**Climate change and the Baltic Sea ecosystem: direct and indirect effects on species, communities and ecosystem function**

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**Abstract**

Climate change has multiple effects on Baltic sea species, communities and ecosystem functioning, through its effects on oceanographic, biogeochemical parameters of the sea, and associated indirect effects on species interactions, trophic dynamics and ecosystem function. Below these effects are reviewed, mainly in the light of literature published after year 2010. Evidence on effects of climate are compiled from field studies, experimental work, and modelling studies.

The responses vary from species group to another, and within groups, even between sibling species. Such differences, as well as many feedbacks and altered trophic pathways, make projections very difficult. Some common patterns arise from the wealth of recent studies, however.

It is probable that the combined effects of increased nutrient loads, increased stratification and increased internal loading will improve the conditions for cyanobacterial blooms in the central basins, as well as the Gulf of Finland. In the northernmost areas the increasing allochtonous DOM may complicate the picture by increasing heterotrophy and by decreasing food web efficiency. This effect may however be counteracted by the intensification of the bacteria-flagellate-microzooplankton-mesozooplankton link, which may change the system from a bottom-up controlled one to a top-down controlled one.

As for the deep benthic communities, increase of nutrients may first promote more sedimentation of organic matter and higher zoobenthos biomasses, but eventually, increasing stratification will weaken benthic-pelagic coupling, resulting in a decreasing benthic biomass. In the photic benthic systems, in turn, nutrient increase probably enhances eutrophication, and, as salinity decline suppresses marine species and temperature increase indirectly favours overgrowth of macroalgae by filamentous algae in summer, major changes in communities can be expected.

Several modelling studies have however concluded that nutrient reductions according to HELCOM BSAP will be a stronger driver for ecosystem functions in the Baltic Sea than climate change. Such studies highlight the importance of studying the Baltic Sea as a socio-ecological system

Knowledge gaps include uncertainties in projecting the future salinity level as well as stratification under different climate forcings. This weakens our ability to project how pelagic productivity, fish populations or macroalgal communities will change in the future. Experimental work could also be better integrated into studies of food web dynamics, to get a more comprehensive view of the responses of the pelagic and benthic systems to climate change, from bacteria to fish. Few studies have investigated the shallow water ecosystems holistically, including macroalgae, filamentous algae, and their grazers and fish at the same time. There are complex climate-induced interactions and multiple feedbacks between algae, grazers and their predators, that are not well known. Finally, both 2D species distribution models and 3D ecosystem models could benefit from better integration of approaches.

**Introduction**

Climate change has multiple effects on Baltic sea species, communities and ecosystem functioning, through its effects on oceanographic, biogeochemical parameters of the sea, and associated indirect effects on species interactions, trophic dynamics and ecosystem function.

These effects have been reviewed by two earlier studies, published in BACC and BACC II. Since then, a wealth of field, experimental and modelling studies have shed more light to the complex interactions between climate and the Baltic Sea ecosystem. Below these effects are again reviewed, mainly based on literature published after year 2010. Evidence is compiled from responses to documented responses of species and communities to climate-induced changes in temperature, salinity, ocean acidification as well as other biogeochemical parameters. Second, a large number of experimental studies, investigating the same parameters are reviewed. Furthermore, the complex food web effects of climate change are scrutinized based on studies where multiple species or trophic levels have been studies. Finally, a number of modelling studies are reviewed.

**Effects on species and communities**

***Microbial communities***

The effects of projected ocean acidification on microbes have been studied together with warming (OAW). For the spring bloom microbial communities (Öland, Baltic Proper), OA alone had a limited impact, but when combined with increased temperature, the communities changed (Lindh et al. 2013). Also in the southern Baltic Sea (Kiel Bight) the impact of OA was limited to certain dominant OTUs (operational taxonomic units); the bacterial community mainly responded to temperature and phytoplankton succession (Bergen et al. 2016).

In experiments using a natural summer microplanktonic community, where CO2 was increased and salinity decreased (from 6 to 3 psu), the biovolume of heterotrophic bacteria of declined (Wulff et al. 2018). In experiments with increasing temperature (from 16 to 18-20 degrees °C) and reduced salinity (from 6.9 to 5.9 PSU) in the Baltic Proper (NW Gotland Sea) the microbial community showed mixed responses. At lower salinity, the heterotrophic bacteria community however changed drastically and resembled communities at high temperature, indicating synergistic effects of temperature and salinity (Berner et al. 2018). It was suggested that the increase in bacterial biomass was caused by the decay of filamentous cyanobacteria. This highlights the importance of considering food web effects (both bottom-up and top-down) on microbial communities under climate change.

***Phytoplankton and Cyanobacteria***

The growing season of phytoplankton has significantly prolonged with warming temperatures during the past few decades (Kahru et al. 2016). E.g. in the western Baltic Sea, it now extends from February to December (Wasmund et al. 2019). The earlier and longer spring bloom has been attributed to changes in environmental conditions associated with global change (Groetsch et al. 2016), including more sunshine and less windy conditions (Hjerne et al. 2019). The spring species communities have also shifted from dominance of early blooming diatoms to later blooming dinoflagellates and the autotrophic ciliate *Mesodinium rubrum* (Klais et al. 2011, Hällfors et al. 2013, Kuosa et al. 2017, Hjerne et al. 2019), due to changes in climate and weather patterns, including ice cover and wind conditions (Klais et al. 2013).

In summer, the amount of Cyanobacteria has increased and the phytoplankton biomass maximum, which in the 1980’s was in spring, is now in July-August. This shift has been explained by a complex interaction between warming, eutrophication and increased top-down pressure (Suikkanen et al. 2013). In the Gulf of Bothnia, salinity decline was also an important factor for phytoplankton community change in 1979 to 2012 (Kuosa et al. 2017).

There is however discrepancy on the relative effects of eutrophication and climate in explaining past changes in phytoplankton biomass and communities. In the long-term data, variable results can be seen, according to area and dominating species group (Wasmund et al. 2011, Groetsch et al. 2016). Certain studies have found evidence of eutrophication effects which have been modified by climate-induced variations in temperature and salinity (Hällfors et al. 2013, Olofsson et al. 2020), and a connection with the Baltic Sea Index has also been demonstrated (Griffiths et al. 2020). Other studies did not find any explanation for the gradual change in community composition, and concluded that phytoplankton community in the Baltic Sea is not in a steady state (Olli et al. 2011), or noted that stochastic dynamics at local scales confound any commonalities between phytoplankton groups (Griffiths et al. 2020).

The projected increase in precipitation is expected to increase river runoff and nutrient load into the sea, especially in the northern Baltic Sea (Huttunen et al. 2015), and together with increased internal loading of nutrients, several modelling studies project an increased phytoplankton biomass until the end of the century (Meier et al. 2012a, Meier et al. 2012b, Skogen et al. 2014, Ryabchenko et al. 2016).

While ocean acidification (OA) has a negative effect on many organisms, it may enhance phytoplankton productivity due to increased CO2 concentration in water. E.g. the biomass of southern Baltic autumn phytoplankton, biomass increased in mesocosms simulating OA, also under warm conditions (Sommer et al. 2015). In many experiments, however, OA had little effects on community composition, fatty acid composition or biovolumes of phytoplankton in spring or autumn (Paul et al. 2015, Bermudez et al. 2016, Olofsson et al. 2019). Even when (positive) effects were detected, they were mainly caused by an associated release of grazing by copepod nauplii in low temperature treatments (Paul et al. 2016).

It has been suggested that climate change may increase blooms and toxicity of species such as the dinoflagellate *Alexandrium ostenfeldii* (Kremp et al. 2012, Kremp et al. 2016), and growth rate, biovolume and intracellular toxin concentration of the Baltic cyanobacterium *Dolichospermum* sp. may increase with elevated temperature (+4°C) (Brutemark et al. 2015, Wulff et al. 2018) and with decreased salinity (from 6 to 3) (Wulff et al. 2018). These studies suggest that Cyanobacteria will get yet another competitive advantage against diatoms and dinoflagellates in a future Baltic Sea.

***Zooplankton***

Several studies have confirmed that marine copepod species have declined, while euryhaline and limnetic, often small-sized, species increase in abundance (Suikkanen et al. 2013, Hänninen et al. 2015). The observed decline of marine taxa has been linked to the decline of salinity, whereas the increase of brackish-water taxa has been, directly or indirectly, positively affected by the temperature increase. (Mäkinen et al. 2017).Species that reside in the upper water layers, such as copepod *Acartia* spp., are mostly affected by temperature driven increase in food availability, whereas species inhabiting the deep layers, such as older stages of *Pseudocalanus acuspes*, are more dependent on salinity and predation pressure (Otto et al. 2014a, Otto et al. 2014b, Ehrnsten 2020).

The effects of climate-driven variations in temperature and ocean acidification (OA) on zooplankton have been studied experimentally. In *Acartia* sp., a dominant copepod in the northern Baltic Sea, warming decreased egg viability, nauplii development and adult survival, and both warming and OA had negative effects on adult female size (Vehmaa et al. 2013, Garzke et al. 2015, Vehmaa et al. 2016). This suggests that the projected OAW may affect the populations of these dominant copepods in the coming decades.

***Macroalgae and vascular plants***

Long-term changes in Baltic Sea macroalgae and charophytes have mostly been attributed to long-term changes in salinity, wind exposure, nutrient availability and water transparency (Gubelit 2015, Blindow et al. 2016, Rinne and Salovius-Lauren 2020), as well as biotic interactions (Korpinen et al. 2007). For bladderwrack *Fucus* spp., light availability, which may also be indirectly affected by climate-induced increase in nutrients, affects the local coverage (Lappalainen et al. 2019). The long-term decrease of water transparency in 1936 to 2017 has been estimated to have reduced favorable sea floor areas for *Fucus* spp. by 45% (Sahla et al. 2020). The conclusion for coastal ecosystems has however been that eutrophication, whether being caused solely by anthropogenic nutrient loads, or amplified by climate change, has been the most important pressure affecting the shallow water areas of the Baltic Sea (Olsson et al. 2015).

The direct effects of increasing temperature and decreasing salinity on bladderwrack *Fucus vesiculosus* have been investigated by a number of experimental studies. Ocean acidification (OA) appears to have a relatively small effect on macroalgae (Al-Janabi et al. 2016a, Wahl et al. 2019), while temperature effects may be significant. The effects of increasing temperature are not linear, however. Growth or photosynthesis is not impaired under projected temperature increase (from 15 to 17.5 °C) but at extreme temperatures, simulating heat waves (27 to 29 °C), photosynthesis declines, growth ceases and necrosis starts (Graiff et al. 2015, Takolander et al. 2017b). Necrosis is also enhanced by low salinity (4 PSU) (Takolander et al. 2017b), and under very low salinity (2.5 PSU) the sexual reproduction of *F. vesiculosus* ceases (Rothäusler et al. 2018, Rothäusler et al. 2019).

OAW may also act in concert with hypoxia, in areas where upwellings bring hypoxic water close to the surface. In a three-day experiment simulating an upwelling event, hypoxic water caused severe mortality of *Fucus* germlings (Al-Janabi et al. 2016b).

Climate induced decline in salinity may also affect communities via its direct effect on species’ physiology. Retreat of marine species towards south and west has been predicted for bladderwrack, eelgrass and blue mussel, and some 40–50 other species affiliated to these (Vuorinen et al. 2015). Species distribution modelling studies have confirmed that this, mainly salinity-induced, decrease will cause habitat fragmentation and significantly reduce the occurrence and biomass of bladderwrack, with large effects on the biodiversity and ecosystem functioning of the shallow water communities of the northern Baltic Sea (Takolander et al. 2017a, Jonsson et al. 2018, Kotta et al. 2019).

It is not certain if *Fucus vesiculosus* can adapt to the anticipated changes. It has been suggested that Baltic marine species have, due to local adaptation, isolation and genetic endemism, an increased risk of local extinction and diminished potential for evolutionary rescue following environmental change (Johannesson et al. 2011). The dispersal rate of locally adapted genotypes may not keep pace with estimated velocity of salinity decline, because of the restricted dispersal and long generation time of *F. vesiculosus* (Jonsson et al. 2018). However, some experimental studies have showed that different sibling groups of *F. vesiculosus* have different responses to OAW (Al-Janabi et al. 2016a, Al-Janabi et al. 2016b), and that *F. vesiculosus* has phenotypic plasticity and tolerance against salinity change (Rothäusler et al. 2018, Rugiu et al. 2018a, b). It has also been shown that *Fucus radicans*, an endemic congener of *F. vesiculosus* which is more tolerant to low salinity, might be able to replace *F. vesiculosus* in the northernmost Baltic (Rugiu et al. 2018a). This adaptive capability may at least delay the most drastic consequences of climate change on bladderwrack.

Similar experiments on climate change effects as done with bladderwrack have also been made with other macroalgae and certain vascular plants. In laboratory and field experiments (in the Gulf of Riga), OA increased the growth of the opportunistic green alga *Ulva intestinalis* (Pajusalu et al. 2013, Pajusalu et al. 2016). This suggests that OA could favour such fast growing species and induce an overgrowth of *Fucus* by annual green algae. Other studies showed that photosynthesis of charophytes increased under high pCO2 treatments, whereas the eelgrass *Zostera marina* did not respond to the elevated pCO2 alone (Pajusalu et al. 2015). Salinity decline is projected to decrease the distributional ranges of *Z. marina* andthe red algae *Furcellaria lumbricalis*, whereas temperature increases probably favours charophytes. Charophytes will however not replace other key habitat forming species because they occupy sheltered soft bottom areas (Torn et al. 2020).

***Benthic animals***

Soft bottom benthic communities are dependent on variables which are influenced by climatic variability. For instance, in the SW coast of Finland, a drastic community change, where amphipods were replaced by Baltic clam *Limecola balthica* and the non-indigenous polychaete *Marenzelleria* spp., took place. It was best explained by an increase in near-bottom temperature and by fluctuations in salinity and oxygen (Rousi et al. 2013). As for benthic biomass, food availability and oxygen conditions have been the most important factors, but it is also suggested that, in the future, climate-induced changes in salinity, temperature and eutrophication will also be of importance (Timmermann et al. 2012, Ehrnsten et al. 2019a, Ehrnsten et al. 2019b).Also in the Åland Islands archipelago, zoobenthos variations were associated with salinity decline during 1983-2012 (Snickars et al. 2015).

The effects of warming on invertebrates are non-linear. In experiments, respiration and growth of the isopod *Idotea balthica* first increased until 20°C, and then decreased at 25°C (Ito et al. 2019)*.* Therefore, heat waves may pose a severe threat to sublittoral invertebrates. Different species show different responses to single and sequential heat waves, however, resulting in a change in community structure (Pansch et al. 2018). Many marine invertebrates will directly and indirectly suffer from decreasing salinity. In experiments simulating projected changes in temperature and salinity, the survival of the isopod *Idotea balthica* decreased, albeit with variations between and within regions (Rugiu et al. 2018c), and a combination of experimental studies and species distribution modelling demonstrated that abundances of *I. balthica* will be significantly reduced, mainly due to the salinity-induced decline of its host macroalgae, *Fucus vesiculosus* (Kotta et al. 2019).

Ocean acidification has various effects on benthic invertebrates. The size and time to settlement of pelagic larvae of the Baltic clam *Limecola/Macoma balthica* increased with OA, suggesting a developmental delay (Jansson et al. 2016), while OA had no effects on larvae of the barnacle *Amphibalanus improvisus* (Pansch et al. 2012). Short (12 h) or long-term (2 week) exposures to OA did not have significant effects on the isopod *Saduria entomon* either (Jakubowska et al. 2013). Controversial results were obtained for the isopod *Idotea balthica*, from three different sea areas: North Sea, Kattegat, and the Baltic Sea. The populations from more saline habitats were not significantly affected by OA, while the Baltic Sea population showed 100 % mortality (Wood et al. 2014). It was suggested that the Baltic *I. balthica* had higher levels of oxidative stress, and the combined stress became lethal to them.

***Non-indigenous invertebrates***

It is often suggested that climate change will favour invasions of non-indigenous species worldwide (Jones and Cheung 2015). It has also been shown that native and non-native species tend to inhabit separate niches in the Baltic Sea. The non-native species typically occur in areas characterized by reduced salinity, high temperatures, high proportion of soft seabed and decreased wave exposure, whereas most native species display an opposite pattern (Jänes et al. 2017). This suggest that the former areas are more prone to further range expansion of non-native species than the latter. Modelled scenarios of temperature and salinity have also been used to project how the change in the abiotic environment could affect NIS already present in the Baltic Sea. The analysis suggests an increase of Ponto-Caspian cladocerans in the pelagic community, and an increase in dreissenid bivalves, amphipods and mysids in the coastal benthic areas of the northern Baltic Sea until 2100 (Holopainen et al. 2016).

***Fish***

Sprat and herring are in the Baltic Sea influenced by multiple factors, including nutrition, predation and fisheries, but also by climatic variations. Sprat has benefited from the increasing seawater temperature (Voss et al. 2011, MacKenzie et al. 2012, Eero et al. 2016). Especially in 1990 to 2020 the populations have been affected by both climate and top-down control, i.e. cod predation and fisheries (Eero et al. 2016).

Increasing seawater temperature has also made it possible for certain warm water Atlantic species, such as anchovy (Reusch et al. 2018) and sole and turbot (Sparrevohn et al. 2013) to occur more abundantly in Kattegat and the westernmost Baltic Sea. Such northward migrations may be caused by both global climate change and by variations in the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO), as well as contraction of the subpolar gyre.

As for coastal fish, the distribution of pikeperch (*Sander lucioperca*) expanded towards north along the coasts of the Bothnian Sea, apparently due to the warming of waters (Pekcan-Hekim et al. 2011). For many coastal piscivores (perch, pike, pike-perch), as well as cyprinids, the eutrophication status of coastal waters is however an equally or more important factor than climate (Snickars et al. 2015, Bergstrom et al. 2016).

Future climatic variations may affect fish in the Baltic Sea through their effects on water temperature, salinity, oxygen and pH, as well as nutrients, which indirectly affect food availability for fish. The responses of cod larvae to ocean acidification (OA), also in combination with warming (OAW), have been studied experimentally. In some studies no effect of OA or OAW on hatching, survival or development rates of cod larvae was found (Frommel et al. 2013), while in others mortality of cod larvae doubled when treated with high end projections (RCP8.5) of OA. When the projected increase of mortality was included into a stock-recruitment model, recruitment of western Baltic Cod declined to an average of 8 % of the current recruitment (Stiasny et al. 2016). Also, several modelling studies project low abundances of cod towards the end of the century, due to the decrease of ‘cod reproductive volume’ (Niiranen et al. 2013, Wåhlström et al. 2020).

Climate change may also have positive effects on fish stocks. Increasing spring and summer temperatures have in modelling studies been projected to gradually increase productivity and stocks of sprat (Voss et al. 2011, MacKenzie et al. 2012, Niiranen et al. 2013). For herring the results are more variable: both increase (Bartolino et al. 2014) and a short-term decrease (until 1950) (Niiranen et al. 2013) have been projected.

**Climate change and ecosystem function**

***Climate change and primary production in the pelagial***

In the global ocean it has been projected that climate change will induce declining of primary production because of intensified stratification and decreased availability of nutrients in the surface layer (IPCC 2019). In the Baltic Sea, primary producers receive nutrients from several sources, both via rivers and through several biogeochemical processes, and the system is more complex than in the ocean.

Several studies using coupled oceanographic-biogeochemical and ecosystem models have indeed projected more phytoplankton and especially cyanobacteria in the warmer and more stratified future Baltic Sea. It has been projected for the central Baltic Sea that increased water temperature causes, together with enhanced mixing and associated increase in nitrogen, an earlier spring bloom, and in summer, more intense cyanobacteria blooms (Meier et al. 2011b, Neumann et al. 2012, Chust et al. 2014, Andersson et al. 2015). Intensified blooms of cyanobacteria are expected especially if hypoxia and internal loading of phosphorus will prevail and increase (Meier et al. 2011a, Funkey et al. 2014).

There are also contrasting results. When pCO2 was experimentally increased, the production of single-celled cyanobacterium *Cyanothece* increased, while that of *Nodularia* sp. decreased (Eichner et al. 2014). Also, increase of temperature from 16 to 18—20 °C, led to an earlier peak of cyanobacteria, while yields were reduced (Berner et al. 2018). In particular, the biomass of nitrogen-fixer *Dolichospermum* sp. decreased. This suggests that there are species specific responses to climate change and associated oceanographic parameters even within Cyanobacteria. If the biomasses of Nodularia asp. and Dolichospermum decrease due to increased acidification, nitrogen input into the Baltic Sea as well as carbon export to heterotrophic bacteria via cyanobacteria might decline (Eichner et al. 2014, Berner et al. 2018).

***Nutrient recycling, benthic-pelagic coupling and trophic efficiency***

While the projected increase in nutrient loading will inevitably affect the pelagic and benthic ecosystems, what eventually determines the productivity is the recycling of carbon and nutrients within the system. Several studies suggest fundamental changes in recycling potential, carbon and nutrient flows, and trophic interactions.

A climate and nutrient load driven model reconstruction of the Baltic Sea state from 1850 to 2006 suggest that the shift from spring to summer primary production is accompanied by an intensification of pelagic recycling of organic matter (Gustafsson et al. 2012). In mesocosm studies warming accelerated (southern Baltic Sea) phytoplankton spring bloom and increased carbon specific primary productivity (Sommer and Lewandowska 2011, Sommer et al. 2012, Paul et al. 2016). The total phytoplankton biomass however decreased due to negative effects of warming on nutrient flux (Lewandowska et al. 2012, Lewandowska et al. 2014).

It has also been projected that the flow of dissolved organic matter (DOM) into the northern Baltic Sea increases in the future climate, especially in the northernmost Baltic Sea (Strååt et al. 2018). By using long-term time series from 1994 to 2006, it was indeed shown that climate change brought about increased riverine DOM, which increased the amount of substrate available for bacteria (Wikner and Andersson 2012). Also experimental studies have demonstrated increased microbial activity and biomass with increasing DOM and temperature (Ducklow et al. 2010). Eventually bacteria compete for nutrients with phytoplankton, and as the brownification of water also reduces light availability, phytoplankton productivity and biomass may decrease. This shifts the carbon flow towards microbial heterotrophy (Wikner and Andersson 2012).

It has also been suggested that climate change may decrease fish productivity, especially in the northernmost Baltic Sea, because when the system towards heterotrophy, the food web efficiency declines, and eventually the fish production may decerase (Berglund et al. 2007, Wikner and Andersson 2012). In most areas, however, also heterotrophic production through the bacteria-flagellates-ciliates chain may remain high, yielding a high amount of copepods, the favourite food of forage fishes (Lefebure et al. 2013), and the consequences of climate change associated changes in trophic efficiency on fish productivity remain unsecure.

For zoobenthos inhabiting soft bottoms, hydrodynamics, oxygen and availability of food are crucial, and several modelling studies have estimated the relative effects of these factors for Baltic Sea zoobenthos. A physiological fauna model linked to a 3D coupled hydrodynamic–ecological Baltic Sea model projected that, in areas previously burdened by hypoxia, benthic biomass will increase (until year 2100) by up to 200 % after re-oxygenating bottom waters, whereas in permanently oxygenated areas the macrofauna biomass will decrease by 35 %, due to lowered food supply to the benthic ecosystem (Timmermann et al. 2012). In another modelling study, zoobenthic production decreased in the coastal zones, and gradually also in the more offshore areas, with increasing temperature and declining salinity and bottom oxygen, regardless of the nutrient load scenarios (Weigel et al. 2015). Warmer temperatures will induce stronger stratification and intensified recycling, and zoobenthos decreases, due to reduced export of organic matter to the benthic ecosystem (Ehrnsten et al. 2020). Large uncertainties in projections exist, however, especially due to difficulties in projecting the future nutrient loads and salinities (Meier et al. 2019b, Saraiva et al. 2019).

***Complex food web responses in the microbial loop***

Experimental studies have also demonstrated that complex responses to climate change may also arise from food web effects within the microbial loop.

In Kvarken, the northern Gulf of Bothnia, increase of DOM enhanced respiration and abundance of bacteria, whereas an increase of temperature (from 12 to 15 °C) induced a decrease of bacteria, probably due to an increase in bacterivorous flagellates (Nydahl et al. 2013). A complex response to warming was also demonstrated for different size classes of heterotrophic flagellates (HF). There was a succession from flagellates feeding on bacteria to omnivorous nanoflagellates preying upon other HF. This intraguild predation pattern probably dampened the response to experimental treatments (Moustaka-Gouni et al. 2016).

As for microzooplankton (MZP), the effects of OA and warming seem to be mostly beneficial. OA does not have a negative effect on MZP, probably because estuarine MZP are adapted to a large natural variability in pCO2. (Horn et al. 2016), and the abundance of the mixotrophic ciliate *Myrionecta rubra* (*Mesodinium rubrum*) even increased in mesocosms with OA, because of increase of its food, picoeukaryotes and Dinophyta at higher CO2 levels (Lischka et al. 2017). In addition, warming improved the growth rate of MZP, and their biomass peaked earlier in warm mesocosm treatments. This led to a reduced time-lag between MZP and phytoplankton peaks, inducing a better food supply to microzooplankton in warm conditions (Horn et al. 2016). The same applied to the MZP-copepod link: at low temperatures MZP escaped from predation by slower growing copepods, whereas at higher temperatures especially small-sized ciliates were more strongly controlled by copepod predation.

OA also promoted the growth of suspension-feeding cladocerans, because of a CO2-driven increase of cyanobacteria (Lischka et al. 2017). Warming may also increase zooplankton grazing on medium-sized algae, which contributes to a change towards smaller-sized phytoplankton species (Klauschies et al. 2012, Paul et al. 2015).

In summary, climate change probably strengthens trophic pathways from phytoplankton and flagellates through ciliates to copepods (Aberle et al. 2015). It has also been suggested, from experimental (mesocosm) evidence, that warming induces a switch from a bottom-up controlled to a mainly top-down controlled system, which may result in increased zooplankton abundance and reduced phytoplankton biomass under warm temperature (Paul et al. 2016).

Such results highlight the importance of considering food web effects (both bottom-up and top-down) on microbial communities under climate change.

***Food web interactions in the littoral ecosystem***

Climate change induced increase in nutrients is bound to affect the algae and vascular plants in the shallow photic zone. The shallow water food webs based on macroalgae and seagrasses may also be affected via the indirect effects of climate change, mediated through the interactions between the algae and their grazers.

In mesocosm experiments mimicking coastal *Fucus vesiculosus* communities in late summer, a heatwave-driven collapse of grazers resulted in overgrowth of *Fucus* by filamentous algae. In the autumn and winter, instead, the process was reversed: warming resulted in more active invertebrates, but the intensified grazing was directed towards the perennial *Fucus* spp. Again, a significant reduction of *Fucus* biomass resulted (Werner et al. 2016). As for the microalgae (diatoms), growing on *Fucus* in spring, temperature effects were stronger than grazing effects, suggesting a positive overall effect of climate change on microalgae (Werner and Matthiessen 2017).

Similar results were obtained in an artificially heated biotest basin (Forsmark nuclear power plant) in the Gulf of Bothnia, the biomass of the non-native gastropod grazer *Potamopyrgus*, gammarids and the snail *Theodoxus* was much higher than in non-heated conditions. The community shift was mainly driven by direct temperature effects on invertebrates and by indirect effects of changes in vegetation cover (Salo et al. 2020). Cascading effects are also possible. In the same biotest basin, perch shifted from feeding on small fish to gammarid crustaceans, which released grazing pressure from filamentous algae (Svensson et al. 2017).

If the same takes place in other sea areas of the Baltic Sea as well, warming may promote the growth of filamentous algae and contribute to the decline of bladderwrack. These results suggest that both summer heatwaves and cold season warming can induce eutrophication-like effects in the photic zone dominated by macroalgae, even without an increase in nutrient loading, and without major changes in salinity.

***Climate change and regime shifts***

In the 1980’s a partly climate induced regime shift took place with drastic changes in the central Baltic food web (Möllmann et al. 2009, Lindegren et al. 2010). Later studies also confirmed that, during that period declines in suitable habitat and ‘reproductive volume’ (where cod egg survival is possible) contributed to the decline of cod population (Hinrichsen et al. 2011, Casini et al. 2016, Bartolino et al. 2017), causing the earlier demonstrated (Casini et al. 2008) cascading effects on its main prey, sprat and herring, as well as zooplankton.

The different effects of temperature and salinity on sprat and cod also resulted in a spatial mismatch between these species, which contributed to the increase of sprat stocks (Reusch et al. 2018). Transition to a lower saline Baltic Sea, and associated decline of marine copepods (Hänninen et al. 2015), also induced a halving of (3-year old) herring weight-at-age, from 50–70 g in the late 1970s to 25–30 g in 2000s (Dippner et al. 2019). These studies have mostly considered the central and southern Baltic fish stocks. In the Bothnian Bay, the northernmost basin of the Baltic Sea, salinity was the major driver for herring as well, but the species involved were different. Here the decline of spawning-stock biomass observed in 1980-2013 was explained by a simultaneously increased competition for food with vendace, a limnic species that had increased with lowering salinity (Pekcan-Hekim et al. 2016).

Multi-species modelling studies have also investigated the factors affecting the populations of cod, herring and sprat under climate change. It was concluded that both fishing and climate strongly affects the size of cod stocks. If fishing is intense but climate remains unchanged, cod declines, but not very dramatically, while if climate changes as projected, cod goes extinct in two models out of seven, even with present low fishing effort (Gårdmark et al. 2013).

Different scenarios may yield very different outcomes, however. Medium CO2 concentrations (RCP4.5), low nutrients and sustainable fisheries resulted in high biodiversity and high numbers of cod and flounder, while high emissions (RCP8.5) and high nutrient loads resulted in diminished biodiversity and high abundance of lower value fish, especially sprat (Bauer et al. 2018, Bauer et al. 2019, Hyytiäinen et al. 2019).

**Knowledge gaps**

There are a number of major knowledge gaps in the present literature. First, despite more than two decades of 3D modelling, there are still large uncertainties in projecting the future salinity level as well as stratification under different climate forcings. This weakens our ability to project all the main changes anticipated, from pelagic productivity and benthic-pelagic coupling to fish populations and geographic shifts in macroalgal communities in the photic zone.

Furthermore, regime shifts mostly looked at through food web changes in the central Baltic Sea, using the cod-sprat-herring-zooplankton trophic links as an example. Only recently have the experimental and mesocosm studies on the dynamics of the lower trophic levels, i.e. bacteria, flagellates and microzooplankton started to shed light on the complex dynamics of the microbial loop under different scenarios of DOM, temperature and OA. The conclusions from the experimental work should be integrated into the wider studies of food web dynamics, to get a more comprehensive view of the responses of the pelagic and benthic systems to climate change, from bacteria to fish.

Furthermore, while experimental studies on macroalgal communities are many, few studies have investigated the shallow water ecosystems holistically, including macroalgae, filamentous algae, and their grazers and fish at the same time. Those that have, have revealed complex interactions and multiple feedbacks between algae, grazers and their predators.

Furthermore, the coupled oceanographic-biogeochemical modelling studies typically study the whole Baltic Sea and often have a horizontal resolution at the scale of 4 km. In contrast the models used to project present or future species distributions are done in 2D, and at much higher resolution, up to 40 m (Jonsson et al. 2018, Virtanen et al. 2018, Kotta et al. 2019). Both modelling types would benefit from integration. Species distribution models could be parametrized with 3D model results, if they were made more locally, and at higher spatial resolution, whereas the 3D models could benefit from high resolution distribution modelling of benthic communities.

**Conclusions**

Climate change induces multiple direct and indirect effects on species and communities, and affects nutrient and carbon dynamics of the Baltic Sea ecosystem in the pelagial, deep sea benthos, as well as the photic zone close to the shores. The responses vary from species group to another, and within groups, even between sibling species. Such differences, as well as many feedbacks and altered trophic pathways, make projections very difficult.

Some common patterns arise from the wealth of recent studies, however. It is probable that the combined effects of increased nutrient loads, increased stratification and increased internal loading will improve the conditions for cyanobacterial blooms in the central basins, as well as the Gulf of Finland. In the northernmost areas - Kvarken and the Bothnian Bay – the increasing allochtonous DOM may complicate the picture by increasing heterotrophy and by decreasing food web efficiency. This effect may however be counteracted by the intensification of the reduction of time lags between bacteria, phytoplankton, microzooplankton, suspension feeding cladocerans and microzooplankton-eating copepods, which may change the system from a bottom-up controlled one to top-down controlled one.

As for the deep benthic communities, increase of nutrients may first promote more sedimentation of organic matter and higher zoobenthos biomasses, but eventually, increasing stratification will weaken benthic-pelagic coupling, resulting in a decreasing benthic biomass. In the photic benthic systems, in turn, nutrient increase probably enhances eutrophication, and, as salinity decline suppresses marine species such as bladderwrack, and as temperature increase also indirectly favours overgrowth of macroalgae by filamentous algae in summer, major changes in the communities dominated by brown algae can be expected.

Naturally, climate change is not the only factor determining the fate of the Baltic Sea in the future. Several modelling studies have concluded that nutrient reductions according to HELCOM BSAP will be a stronger driver for ecosystem functions in the Baltic Sea than climate change (Friedland et al. 2012, Niiranen et al. 2013, Ehrnsten et al. 2019b, Pihlainen et al. 2020). In moderate nutrient loading scenarios also climate change will play a role, but under full implementation of BSAP, the environmental state of the Baltic Sea will be significantly improved by the end of the century (Meier et al. 2018, Saraiva et al. 2018, 2019). This also means that extreme cyanobacteria blooms will no longer occur, despite the proceeding climate change (Meier et al. 2019a).

These studies highlight the importance of studying the Baltic Sea as a socio-ecological system, responding to both environmental and societal changes (Bauer et al. 2018, Bauer et al. 2019, Hyytiäinen et al. 2019).

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