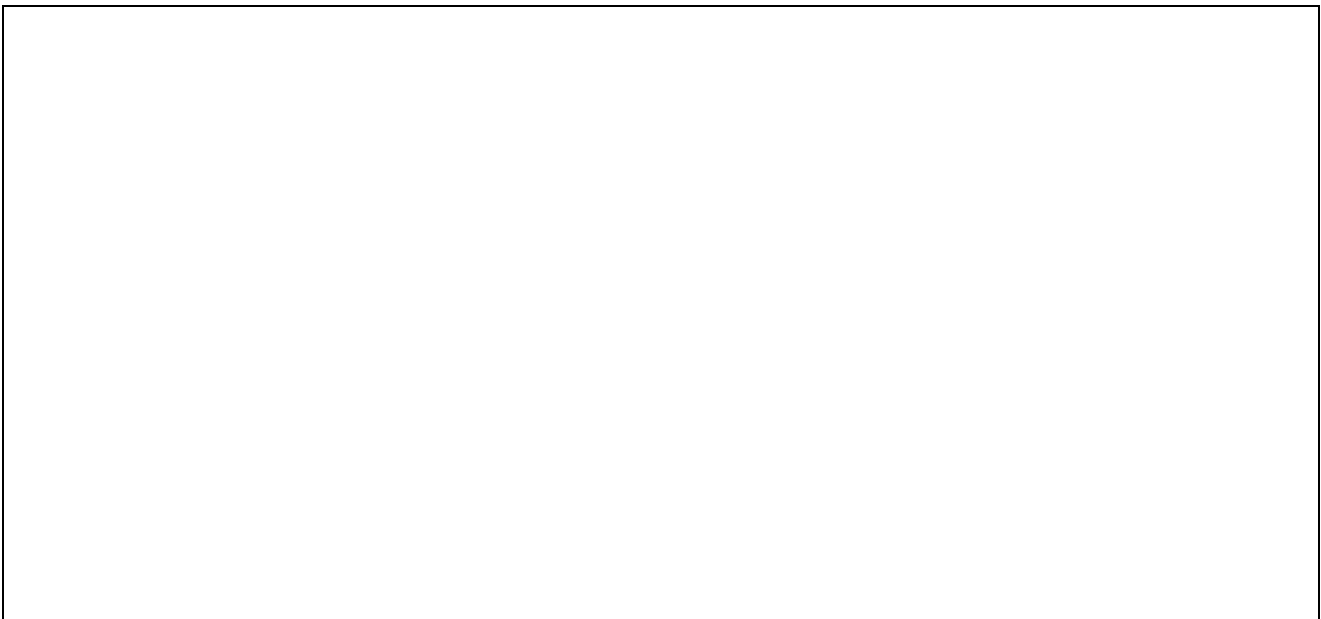

Figure X. Average genus richness of phytoplankton (α -diversity) along the Baltic Sea salinity gradient. The data points are weighted by the sampling effort at each salinity slot. Note the log scale of the salinity axis.

5.2.5.5 Modelling approaches to climate change – what can we learn from simulations of future ecosystems?

(Gårdmark)

Understanding future ecological responses to climate change involves simulation of potential futures in ecological models. Scenario analyses of alternative potential responses (Coreau et al. 2009) can be used to identify key processes influencing the type and variation in responses, as well as form information for management in the face of climate change. 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, including conceptual models (MacKenzie et al. 2007), single species population dynamic models (MacKenzie et al. 2011), multi-species models (Heikinheimo 2011), models of small (Lindegren et al. 2009, 2010) or large food-webs (Österblom et al. 2007), and coupled physical-biogeochemical models (Meier et al. 2011).

Available studies of ecological responses to climate change in the Baltic Sea have focussed on species and the food-web of the offshore central Baltic Sea (Österblom et al. 2007, Lindegren et al. 2009, Heikinheimo 2011, MacKenzie et al., 2007, 2011, Meier et al. 2011). No model studies of climate change impacts have so far been made in other basins, or in coastal areas, of the Baltic Sea. For example, as available physical-biogeochemical models show large biases in the Bothnian Sea and Bothnian Bay (Eilola et al. 2011).

What can be learnt from these diverse model studies? Here we identify key issues for future simulation-based studies of climate change effects on Baltic Sea ecosystems, and discuss how these can be used to further our understanding of ecological responses to climate change.

The diversity of ecological models raises the question which models are suitable for analysing ecological impacts of climate change. The responses of single (often exploited) marine species to climate change, or in general to environmental variation, have often been addressed using single-species models (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 (Stenseth et al. 2002). Thus, future species responses to climate change needs to be addressed in a food-web setting.

Which food-web setting should be used for studying climate effects on a particular species? Climate effects on a species may vary with species interactions (Stenseth et al. 2002) because of the feed-backs these create. Thus, models that include multiple species, but do not account for the feed-backs between them (e.g. by accounting for predation effects on prey, but not the energy gained by the predators; Heikinheimo 2011,

MacKenzie et al. 2011) may result in simulated responses to climate changes that are very different from food-web models that do include such feed-backs (Österblom et al. 2007, Lindegren et al. 2009).

Furthermore, it is not known how increasing complexity of the modelled food-webs affects 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, are needed. Calls for such 'ensemble modelling' of marine ecological models have arisen (Stock et al. 2011), but have not yet been met.

In addition to ecological-climate interactions, marine food-web processes are also interlinked with geochemical cycles through, for example, nitrogen fixation of 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 done in coupled physical-biogeochemical models (Meier et al. 2011). 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 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 et al. 2004, 2007). These are highly detailed biogeochemical ecosystem models, which couple physical, biological, social, economic, and management modules. Although it is unclear how underlying climate variation propagates through the coupled modules (leading to uncertainty in simulated ecological responses), inclusion of such highly complex models may prove useful in comparative model studies of climate change impacts on marine food-webs.

There are further aspects of the ecological models that may affect simulated ecological responses to climate change. For example, available studies of the responses of species or food-webs in the Baltic Sea to climate change rely on models with population level implementations or even at the level of species groups (Österblom et al. 2007, Lindegren et al. 2009, Heikinheimo 2011, MackKenzie et al. 2011, Meier et al. 2011), whereas ecological processes occur between individuals. Similarly, climate forcing on the model species or food-webs has often been based on observed correlations of climate and e.g., recruitment of species, rather than on actual mechanisms (Lindegren et al. 2009, Heikinheimo 2011, MacKenzie et al. 2011). This may prove problematic if simulated forcing scenarios go beyond observed climate conditions – an inherent feature of future predicted climate change.

The way forward, to further our understanding of how climate change affects Baltic Sea ecosystems through simulation modelling, thus includes comparative scenario analyses in sets of ecological models of varying complexity as well as extending modelling approaches beyond the central Baltic Sea.

5.2.5.6 Conclusions

<mark>(NOT STRUCTURED, NOT FINISHED!)</mark>

Recently, the ecosystem approach to management has been mentioned in marine policy documents (Österblom et al. 2010 and references therein). However, behaviour of complex systems and their potential to regime shifts is yet to be incorporated in marine ecosystem-based management (Hughes et al. 2005). An ecosystem approach to management of human actions can therefore only be implemented in the co-evolution between science and policy (Rice 2005). Integrated research assessments and monitoring programmes are required to disentangle multiple drivers and their stochastic interplay. Both *in situ* monitoring of physical and biological variables and phenological observations and field experiments are necessary to understand ecosystem level responses to climate change. This knowledge is necessary to develop effective management and adaptation strategies and to ensure provision of ecosystem services (Beamish et al. 2004, Kraberg et al. 2011). *(Blenckner – Policy)*

The capacity of an ecosystem to persist in the face of change depends on its resilience. Resilient ecosystems are able to absorb external pressures without changing their essential structure and function. If the system is not resilient, even a relatively small change in external drivers can trigger a restructuring of the system.

The Baltic Sea has experienced several climate-induced or climate-affected 'regime shifts' during its recent history. The reversibility of these shifts can be debated. While the Central Baltic Sea regime shift may have characteristics of hysteresis (internal feedbacks prevent returning to the eearlier state), the Sound regime shift shows no signs of trophic cascade or shift in trophic control (i.e., between top-down and bottom-up regulation) (Lindegren et al. 2010a). Given similar external physical forcing, the observed difference between regime shifts within the Baltic Sea are likely due to a different magnitude of anthropogenic influences, e.g., with respect to eutrophication and fishing pressure, which both affect the internal structure and resilience of the ecosystem to climate change (Blenckner et al., in prep).

From a species diversity and secondary productivity perspective, the combined synergistic effects of the climate change are likely to be expressed in different ways in different regions. Importantly, how changes in these major drivers will interact with primary productivity and the subsequent delivery of organic matter to the seafloor will be key in defining the responses of benthic communities. The potential combined and synergistic effects of these drivers and their feedbacks will most certainly remain a significant challenge for understanding climate change effects. *(Norkko – Benthic)*

Throughout history climate variability has affected the higher trophic levels of the Baltic Sea (e.g., Österblom et al. 2007) and future changes in ecosystem structure and functioning in general and community

composition and population dynamics of fish populations in particular (i.e., involving regime shifts and trophic cascades) should be expected in response to future climate change (MacKenzie et al. 2007; Lindegren et al. 2010b). *(Lindegren – Cascading)* Whether the climate change also influences the internal nutrient dynamics, primary productivity and trophic efficiency of the Baltic Sea remains to be seen.

Also, it is still not known whether the magnitude of internal loading of phosphorus from the anoxic bottoms of the Baltic Sea will increase, decrease, or remain the same: the models predicting the density stratification and vertical processes are currently not developed enough.

Some of the most profound effects involve losses in functional diversity that will accompany the loss of marine elements in the fauna. Reductions in functional diversity will likely reduce benthic bioturbation potential with consequences for ecosystem functioning. These aspects are perhaps particularly critical in the Baltic Sea, where functional redundancy is low due to the low overall species and functional diversity (Norkko & Villnäs 2008). *(Norkko – Benthic)*
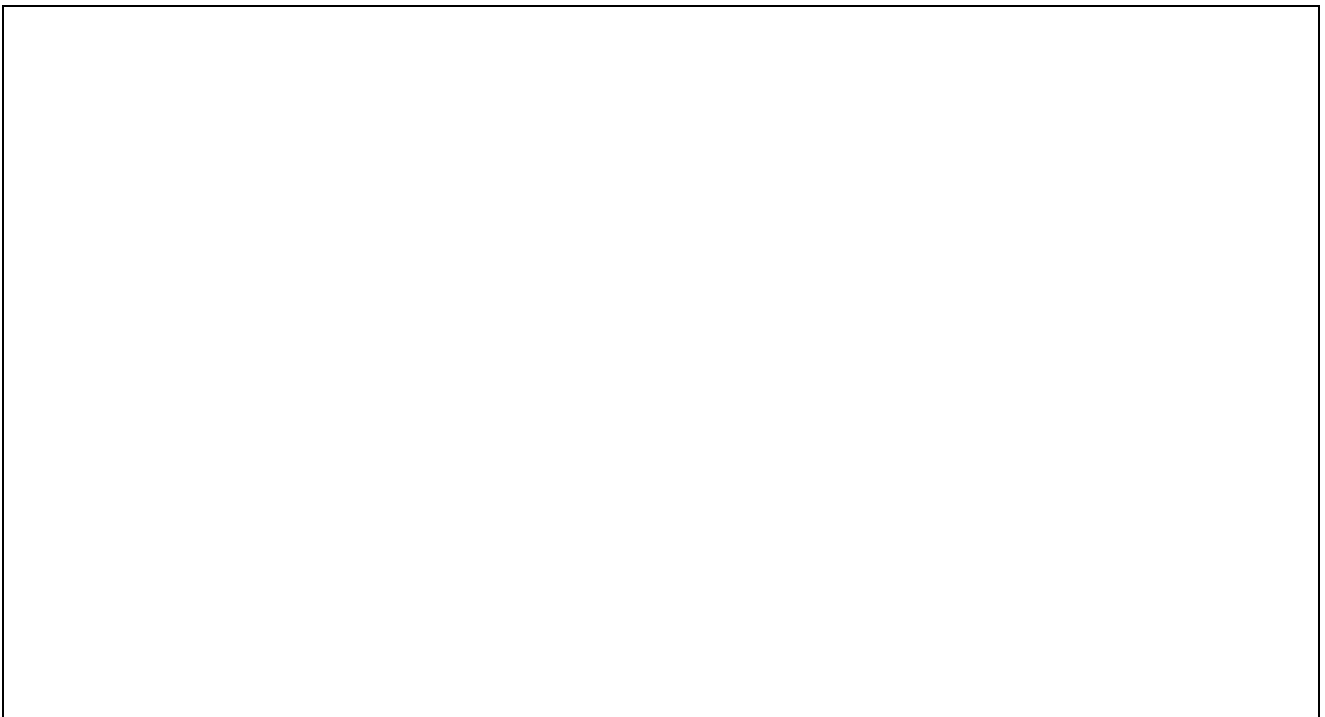
Fig. X. Conceptual model of the effects of climate change on the ecosystem of the Baltic Sea.

5.2.5.7 References

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