Muotoiltu: Numerointi: jatkuva

Global climate change and the Baltic Sea ecosystem: direct and indirect effects on species, communities and ecosystem functioning

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Abstract

Climate change has multiple effects on Baltic Sea species, communities and ecosystem functioning, through changes in physical and biogeochemical environmental characteristics of the sea. Associated indirect and secondary effects on species interactions, trophic dynamics and ecosystem function are expected to be significant. We review studies investigating species-, population- and ecosystem-level effects of abiotic factors that may change due to global climate change, such as temperature, salinity, oxygen, pH, nutrient levels, and the more indirect biogeochemical and food web processes, primarily based on peer-reviewed literature published since 2010.

For phytoplankton, clear symptoms of climate change, such as prolongation of the growing season are evident, and can be explained by the warming, but otherwise climate effects vary from species to species and area to area. Several modelling studies project a decrease of phytoplankton bloom in spring and an increase in cyanobacteria blooms in summer. The associated increase in N:P ratio may contribute to maintaining the ‘vicious circle of eutrophication’. However, uncertainties remain because some field studies claim that cyanobacteria have not increased and some experimental studies show that responses of cyanobacteria to temperature, salinity and pH vary from species to species. An increase of riverine DOM may also decrease primary production, but the relative importance of this process in different sea areas is not well known. Bacteria growth is favoured by increasing temperature and DOM, but complex effects in the microbial ~~loop~~ food web are probable.

Warming of seawater in spring also speeds up zooplankton growth and shortens the time lag between phytoplankton and zooplankton peaks, which may lead to decreasing of phytoplankton in spring. In summer, a shift towards smaller size zooplankton and a decline of marine copepod species has been projected.

In deep benthic communities, continued eutrophication promotes high sedimentation and keeps food conditions for zoobenthos good. If nutrient abatement proceeds, improving oxygen conditions will first increase zoobenthos biomass but the subsequent decrease of sedimenting matter will disrupt the pelagic-benthic coupling and lead to a decreased zoobenthos biomass. In the shallower photic systems, heatwaves may produce eutrophication-like effects, e.g., overgrowth of bladderwrack by epiphytes, due to a trophic cascade. If salinity also declines, marine species such as bladderwrack, eelgrass and blue mussel may decline. Freshwater vascular plants will be favoured but they cannot replace macroalgae on rocky substrates. Consequently also invertebrates and fish benefiting from macroalgal belts may suffer. Climate induced changes in the environment also favour establishment of non-indigenous species, potentially affecting food web dynamics in the Baltic Sea.

As for fish, salinity decline and continuing of hypoxia is projected to keep cod stocks low, whereas the increasing temperature has been projected to favour sprat and certain coastal fish. Regime shifts and cascading effects have been observed in both pelagic and benthic systems, as a result of several climatic and environmental effects acting synergistically.

Knowledge gaps include uncertainties in projecting the future salinity level as well as stratification, and potential rate of internal loading, under different climate forcings. This weakens our ability to project how pelagic productivity, fish populations and macroalgal communities may change in the future. 3D ecosystem models, food web models and 2D species distribution models would benefit from integration, but progress is slowed down by scale problems and inability of models to consider the complex interactions between species. Experimental work should be better integrated into empirical and modelling 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. Also, to better understand the effects of climate change on biodiversity of the Baltic Sea, more emphasis should be placed on studies of shallow photic environments.

The fate of the Baltic Sea ecosystem will depend on various intertwined environmental factors, and on development of the society. Climate change will probably delay the effects of nutrient abatement and tend to keep the ecosystem in its ‘novel’ state. Several modelling

studies however conclude that nutrient reductions will be a stronger driver for ecosystem functioning of the Baltic Sea than climate change. Such studies highlight the importance of studying the Baltic Sea as an interlinked socio-ecological system.

Keywords: Climate change, biodiversity, species, communities, food webs, ecosystem functioning, Baltic Sea

1. Introduction

Global climate change affects the marine ecosystem through ocean warming, acidification, deoxygenation and through changes in nutrient loading and water circulation, which may all impact marine biological processes from genes to populations, communities, and ecosystems (Brierley and Kingsford, 2009; Henson et al., 2017). The biological consequences range from shifts in species abundance and distributions, changes in dispersal patterns and modification of species interactions to altered food webs and decreasing ocean productivity (Hoegh-Guldberg and Bruno, 2010; Philippart et al., 2011; Doney et al., 2012; Burrows et al., 2019). The changes in biological processes also affect marine ecosystem services and threaten human food security, especially in the most vulnerable areas (Barange et al., 2014).

Climate change has multiple effects also on the Baltic Sea, impacting species, communities, and ecosystem functioning. As in the ocean, the effects are usually mediated via climate affected oceanographic or biogeochemical processes and via associated indirect effects on species interactions, trophic dynamics, and ecosystem function mechanisms. These potentially affect the biota inhabiting the Baltic Sea, as well as the human society (Paasche et al., 2015; Hyytiäinen et al., 2019; Pihlainen et al., 2020; Stenseth et al., 2020).

The effects of climate change on the Baltic Sea ecosystem may differ from those projected for the oceanic areas as the Baltic Sea differs in many respects from the oceans and even from the coastal ecosystems surrounding the other regional seas and oceans. The communities of the Baltic Sea are formed of a peculiar combination of marine, limnetic and brackishwater taxa. The long winter and the strong seasonal cycle give the area sub-arctic properties, especially in the northern areas. The Baltic Sea has also been shown to warm up faster than most other sea areas of the world (Belkin, 2009; Sherman et al., 2009), albeit with large differences between sub-basins (Kniebusch et al., 2019; Dutheil et al., 2021).The Baltic Sea is also strongly affected by its watershed, which is more than four times larger than its surface area and is inhabited by ca. 85 million people (Omran and Negm, 2020). The marine ecosystem therefore receives excess nutrients and other elements and contaminants from the land via rivers, through the air, and by leaking from the sediments of the Baltic Sea. Furthermore, the irregular inflows of more saline and oxic North Sea water, which at specific basin-wide weather conditions enter the Baltic sea through the Danish Straits (Matthäus and Schinke, 1994; Lehmann et al., 2022) and influence the state and functioning of the Baltic Sea.

All these pathways of chemical elements and oceanographic and biogeochemical processes may be affected by global climate change and the quasi-cyclic climate phenomena such as the North Atlantic Oscillation (NAO). It has also been suggested that impacts and symptoms of global climate change are accumulating faster in the Baltic Sea than in other coastal areas of the oceans, and that Baltic Sea thus can be considered as “a time machine for the future coastal ocean” (Reusch et al., 2018).

However, attribution of the observed ecosystem changes to global (anthropogenic) climate change is challenging because of the multiple synergistic effects between climate and other environmental drivers, such as eutrophication, harmful substances, habitat modification, fishing and introduction of non-indigenous species, which all may have strong impacts on ecosystems and their functioning in time and space (Reusch et al., 2018; Stenseth et al., 2020; Bonsdorff, 2021). Therefore, profound knowledge of the mechanisms and processes governing Baltic Sea ecosystem under climate change are vital for the understanding and management of the Baltic Sea (Reusch et al., 2018; Bonsdorff, 2021; Blenckner et al., 2021).

The overall effects of climate change on the Baltic Sea have been reviewed in earlier synthesis-studies (The BACC Author Team, 2008; The BACC II Author Team, 2015), in which also climate impacts on the marine ecosystem were assessed (Dippner et al., 2008; Viitasalo et al., 2015). Since then, a wealth of field, experimental and modelling studies have shed more light onto the complex interactions between the climate change and the Baltic Sea system (Meier et al., 2022b).

In this paper, we review research on climate change effects on the Baltic Sea species, habitats, and ecosystem functioning, primarily based on research published in 2010—2021. We include both studies investigating direct effects of climate related parameters on organisms, as well as studies that investigate the more indirect processes affecting the structure and functioning of the Baltic Sea ecosystem through biogeochemistry and food web interactions. Evidence is compiled from empirical field studies that show past changes and responses of species, populations, and communities to climate-affected parameters such as temperature, salinity, oxygen and pH. A large number of experimental studies, investigating species responses to the same parameters in micro- or mesocosms, are reviewed. Studies investigating the complex effects of climate change on the interactions between species and trophic groups, i.e., phytoplankton, bacteria, cyanobacteria, zooplankton, and fish, as well as algae or vascular plants and invertebrates grazing on them, are also analysed. Modelling studies, based on coupled oceanographic-biogeochemical models or other types of species-level or food web models, are reviewed. Based on the published research we draw conclusions about the role of climate driven environmental variables on shaping the structure and functioning of the Baltic Sea ecosystem and identify knowledge gaps and current issues of dissensus. Areas in need of more research are recommended.

2. Definitions

We review studies that shed light to the possible climate effects on the Baltic Sea ecosystem, by studying oceanographic and biogeochemical parameters which have been projected to change due to climate change. As such changes may be affected by both anthropogenic global climate change and by natural climate variations, it is first necessary to define certain key terms used in this review.

By *global climate change* we refer to the past and contemporary increase in global temperature, caused by anthropogenic emissions of CO_2 and other greenhouse gases, and its effects on various climatic as well as oceanographic and biogeochemical parameters. By *climate change*, in turn, we refer to a large-scale shift in climatic parameters affecting the Baltic Sea region, that may be caused either by global climate change, by cyclic climate fluctuations (such as North Atlantic Oscillation, NAO) or by irregular or stochastic variation in climate parameters. We are not ~~referring to~~ considering short-term (between-year or seasonal) ~~weather patterns~~weather variations, but mainly include studies ~~consider~~ that attempt to reveal organisms' responses to longer term (several years – decades) variability in climate.

Kommentoinut [VM1]: R2:
r. 150 Variation between year is weather variations as climate variations are defined as differences between 30-year periods

For *ecosystem functioning* we use Tilman's (2001) definition, "the rate, level, or temporal dynamics of one or more ecosystem processes such as primary production, total plant biomass, or nutrient gain, loss, or concentration". By *functional diversity* we mean "the range and value of those species and organismal traits that influence ecosystem functioning" (Tilman, 2001). A *functional group*, is "a set of species that have similar traits and that thus are likely to be similar in their effects on ecosystem functioning" (Tilman, 2001).

With *biogeochemical processes*, we refer to various biogeochemical cycles and processes, which often involve cycling and transfer of allochtonous or autochtonous essential nutrients and/or minerals and organic carbon, and which are either driven or influence biological activity in species. With *trophic dynamics* we refer to interactions between trophic levels or functional groups, such as phytoplankton, bacteria, cyanobacteria, nano- and microflagellates, micro-, meso- and microzooplankton, zoobenthos and fish, as well as algae and vascular plants and invertebrates living amongst them.

Trophic efficiency is defined as “the efficiency of energy flow between trophic levels, and is the percentage of energy from a trophic level that is used by the organisms of the next trophic level for growth and reproduction” (Hine, 2019).

3. Review methods

The search for relevant papers was implemented mainly using Web of Science (WoS) website tool (https://apps.webofknowledge.com/), maintained by Clarivate. The search was focused on years 2010-2021 and was performed using several search terms in various combinations. These included (always) “Baltic Sea” and (in various combinations) “climate”, “climate change”, “global climate change”, “marine ecosystem”, “temperature”, “salinity”, “acidification” and “pH”, as well as taxonomic groups such as “phytoplankton”, “cyanobacteria”, “bacteria”, “zooplankton”, “microzooplankton”, “mesozooplankton”, “flagellates”, “macroalgae”, “zoobenthos”, “benthic animals” and “fish” as well as “microbial loop”. Marine birds and mammals were not included. The words were used as both search terms Title and Topic, and several reference lists were derived and merged.

Some papers from 2021 and 2022 were found and downloaded with an unstructured search performed with Google Scholar, as this website tool includes more recent publications than WoS. In some cases, references before 2010 were also included, if it was necessary to back up the statements with older studies.

The search resulted in 500+ papers, of which many were not relevant with the current review, i.e., were not concerning effects of climate change on species, habitats or ecosystem functioning in the Baltic Sea. The most relevant studies were saved into library groups of EndNote X9.2 reference management software (Clarivate Analytics), and the contents were scrutinized in more detail.

Because of the focus period, 2010-2021, the review is not a full systematic review of all research done on climate change effects on the Baltic Sea ecosystem this far. Also, certain taxonomic groups and study types were less thoroughly reviewed than others. Fish studies in particular were not comprehensively scrutinized, because the complex responses of fish populations to climate, eutrophication and fisheries have recently been addressed by a large number of studies and would merit their own review. Also, we have not reviewed all experimental studies that have dealt with environmental variables that may change with climate change. Our goal is to highlight the variety of field, experimental and modelling studies and to summarise what can be concluded from the recent evidence on the possible effects of climate change on the Baltic Sea.

Kommentoinut [VM2]: R2 General comments: The fact that many more mesocosm studies relevant for climate-change effect has been reported need to be clarified and preferably some references added. Also, clarify that just a selected number of studies using defined test variables are presented in table 1

4. Effects on species and communities

4.1. Phytoplankton

Climate change may have direct effects on the physiology and phenology on phytoplankton, through physical and chemical parameters, and indirectly through hydrodynamics, e.g., stratification, and availability of light and nutrients. Top-down forces, i.e., grazing on phytoplankton, may also be modified in various ways if grazer populations change.

The growing season of phytoplankton has been significantly prolonged with warming temperatures during the recent past decades. A satellite-based study suggested that the length of the period with chlorophyll concentration of at least 3 mg m^{-3} has in the Baltic Sea doubled, from 110 days in 1998 to 220 days in 2013 (Kahru et al., 2016). Another study using phytoplankton sampling data from the Bay of Mecklenburg, western Baltic Sea, confirmed that the phytoplankton growing season, which in 1988—1992 on average lasted from March to August, now (2014-2017), now extends from February to December (Wasmund et al., 2019), with a longer gap between the spring and late summer peaks. This prolongation was tentatively explained by increased sunshine in spring and higher temperature in the autumn, inducing changes in species composition and settling rates of phytoplankton, remineralization of organic matter by bacteria, and grazing rates by zooplankton (Wasmund et al., 2019).

The spring species communities have also shifted from dominance of early blooming diatoms to later blooming dinoflagellates and the mixotrophic ciliate *Mesodinium rubrum*

(Klais et al., 2011; Hällfors et al., 2013; Kuosa et al., 2017; Hjerne et al., 2019), probably due to changes in climate and weather patterns, including ice cover, solar irradiation and wind conditions (Klais et al., 2013; Hjerne et al., 2019). In the long-term data, variable results can be seen, according to area and dominating species group. For instance, spring phytoplankton biomass increased in the Baltic Proper but decreased in the Belt Sea area (1979-2005); both areas showed antagonism between communities dominated by diatoms or dinoflagellates, and the trends were therefore oscillating rather than linear (Wasmund et al., 2011). Symptoms of a regime shift were identified, and changes were attributed to approximately 10-year fluctuations in temperature, salinity, and nutrients. A linkage to global climate change was not detected (Wasmund et al., 2011).

Some studies have attributed the springtime shifts in phytoplankton phenology and community structure to changes in environmental conditions driven by global climate change. A fifteen-year study (2000-2014) using FerryBox observations, covering the area between Helsinki (Gulf of Finland) and Travemünde (Mecklenburg Bight), confirmed that spring bloom intensity was mainly determined by winter nutrient concentration, while bloom timing and duration co-varied with meteorological conditions. The authors conclude that the bloom magnitude has been affected by the reduction of nutrient loading from land, while bloom phenology can also be modified by global climate change affecting seasonal oceanographic and biogeochemical processes (Groetsch et al., 2016).

It has also been suggested that, in the future climate, higher temperatures and less ice will cause an earlier bloom of both diatoms and dinoflagellates, with increased dinoflagellate dominance (Hjerne et al., 2019). Experimental (mesocosm) evidence supports findings that warming up of water and changes in light conditions will accelerate the spring bloom, induce a decline in peak biomass and favour small size cells, either directly or via increased grazing by copepods (Sommer et al., 2012). On the other hand, this development may be counteracted by increases of windiness and cloudiness, which have also been projected by certain modelling studies (Hjerne et al., 2019). Recent studies have however indicated that the projections for spring and summer wind and radiation are uncertain (Christensen et al., 2022), and future weather changes and associated spring bloom dynamics therefore remain obscure.

Climate change effects, i.e., temperature increase, salinity decline and acidification have been shown to have variable results on the toxic dinoflagellate *Alexandrium ostenfeldii*. Generally, the growth rates, as well as saxitoxin production, increased with higher temperature and elevated pCO_2, but the responses were variable between strains (Kremp et al., 2012; Kremp et al., 2016). In contrast, temperature or salinity changes did not have a significant effect on cyst germination of this species (Jerney et al., 2019).

Climate change also increases concentration of water carbon dioxide, a compound necessary for primary production, and ocean acidification (OA) could therefore enhance productivity of phytoplankton. However, the results of experimental studies investigating effects of pCO_2 on phytoplankton are variable. The biomass of southern Baltic autumn phytoplankton (kept in 1400-L indoor mesocosms for 21 days) increased when pCO_2 was increased from 439 ppm to 1040 ppm, also under warm conditions (Sommer et al., 2015). In other experiments, 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 decrease of grazing by copepod nauplii in low temperature treatments (Paul et al., 2016).

There are also studies that have indicated a connection between phytoplankton and the North Atlantic Oscillation (NAO). A decline in the intensity of NAO in the 1990s was suggested to have caused by less cloudy conditions, giving more irradiance, and less windy conditions, inducing stronger stratification of surface water (Hjerne et al., 2019). If the shifts are driven by variations in NAO or the Baltic Sea Index (BSI, a regional index similar to the NAO), they may be temporary and reversable, whereas shifts caused by global climate change may be more enduring.

In the northern Baltic Proper, Åland Sea and the Gulf of Finland, the biomasses of Chrysophyceae, Prymnesiophyceae and Cyanophyceae have increased and the phytoplankton biomass maximum, which in the 1980’s was in spring and mainly consisted of diatoms, is now in July-August and is dominated by filamentous cyanobacteria (Suikkanen et al., 2013). This shift was explained by a complex interaction between eutrophication, climate induced warming, and increased top-down pressure, as well as changes in DIN:DIP ratio in summer (Suikkanen et al., 2013). In the Gulf of Bothnia, a gradual decline in salinity was also an important factor for phytoplankton community change in 1979 to 2012 (Kuosa et al., 2017).

It is obvious that climatic influences are intertwined with other processes and parameters affecting phytoplankton, especially anthropogenic nutrient loading from land and internal loading of nutrients from the sediments. There is however a discrepancy on the relative effects of eutrophication, climate change and other environmental and anthropogenic factors in explaining past variations in phytoplankton communities and biomass. Also, several studies have identified complex variations in phytoplankton communities that cannot be easily explained by any of the studied factors or environmental parameters.

A study comparing historic phytoplankton communities from 1903-1911 with the present ones (1993-2005) in the northern Baltic Proper and the Gulf of Finland observed an undefined “period effect”, characterized by a decline of diatoms and increase of dinoflagellates, that was not well explained by the available environmental variables (temperature, salinity, and general regional climatological data). Although data on biogeochemical parameters was not available for the period 1903-1911, the authors interpreted the observed community change as evidence of the direct and/or indirect influence of eutrophication (Hällfors et al., 2013).

Kommentoinut [VM3]: R2:
r. 293 The reported period is wrong.

A study investigating summer phytoplankton time series (HELCOM monitoring 1979-2012) across the Baltic Sea found that there were no common interannual patterns. Instead, the class trends, e.g. that of cryptophytes, may be affected by anomalies in the BSI, although a mechanistic explanation for the relationship could not be found (Griffiths et al., 2020). Other studies did not find any explanation for the observed changes in the biovolumes of different taxa, e.g. decrease of diatoms and increase of certain dinoflagellate taxa, 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).

To sum up, the past changes in phytoplankton community composition have been very variable, and usually cannot be explained by a single factor. Some clear signs of climate change, such as prolongation of the growing season are evident, and can be explained by the warming and associated biogeochemical processes, but the changes in species and communities vary from area to area and have multiple reasons, including climate change, changes in nutrient dynamics, as well as changes in trophic interactions.

4.2. Cyanobacteria

Filamentous diazotrophic cyanobacteria benefit from warm temperatures and stratified water, and they tend to bloom during the hottest and calmest periods of summer (Munkes et al., 2021). Several modelling studies suggest that the climate induced increase in stratification (Liblik and Lips, 2019), together with potentially increasing hypoxia, and consequent release of phosphorus from the anoxic sediments, will increase cyanobacteria blooms in the Baltic

Sea (Meier et al., 2011a; Neumann et al., 2012; Chust et al., 2014; Lessin et al., 2014; Andersson et al., 2015; Ryabchenko et al., 2016).

Many field studies have also stated that cyanobacteria have already increased along with the warming of the Baltic Sea. In the northern Baltic Proper, Åland Sea and the Gulf of Finland, the biomasses of Cyanophyceae have increased, which has been explained by an interaction between warming, eutrophication and increased top-down pressure on species of the spring bloom, as well as changes in DIN:DIP ratio in summer (Suikkanen et al., 2013).

Also, in the Gulf of Bothnia, eutrophication and cyanobacteria have increased in summer (Fleming-Lehtinen et al., 2015; Kuosa et al., 2017), and extensive cyanobacteria blooms have in the past few years been detected with satellite methods in the Bothnian Sea, an area usually devoid of such phenomena (unpublished monitoring and satellite records collected by the Finnish Environment Institute). The increase of cyanobacteria in the Bothnian Sea has been attributed to an increased freshwater flow and, since 2000, to an increased intrusion of more saline and phosphorus rich Baltic Proper water into the Bothnian Sea. These changes have increased stratification, lowered oxygen conditions, and led to a decline in N:P ratio of the Bothnian Sea, which has favoured the development of cyanobacteria blooms in the area (Rolff and Elfwing, 2015; Ahlgren et al., 2017; Kuosa et al., 2017)

It has also been suggested that the various drivers of climate change may contribute to increase blooms and toxicity of cyanobacteria in the Baltic Sea~~species such as the dinoflagellate *Alexandrium ostenfeldii* (Kremp et al., 2012; Kremp et al., 2016; Jerney et al., 2019)~~. ~~Also, t~~For instance, the intracellular toxin concentration of the 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). As toxins of both dinoflagellates (Sopanen et al., 2011) and cyanobacteria (Karjalainen et al., 2006; Karjalainen et al., 2007; Engström-Öst et al., 2017) can accumulate in Baltic Sea zooplankton and induce lower grazing rates and higher mortality, these studies suggest that toxic dinoflagellates and filamentous cyanobacteria may get, due to their toxic effects and unpalatability, a competitive advantage over diatoms and other phytoplankton in a future Baltic Sea.

A few long-term studies have not found an increase in cyanobacteria during the past. Two recent studies compiling monitoring data from the Baltic Sea for 1979-2012 (Griffiths et al., 2020) and 1979-2017 (Olofsson et al., 2020) did not find any evidence for an overall increase of diatzotrophic filamentous cyanobacteria during this period. Biovolume of the hepatotoxic *Nodularia spumigena* did not change, and that of the non-toxic *Aphanizomenon* sp. increased in the north and declined in the south (Olofsson et al., 2020). Also, a study that compared years 1903-1911 and 1993-2005 concluded that cyanophyte biomass has not increased in summer and have decreased in spring and autumn (Hällfors et al., 2013). It has been suggested that, although cyanobacteria do prefer warmer temperatures, the effect of ongoing warming can better be seen in changes in phenology of cyanobacteria rather than as an increase of biomass (Griffiths et al., 2020). Also, a connection between the amount of cyanobacteria and the Baltic Sea Index has been identified (Griffiths et al., 2020).

Hypothetically, ocean acidification could benefit cyanobacteria through increased availability of carbon dioxide in water. The available studies do not give a definitive answer, however. When pCO_2 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 the biomass of cyanobacteria, especially that of nitrogen-fixer *Dolichospermum* sp. declined (Berner et al., 2018). Further, in mesocosm studies an increase of pCO_2 (from 360 to 2030 µatm) coupled with an increase in water temperature (from 16.6 to 22.4 °C) had a *negative* impact on the biomass of the diatzotrophic cyanobacteria *Nodularia spumigena* (in 1400-L mesocosms, 28 days) (Paul et al., 2018). Another experimental study (using 75 ml cell culture flasks), investigating the effects of increased temperature (from 12 to 16 °C), decreased salinity (from 7 to 4), and elevated pCO_2 (from 380 to 960 ppm), found that only temperature had an effect on biovolume and photosynthetic activity of *Nodularia spumigena* and *Aphanizomenon* sp. (Karlberg and Wulff, 2013). The two species however had antagonistic effects on each other: biovolumes were lower when grown together than when grown separately, indicating species interactions.

If the biomasses of *Nodularia* sp. 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). This could however be balanced by the potential increase of *Cyanothece*, which is also a nitrogen-fixer (Eichner et al., 2014).

To sum up, there are species specific responses to climate change and associated oceanographic parameters within cyanobacteria. Several field and modelling studies suggest that the climate induced increase in temperature and stratification, together with increasing hypoxia and release of phosphorus from the sediments, has increased cyanobacteria biomass and will continue to favour cyanobacteria blooms also in the future . However, the results of certain empirical and experimental studies give a more multifaceted picture of cyanobacteria response to climate change. The past increase of cyanobacteria is not as obvious as might be expected, responses vary from species to species, and processes affecting amount of cyanobacteria in the Baltic Sea can be modified, counteracted, or amplified by various environmental processes and food web interactions.

4.3. ~~Zooplankton~~Mesozooplankton

The Baltic Sea mesozooplankton species originate either from marine or freshwater environments, and some are typically brackishwater. It is therefore plausible that they respond to long-term variations in oceanographic parameters. Several field studies have confirmed that marine copepod species (e.g., *Pseudocalanus* spp. and *Temora longicornis)* declined during the 1980s and 1990s, while euryhaline and limnetic, smaller-sized copepod species (*Acartia* spp. and *Eurytemora* spp.) increased in abundance (Suikkanen et al., 2013; Hänninen et al., 2015), and the decline of marine taxa has usually been proposed to be linked to a decrease of salinity (Suikkanen et al., 2013; Hänninen et al., 2015). It has also been experimentally shown that close to the physiological tolerance limit for salinity (below 7 psu), respiration of copepods (*Acartia longiremis*) increases and feeding rate decreases (in 610 ml bottles, 24 h experiments), indicating a disruption of the energetic balance under low salinity (Dutz and Christensen, 2018).

Environmental impacts on the physiology of the more sensitive species may also affect the reproductive success of zooplankton (Möller et al., 2015). The increase of euryhaline taxa has been, directly or indirectly, attributed to the temperature increase (Mäkinen et al., 2017). It has also been suggested that species that reside in the upper water layers, such as the copepod *Acartia* sp., 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; Mäkinen et al., 2017).

The effects of climate-driven variations in temperature and ocean acidification (OA) on zooplankton have been studied experimentally. In *Acartia* sp., warming decreased egg viability, nauplii development and adult survival (in 1.2-L bottles, during 60-hours) (Vehmaa et al., 2013). In other experiments, both warming (Garzke et al., 2015) and OA (Vehmaa et al., 2016) had negative effects on adult female size. This suggests that the projected warming combined with ocean acidification may have negative effects on the populations of these copepods in the future Baltic Sea.

Changes in zooplankton functional groups, such as a shift from raptorially and suspension-feeding copepods and cladocerans to a dominance by small filter-feeding rotifers and cladocerans, have also been shown as results of warming (Suikkanen et al., 2013; Jansson et al., 2020). OA also promoted the growth of suspension-feeding cladocerans, because of a CO_2driven increase of cyanobacteria (Lischka et al., 2017).

Furthermore, a switch from predominantly herbivorous feeding by copepods to predation on ciliates has been observed in a field study in the southern and central Baltic Sea, during cyanobacterial blooms (Loick-Wilde et al., 2019). This was caused by decomposing of the otherwise unpalatable filamentous cyanobacteria, and an associated increase of the bacteria, nanoflagellates and ciliates (Hogfors et al., 2014). Warming may also increase zooplankton grazing on medium-large-sized algae, which could contribute to a change towards smaller-sized phytoplankton species (Klauschies et al., 2012; Paul et al., 2015). It is therefore possible that the dominant traits of zooplankton communities will change if climate-induced warming and reduced salinity trends continue. It has also been suggested, from experimental (mesocosm) evidence, that warming speeds up the growth of copepods but leaves phytoplankton unaffected, which shortens the time lag between phyto- and zooplankton. This may lead to a larger and earlier zooplankton peak and increase the possibility of zooplankton controlling phytoplankton, which may lead to a reduced phytoplankton biomass under warm temperature (Paul et al., 2016).

Sufficient supply of essential compounds such as amino acids (AA) produced by phytoplankton and cyanobacteria is essential for the growth and productivity of zooplankton grazers. A field study performed in the Baltic Proper shows that, during a warm summer, thermophilic rotifers and cladocerans (e.g. *Bosmina* spp.) acquired ample AA through filter feeding on the abundant diazotrophic cyanobacteria, whereas the temperate copepods (e.g. copepods *Temora longicornis* and *Pseudocalanus* spp.) avoided the warm surface layer and acquired AA mainly through sinking organic matter and/or via grazing on chemoautotroph based microbial food web in the suboxic zone (Eglite et al., 2018). Mesocosm experiments have also demonstrated that a high bacterial production can maintain copepod production (Lefébure et al., 2013), but that increased heterotrophy leads to a decreased fatty acid content and lower individual weight of copepods (Dahlgren et al., 2011). This may imply that thermophilic zooplankton species, such as rotifers and certain cladocerans gain more AA than copepods in a future warmer ~~and more stratified~~ Baltic Sea.

Kommentoinut [VM4]: R2 General comments:
The fact that many more mesocosm studies relevant for climate-change effect has been reported need to be clarified and preferably some references added.

Little is known on the adaptation capabilities of zooplankton against physicochemical stress, but some degree of temperature adaptation has been demonstrated experimentally for the copepod *Eurytemora affinis* (Karlsson and Winder, 2020). Interestingly, the adaptability was better in populations reared in warm temperatures (≥17°C), which suggests that southern populations can better cope with increasing temperatures than the northern ones, and that the adaptation capability of all (surviving) populations may improve with proceeding climate change.

To sum up, a shift towards smaller size zooplankton and a stronger linkage between mesozooplankton and the microbial ~~loop~~ food web is probable in a warmer Baltic Sea. A decline of certain marine species has also been projected, but this will depend on the future velocity of salinity decline, patterns of stratification, realized time lag between phyto- and zooplankton peaks, predation pressure by fish, and on the possible adaptation of zooplankton species to the subtle changes in salinity.

4.4. Bacteria and the microbial ~~loop~~food web

Kommentoinut [VM5]: R2:
r. 467 I would avoid “loop” as having an unclear and even misleading meaning (instead “microbial (part of the) food web”. How is “loop” justified? Microorganisms constitute the original food web in the biosphere and is an integral part of the modern food web. It both contribute to biomass flow and remove biomass by respiration. As most organisms.

Bacteria are key components of the ecosystem, as they decompose organic material, and serve as food for heterotrophic nanoflagellates and the associated microbial ~~loop~~food web. They affect the nutrient and carbon dynamics of the marine ecosystem and it is therefore possible that climate impacts on bacteria may radiate to the structure and functioning of the entire Baltic Sea ecosystem.

The effects of climate induced changes in environmental factors to pelagic bacteria and the other components of the microbial ~~loop~~ food web have been studied experimentally. The effects of projected ocean acidification (OA) on bacteria have been studied alone and also in combination with with other abiotic variables, such as temperature (OAW) and salinity (OAS). OA alone had a limited impact on spring bloom microbial communities (sampled from the sea area around the island Öland in the Baltic Proper and kept in 100-liter mesocosms for 21 days), but when combined with increased temperature, certain bacterial phylotypes, such as betaprote~~r~~obacteria, increased. It was suggested that synergistic effects of increased temperature and acidification selectively promote growth of specific bacterial populations (Lindh et al., 2013). In the southern Baltic Sea (Kiel Bight) the impact of OA was studied in 1400-liter indoor mesocosms for 21-24 days. Acidification only affected few operational taxonomic units (OTUs), such as *Bacteroidetes* `NS3a marine group´, as the bacterial community mainly responded to temperature and phytoplankton succession.

Kommentoinut [VM6]: R2:
r. 481 Correct to “betaproteobacteria”. Indeed, all “proteo” phrases need correction.

Depending on studied season and temperature treatment, Cyanobacteria, *Bacteroidetes*, Alphaprote~~r~~obacteria and/or Gammaprote~~r~~obacteria increased under OA (Bergen et al., 2016).

In an OAS experiment (4-liter aquaria, 12 days) using a natural summer microplanktonic community, the biovolume of heterotrophic bacteria declined when pCO_2 was increased (from 380 to 960 µatm) and salinity was decreased (from 6 to 3 psu) (Wulff et al., 2018). In experiments done in the Baltic Proper (NW Gotland Sea, 25-liter microcosms for 23 days), where temperature was increased (from 16 to 18-20 °C) and salinity reduced (from 6.9 to 5.9 PSU), the microbial community showed mixed responses. No conclusive evidence of direct climate-induced change could be detected (Berner et al., 2018). At reduced salinity levels, certain Actinobacteria and *Bacteroidetes* OTUs increased, and the heterotrophic bacteria community resembled communities at high temperature, indicating synergistic effects of temperature and salinity. Biotic interactions were more dominant than abiotic ones, however. The largest increase in heterotrophic bacterial biomass was detected when filamentous cyanobacteria started to decay, regardless of temperature or salinity. It was suggested that this indirect coupling between heterotrophic bacteria and filamentous cyanobacteria is more important for bacterial communities than the direct effects of climate induced changes in temperature or salinity (Berner et al., 2018).

Experimental studies have demonstrated that complex food web responses to climate change may also arise. In ~~Kvarken~~the Quark, the Gulf of Bothnia, increase of dissolved organic matter (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). Mesocosm experiments done in the Gulf of Bothnia area have however demonstrated that increasing dissolved organic carbon (DOC) enhances bacterial production and leads to a promotion of heterotrophy (Dahlgren et al., 2011; Andersson et al., 2013)~~,~~. ~~but that a~~Also mixing depth influences the ratio of heterotrophic to autotrophic production: with a shallow pycnocline, the autumn plankton community in the northern Bothnian Sea remained net-autotrophic irrespective of DOC, whereas with increased mixing depth and with added DOC the system became net-heterotrophic (Båmstedt and Wikner, 2016).

Kommentoinut [VM7]: R2:
r. 506 Please correct to "In the northern Quark, …"

Kommentoinut [VM8]: R2 General comment:
The fact that many more mesocosm studies relevant for climate-change effect has been reported need to be clarified and preferably some references added.

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 pCO_2 (Horn et al., 2016). The abundance of the mixotrophic ciliate *Mesodinium* sp. even increased in mesocosms with OA, because of increase of its prey and food, e.g. picoeukaryotes, at higher CO_2 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.

To sum up, different components of the microbial ~~loop~~ food web show very variable responses to climate induced changes in temperature, salinity, and pH. Bacteria growth is generally favoured by increasing temperature, but mixed effects are common, and indirect processes affecting decay and availability of organic matter, and abundances of species predating on bacteria, are also important. This highlights the importance of considering the effects of abiotic factors and the delicate indirect food web effects on the dynamics of the microbial ~~loop~~food web, and the pelagic ecosystem in general.

4.5. Macroalgae and vascular plants

Long-term changes in Baltic Sea macroalgae and charophytes have mostly been explained by combined or synergistic effects of changes in salinity, wind exposure, nutrient availability and water transparency (Gubelit, 2015; Blindow et al., 2016; Eveleens Maarse et al., 2020; Rinne and Salovius-Laurén, 2020), as well as biotic interactions (Korpinen et al., 2007).

For the brown alga bladderwrack *Fucus* spp., light availability, which may also be affected by partly climate-driven changes in eutrophication, affects their local coverage (Lappalainen et al., 2019). A documented long-term decrease of water transparency in 1936 to 2017 has reduced favourable sea floor areas for *Fucus* spp. by 45% (Sahla et al., 2020), and resulted in a halving of the depth range of *F. vesiculosus* in the Åland Islands (Eveleens Maarse et al., 2020). For many shallow coastal ecosystems of the Baltic Sea, it has been concluded that eutrophication is the most important pressure affecting the ecosystem structure and functioning (Olsson et al., 2015). This is plausible, because of the strong influence of anthropogenic nutrient loading in coastal areas (Vigouroux et al., 2021), especially those that are prone to hypoxia due to complex topography (Virtanen et al., 2018a), and which often are affected by internal loading of phosphorus from the sediment (Puttonen et al., 2014; Puttonen et al., 2016).

The effects of anthropogenic eutrophication on macroalgae may however be amplified or counteracted by climate induced changes in environmental parameters. Such interactions are reviewed below.

The direct effects of climate induced changes in temperature, salinity and ocean acidification (OA) on bladderwrack *Fucus vesiculosus* have been investigated by a number of experimental studies. 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 impacts of increasing temperature are not linear, however. Growth or photosynthesis is not impaired under temperatures of 15 to 17.5 °C but at extreme temperatures, simulating heat waves of 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).

The timing of temperature stress is however important for the damage experienced by algae. Experiments done with bladderwrack *Fucus vesiculosus* (in 1500-L tanks in Kiel, the western Baltic Sea) showed that in the early and late summer warming of 1 to 5 ℃ above ambient had mostly beneficial effects on bladderwrack, whereas in midsummer a similar warming had negative effects (Wahl et al., 2021). During midsummer, the heat waves surpassed the physiological tolerance limits of the species, with detrimental effects on growth.

Ocean acidification combined with warming (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 if they were already stressed by OAW (Al-Janabi et al., 2016b).

Climate induced decline in salinity may affect communities via its direct effect on the physiology of individual populations and species. A retreat towards the south/south-west has been predicted for marine species such as bladderwrack and eelgrass, and for species affiliated to them (Vuorinen et al., 2015). Species distribution modelling studies have suggested that this mainly salinity-induced decrease of bladderwrack will cause habitat fragmentation 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 to what degree *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, diminished potential for adaptation and therefore, an increased risk of local extinction (Johannesson et al., 2011). E.g., *F. vesiculosus* has long generation time and relatively restricted dispersal, and therefore the dispersal rate of locally adapted genotypes may not keep pace with the projected velocity of salinity decline (Jonsson et al., 2018). However, a growing body of evidence from experimental studies shows that *F. vesiculosus* has phenotypic plasticity and tolerance against salinity change (Rothäusler et al., 2018; Rugiu et al., 2018a, b), and genetic studies show that different sibling groups of *F. vesiculosus* have different responses to environmental change, including OAW (Al-Janabi et al., 2016a; Al-Janabi et al., 2016b). There may also be population-specific responses to different stressors, especially if populations are genetically isolated. In a study performed in the Danish Straits, certain populations of *F. vesiculosus* were only slightly affected by a salinity decline, while others displayed clearer responses; one population even showed severe stress symptoms and stopped growing (Kinnby et al., 2020).

It has also been shown that *Fucus radicans*, an endemic congener of *F. vesiculosus*, which is tolerant to low salinity, might be able to occupy the niche of *F. vesiculosus* in the northernmost Baltic if salinity declines (Rugiu et al., 2018a). If *F. radicans* can replace the ecological functions of its congener, its increase may potentially delay or modify the most drastic consequences of climate change on the invertebrate and fish species dependent on bladderwrack belts. Changes in species interactions involved in climate induced environmental changes are however very difficult to project. Some studies project a decrease of grazers of *Fucus* spp. in the northern areas (Kotta et al., 2019), while others predict an increase (Leidenberger et al., 2015).

Similar experiments on climate change effects as done with bladderwrack have also been made with other macroalgae and certain vascular plants. In field mesocosm experiments, OA increased the growth of the opportunistic green alga *Ulva intestinalis* in the Kõiguste Bay, Gulf of Riga, Estonia (Pajusalu et al., 2013; Pajusalu et al., 2016). This suggests that OA could favour such fast-growing species and induce an overgrowth of *Fucus* sp. by annual green algae.

Salinity decline is projected to decrease the distributional ranges of the marine eelgrass *Zostera marina* and the red alga *Furcellaria lumbricalis* (Torn et al., 2020) The changing environment poses an evolutionary risk for populations that live close to the limits of their geographical ranges (Johannesson et al., 2011), including *Z. marina* (Billingham et al., 2003). Indeed, mesocosm studies have indicated that, while OA has little effect on the eelgrass *Zostera marina* (Pajusalu et al., 2015), they suffer from heatwaves in summer (Ehlers et al., 2008) and elevated temperatures in winter-spring period (Sawall et al., 2021). On the other hand, the viability of eelgrass beds also strongly depends on water clarity. A study performed for the southernmost Baltic Sea coupled biogeochemical and species distribution modelling to assess how projected wind fields, hydrodynamic conditions and nutrient abatement scenarios affect the distribution of eelgrass *Z. marina* in the future (2062-2066). It was concluded that nutrient reductions that fulfil the Baltic Sea Action Plan of the Helsinki Commission (HELCOM BSAP) will lead to an expansion of eelgrass coverage, despite potentially harmful effects on eelgrass distribution caused by the climate change (Bobsien et al., 2021).

Certain species may be favoured by the projected climate change. Lowering of salinity generally favours vascular plants originating from freshwater, and temperature increase favours thermophilic species, such as charophytes (Torn et al., 2020). In mesocosm studies made in Kõiguste Bay, photosynthesis of charophytes (*Chara aspera*, *C. tomentosa* and *C. horrida*) increased under high pCO_2 treatments (Pajusalu et al., 2015), which suggests that they may be favoured by ocean acidification.

To sum up, recent studies suggest that changes in species composition of macroalgae and vascular plants are likely, due to temperature, pH, and salinity changes. Climate change, in conjunction with other environmental changes (especially eutrophication) may also influence carbon storage in both macroalgae and vascular plants in the Baltic Sea (Röhr et al., 2016; Takolander et al., 2017a; Jonsson et al., 2018; Salo et al., 2020; Bobsien et al., 2021). It has been projected that macroalgae will decline in hard bottoms and vascular plants increase in the more sheltered soft bottom areas (Torn et al., 2020). Because algae and plants mostly occupy different habitats, the possible increase of vascular plants or charophytes cannot counteract the negative effects of the disappearance of macroalgae from hard bottom areas. Consequently also the invertebrates, fish and birds benefiting from habitats formed by macroalgae will suffer from the climate change.

As with other species groups, projecting the fate of macroalgae and vascular plants is challenging. This is caused by the uncertainties in projections concerning salinity and stratification (Lehmann et al., 2022), discrepancy on which physicochemical factors determine the distribution of invertebrates, unknown adaptation capabilities of algae and plants, and by uncertainties concerning future trophic interactions within macroalgae and vascular plant communities.

4.6. Benthic invertebrates

Soft bottom benthic communities are dependent on several hydrographic and biogeochemical variables, and parameters that change with climatic variations have been shown to drive the long-term progression of zoobenthic communities (Weigel et al., 2015; Rousi et al., 2019; Ehrnsten, 2020). In the SW coast of Finland, a drastic community change took place, with amphipods being replaced by Baltic clam *Limecola balthica* and the non-indigenous polychaete *Marenzelleria* spp. This major community change was explained by an increase in near-bottom temperature and by fluctuations in salinity and oxygen (Rousi et al., 2013). In the Åland Islands (northern Baltic Sea), zoobenthos variations in 1983-2012 were associated with salinity decline, and environmentally driven shifts in the links between zoobenthos and benthic-feeding fish assemblages were recorded (Snickars et al., 2015). Long-term climate-induced shifts in zoobenthos and other trophic levels have also been described in various parts of the Baltic Sea (Törnroos et al., 2019; Forsblom et al., 2021). In all these cases, interactions between the physico-chemical climate-affected parameters and secondary impacts (mainly eutrophication and/or hypoxia) have been identified.

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 differences between and within regions (Rugiu et al., 2018c). Also, effects of warming on invertebrates are often non-linear, with stress effects being manifested after a certain threshold. 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). Heat waves, which have been projected to increase in frequency (Meier et al., 2019a), may therefore pose a severe threat to sublittoral invertebrates (Pansch et al., 2018). Different species show different responses to single and sequential heat waves, however, resulting in a change in community structure. E.g., the bivalve *Limecola balthica* suffered from repeated heat waves, whereas the sessile amphipod *Corophium* sp. benefited from them. The polychaete *Polydora cornuta* seemed to get acclimated to heat waves when they were repeated, showing some signs of adaptation. In general, heat waves favoured crawling or burrowing predators and suspension feeders, while the abundance of detritivores decreased, suggesting a climate-induced change in dominant zoobenthic traits (Pansch et al., 2018).

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 in mesocosms (in the western Gulf of Finland) with OA, suggesting a developmental delay (Jansson et al., 2016), while OA had no effects on larvae of the bay barnacle *Amphibalanus improvisus* originating from Kiel Fjord, southern Baltic Sea (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 the more oceanic and 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.

Several modelling studies have suggested that climate-induced changes in temperature, salinity and eutrophication, affecting oxygen levels and food availability for benthos, drive the development of benthic communities and their biomass in the future (Ehrnsten et al., 2019a; Ehrnsten et al., 2019b). A physiological fauna model linked to a 3D coupled hydrodynamic–ecological 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). The fate of zoobenthos also depends on human intervention, i.e., success of nutrient reduction schemes. For instance, it has been projected that, if the HELCOM BSAP will be implemented, the biomass of benthic animals, and hence food for benthic-eating fish, will first increase and then decrease (Ehrnsten et al., 2020).

There are very few modelling studies focusing on invertebrates inhabiting shallower hard bottom habitats. One study, where experimental work and species distribution modelling were combined, projected a decline of the isopod *Idothea balthica* in the future, mainly due to the salinity-induced decline of its host macroalgae, *Fucus vesiculosus* (Kotta et al., 2019). Another study reached quite different conclusions. Species distribution models combined with oceanographic-biogeochemical scenarios for 2050 projected an increase in habitat suitability for *Idotea balthica* and *I. chelipes*, and concluded that changes in temperature and ice cover will be more important determinants for these species than changes in salinity (Leidenberger et al., 2015).

One modelling study also investigated how *Saduria entomon*, a cold-water crustacean that occupies brackish and limnic parts of the Baltic Sea, will be affected by climate change and eutrophication (Gogina et al., 2020). The applied models project a net increase (and some local declines) for *S. entomon*, and conclude that the positive effects of declining salinity will override the effects of the two nutrient load scenarios (business as usual and BSAP). The success of this species in the future warmer conditions is also facilitated by its good tolerance for temperature changes.

It is notable that hypoxia, which is a key factor affecting zoobenthos, is by no means limited to the deep basins of the Baltic Sea (Conley et al., 2011). Especially the archipelagos of the northern Baltic Sea are, due to their complex topography and limited water exchange, prone to hypoxia (Virtanen et al., 2018a). Increasing sea surface temperature will strengthen stratification and enhance mineralization of organic matter by microbes, which may increase the release of phosphorus from sediments (Puttonen et al., 2016) and lead to a “vicious circle of eutrophication” (Vahtera et al., 2007). The sheltered archipelago areas and enclosed bays may therefore become “climate change hotspots” (Queiros et al., 2021), where also zoobenthic communities are most drastically changed.

To sum up, zoobenthic communities are affected by all environmental parameters that are projected to change with climate change, i.e., temperature, salinity, pH and oxygen, as well as benthic-pelagic coupling. However, the effects are not unidirectional and several processes may amplify or counteract the possible changes. The magnitude of the future salinity decline is unclear, and other factors, such as decreasing ice cover and changes in future wind conditions (of which no consensus exists) may also affect nutrient and oxygen dynamics of the Baltic Sea. Also, there may be feedback effects on sediment oxygen levels, as different benthic species have different bioirrigation activities (Norkko et al., 2012; Guy-Haim et al., 2018). Such processes, that are dependent of traits of a few species, may be of particular importance in low-diversity systems such as the northern Baltic Sea (Gladstone-Gallagher et al., 2021).

4.7. Non-indigenous invertebrates

It is often suggested that global climate change favours invasions of non-indigenous species (NIS) worldwide (Jones and Cheung, 2015). This is plausible, because increase of temperature will open new niches and induce a poleward shift of the ranges of species inhabiting tropical and temperate sea areas. In the Baltic Sea, it has been shown that non-native species typically occur in areas characterized by high temperatures, reduced salinity, 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 climate induced range expansion of non-native species than the latter. This is consistent with the hypothesis of climate change hotspots, which suggests that some coastal areas may be more susceptible to effects of climate change than others (Queiros et al., 2021).

Modelled scenarios of temperature and salinity have been used to project how changes in the abiotic environment could affect NIS already present in the Baltic Sea. One modelling study 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).

To sum up, the global climate change induces many environmental changes that may favour establishment of NIS in the Baltic Sea. However, attribution of the observed establishments to the climate change is difficult. It has even been claimed that there is no conclusive evidence that NIS will gain significant advantage from environmental alterations caused by climate change (Henseler et al., 2021). Stochastic processes related to maritime transport and other types of human activities are obviously important for the chances of NIS to be introduced and established into a given sea area. Long-term surveys, and comparisons with areas where NIS have not been established, are needed to distinguish climate-related effects from other ecosystem-level drivers (Bailey et al., 2020).

4.8. Fish

Fish populations in the Baltic Sea are influenced by various environmental and anthropogenic factors, including nutrition, predation, habitat destruction, and fisheries, but also by climatic variations.

Sprat probably benefits from global climate change, because increasing spring and summer temperatures have in empirical studies been observed to increase survival of sprat eggs and larvae (Voss et al., 2012) and in modelling studies to increase productivity and biomass of sprat (Voss et al., 2011b; Mackenzie et al., 2012; Niiranen et al., 2013).

For herring the results are more variable. The growth rate of herring larvae is positively affected by temperature (Hakala et al., 2003), but weight-at-age and stock biomass of herring adults has in several studies been linked to the availability of food, mainly determined by the abundance of marine copepods and competition with sprat (Flinkman et al., 1998; Möllmann et al., 2003; Casini et al., 2011; Heikinheimo, 2011; Otto et al., 2014b). In modelling studies both increase (Bartolino et al., 2014) and a short-term decrease (until 1950) (Niiranen et al., 2013) of herring populations have been projected.

Both herring and sprat populations have probably benefited from the eutrophication during the 1950s to 1980s (Eero et al., 2016), during the same period as the Baltic Sea eutrophication status changed from good to poor (Andersen et al., 2017; Murray et al., 2019). Since then, sprat biomass has varied independently of nutrient dynamics, and has been more strongly affected by climatic variation and top-down control, i.e. cod predation and fisheries (Eero et al., 2016).

Based on experimental and modelling studies, future climatic variations may affect Baltic cod through their effects on water temperature, salinity, oxygen, and pH, as well as nutrients, which indirectly affect both the availability and quality of food (Limburg and Casini, 2019; Möllmann et al., 2021). The responses of cod larvae to ocean acidification (OA), have been studied experimentally, also in combination with warming (OAW). In some studies, no effects of OA or OAW on hatching, survival or development rates of cod larvae were found (Frommel et al., 2013), while in others mortality of cod larvae doubled when they were treated with high end projections of OA (based on RCP8.5). When the projected increase of mortality was included into a stock-recruitment model, recruitment of western Baltic cod declined to only 8 % of the baseline recruitment (Stiasny et al., 2016), suggesting a dramatic effect of OA on cod populations.

A thorough review including long-term data and modelling demonstrated how predation, fishing, eutrophication, and climate have sequentially affected eastern Baltic cod during the past century (Eero et al., 2011). In the early decades of the 20th century, cod reproduction was successful but seal predation and food availability kept the size of cod stock at a moderate level. From the 1940s, fishing replaced seal predation in controlling cod population, whereas the slowly increasing eutrophication had a minor positive influence on cod spawning stock biomass in 1950s to 1970s. In the late 1970s, a series of large saline inflows increased the salinity of the Baltic Sea and kept oxygen conditions in the deep basins favourable for cod. Consequently, reproduction peaked in 1978-1982 and, as also fishing pressure was temporarily low, the spawning stock biomass increased to a record-breaking level of ca. 700,000 tonnes in 1980-1984 (Eero et al., 2011). After this peak period, cod stock started to decline, due to a drastic reduction of the ‘cod reproductive volume’ (RV), water layer sufficiently saline and oxic for survival of cod eggs and larvae. The decline of RV was associated to a stagnation period with low oxygen, caused by a combination of anthropogenic eutrophication and climate-induced paucity of major saline inflows. Since then, the productivity of cod stocks has remained low (Eero et al., 2020), and also the average maximum length of cod individuals has been constantly declining (Orio et al., 2021). The reason for low growth may have been the low availability of both benthic and pelagic food (Neuenfeldt et al., 2020). Alternatively, a long-term exposure to low oxygen conditions may affect body chemistry (Limburg and Casini, 2019) and decrease digestion rate and food consumption of cod (Brander, 2020). The physiological hypothesis is strengthened by the observed increase in depth distribution of cod and consequent dwelling of cod in low oxygen water (Casini et al., 2021).

Several studies project low abundances of cod towards the end of the century, due to the climate and eutrophication induced decrease of RV (Eero et al., 2011; Gårdmark et al., 2013; Niiranen et al., 2013; Eero et al., 2020; Wåhlström et al., 2020). It has also been speculated that seal predation could contribute to keeping cod stocks low. However, although seal predation can cause damage to cod fisheries in coastal areas (Blomquist and Waldo, 2021), it has been concluded that the increased seal predation is a less important factor for the future size of fish stocks in the Baltic Sea than climate, eutrophication and fisheries (Mackenzie et al., 2011; Tomczak et al., 2021).

There is some disagreement on the effect of fisheries on cod stocks in the future. Earlier studies suggested that fisheries limitations may well enable stock recovery even in a ‘cod-hostile’ environment (Cardinale and Svedäng, 2011; Heikinheimo, 2011). Certain recent modelling studies have however been less optimistic, and projected that cod productivity will remain low, due to the large impact of environmental drivers, especially oxygen and availability of food (Eero et al., 2020). For the western Baltic cod (inhabiting the Danish straits and the Arkona Sea) it has even been suggested that cod is now beyond a tipping point, with severe ecological, economic, and social consequences. At a critical moment, fisheries management failed to fully consider the changed environmental conditions, and climatic factors now prevent the recovery of cod stocks (Möllmann et al., 2021).

Increasing seawater temperature has also made it possible for certain warm water Atlantic species, such as anchovy (Alheit et al., 2012) and sole and turbot (Sparrevohn et al., 2013) to occur more abundantly in Kattegat and the southernmost Baltic Sea. Such north- and eastward migrations of these warm-water species may be caused by both global climate change and by variations in the Northern Hemisphere temperature Anomalies (NHA), North

Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO), as well as contraction of the subpolar gyre (Alheit et al., 2012; Sparrevohn et al., 2013).

As for coastal freshwater 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) and cyprinids, eutrophication status of coastal waters is however a more important factor for distribution than climatic variation (Snickars et al., 2015; Bergström et al., 2016). A long-term study covering four decades (1970s to 2010s), made at different coastal areas of the Baltic Sea, illustrated that it is hard to disentangle the effects of abiotic factors from biotic interactions affecting fish and their benthic food-sources (Törnroos et al., 2019).

To sum up, temperature, salinity, oxygen and pH have a big impact on Baltic fish recruitment and growth and, as all these variables respond to climatic variations, it seems evident that fish communities in the Baltic Sea will undergo changes, with the open sea ecosystem remaining clupeid dominated, and certain freshwater fish increasing in coastal areas (Reusch et al., 2018; Stenseth et al., 2020; Möllmann et al., 2021). Together with other environmental changes, especially eutrophication, changes in fish populations may lead to altered food web dynamics (Eero et al., 2021), necessitating ecosystem-based management of fisheries and socio-ecological adaptation (Woods et al., 2021).

5. Climate change and ecosystem structure and function

~~As seen from the above studies, t~~The Baltic Sea ecosystem is impacted by climate induced changes in the physical and biogeochemical environment in various ways. Climatic changes affect species and populations directly and indirectly, also impacting micro-evolution of species and having synergistic effects on other environmental drivers such as eutrophication and hypoxia (Wikner and Andersson, 2012; Niiranen et al., 2013; Ehrnsten et al., 2020; Pecuchet et al., 2020; Schmidt et al., 2020). In synergy, these impacts have already boosted the emergence of ‘novelty’ in the system and profoundly altered pathways of energy (Ammar et al., 2021). This development will probably continue, at least if the environmental conditions of the Baltic Sea will continue to change as projected by modelling studies. Below, recent findings regarding climate impacts on structure and functioning on the Baltic Sea ecosystem are summarized.

5.1. Projections of primary production and eutrophication

For the global ocean it has been projected that climate change will decrease both primary and secondary production because of intensified stratification and decreased availability of nutrients in the surface layer (Blanchard et al., 2012; IPCC, 2019). The effects of climate change on the Baltic Sea ecosystem may however be different, because of the special hydrographical characteristics, peculiar communities, strong seasonal cycle, and the strong dependency of the Baltic Sea of both its watershed and the adjacent North Sea.

In the Baltic Sea, changes in ice conditions, water temperature, density stratification, and especially supply of nutrients through rivers and from the sediment, affect the nutrient dynamics and primary productivity in both coastal areas and the open sea. Different species however respond in different ways to changes in the environmental parameters, and both increases and decreases in primary production have been reported and projected along with climate induced changes in the environment.

Climate change will most probably mean milder winters and if soils remain thawed, more nutrients will leak from the terrestrial areas into the freshwater system. The nutrient load into the sea will probably increase, especially in the northern Baltic Sea where precipitation is probably increasing the most (Lessin et al., 2014; Huttunen et al., 2015; Christensen et al., 2022), but also in the southern Baltic Sea (Voss et al., 2011a). It has also been projected that the total phosphorus loading (from terrestrial areas of Finland) will increase relatively more than that of nitrogen (Huttunen et al., 2015) and, together with the internal loading of phosphorus from sediments (Lessin et al., 2014; Stigebrandt et al., 2014; Stigebrandt and Anderson, 2020), phosphorus availability to primary producers may increase. If the N:P ratio of the surface layer will decline, the spring bloom will decline and more excess phosphate will be available for the summer cyanobacteria communities after the spring bloom (Lessin et al., 2014). This hypothesis concerns especially the Baltic Proper and the Gulf of Finland, perhaps also the southern Bothnian Sea.

Kommentoinut [VM9]: R2:
r 907-909 This is likely relevant for the Baltic proper and Kattegat but less for the Gulf of Bothnia. The potential effects of simultaneously increasing DOC discharge is neglected in the scenario proposed.

In the central Baltic Sea, increased spring water temperature causes, together with increased irradiation and enhanced wind-induced mixing of the surface-layer, an earlier but less intense spring bloom. In summer, in contrast, increase of temperature is coupled with increased thermal stratification, which is projected to favour production of cyanobacteria (Meier et al., 2011a; Neumann et al., 2012; Chust et al., 2014; Andersson et al., 2015). Intensified blooms of cyanobacteria are expected especially if hypoxia will prevail and internal loading will decrease the N:P ratio (Meier et al., 2011b; Funkey et al., 2014; Lessin et al., 2014). If the biomass of diatzotrophic cyanobacteria will increase, nitrogen fixation could also increase, further contributing to the decrease in the N:P ratio (Lessin et al., 2014).

Several modelling studies project an increase in total phytoplankton concentration (chlorophyll, in mg m^{-3}), until the end of the century, with the increase manifested especially in summer (Meier et al., 2012a; Meier et al., 2012b; Lessin et al., 2014; Skogen et al., 2014; Ryabchenko et al., 2016). As hypoxia and associated internal loading of phosphorus will probably be enforced by global warming (Meier et al., 2019b; Tomczak et al., 2021), it has even been suggested that this “vicious circle of eutrophication” (Vahtera et al., 2007), will prevent the success of nutrient abatement measures, unless internal loading of phosphorus will be reduced (Gustafsson et al., 2012; Stigebrandt and Anderson, 2020).

Nutrient abatement may however counteract climate effects. For instance ~~Interacting effects of nutrient abatement and climate were observed~~ in Kattegat ~~already~~ in mid 1990s, ~~-~~ ~~R~~reduction of nutrient loading led to a shift from a highly eutrophic state, characterized by small phytoplankton species and low water transparency, to an improved state, with a larger share of diatoms, decreased phytoplankton biomass and increase of water transparency (Lindegren et al., 2012). An opposing trend has taken place in the Bothnian Sea. Because of the lack of halocline and lower anthropogenic nutrient loading, the Bothnian Sea has this far remained in a relatively good condition. However, since year 2000 also the Bothnian Sea has shown symptoms of eutrophication (Kuosa et al., 2017), and also open sea cyanobacteria blooms have in recent years become more common, due to a “leaking” of phosphorus rich water from the central Baltic Sea through the Åland Sea (Rolff and Elfwing, 2015; Ahlgren et al., 2017). The connection of this process to climate change is not certain. Rather, the severe hypoxia of the central Baltic Sea has brought the anoxic layer so close to the sill separating the Baltic Proper from the Åland Sea that flow of nutrient rich water across the Åland Sea is at times possible. Whether or not the proceeding climate change will amplify the ongoing eutrophication of the Bothnian Sea remains to be seen, but if temperature stratification will increase and N:P ratio continues to decline, this will create conditions that are favourable for cyanobacteria blooms also in this relatively pristine sea area.

Several recent modelling studies conclude that nutrient abatement according to HELCOM BSAP will in the long run counteract the climate induced increase in nutrient loading and lead to decreased eutrophication (Meier et al., 2018; Ehrnsten et al., 2019b; Murray et al., 2019; Pihlainen et al., 2020). Based on oceanographic-biogeochemical modelling, it has also been suggested that hypoxia will eventually diminish (Meier et al., 2021) and that extreme cyanobacteria blooms will no longer occur in the future, if nutrient loadings will be lowered according to BSAP, despite the proceeding climate change (Meier et al., 2019a).

To sum up, the fate of the level of primary production and level of eutrophication will depend on various intertwined factors and processes, and on development of both climate and the society. Changes in primary production will impact interactions between the main trophic levels, i.e., phytoplankton, detritus and zoobenthos as well as detritivores, benthivores, grazers, zooplanktivores and piscivores (Kiljunen et al., 2020; Kortsch et al., 2021).

5.2. Trophic efficiency and consequences to the secondary production

Recycling and build-up of carbon within the ecosystem determines the overall productivity and biomass of different trophic levels. Several studies suggest fundamental changes in trophic dynamics, and eventually in the pathways of carbon in the Baltic Sea.

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 decreased, because increased stratification decreased nutrient flux to the surface layer, however (Lewandowska et al., 2012; Lewandowska et al., 2014). Furthermore, in stratified conditions the relative importance of ~~the microbial loop~~ pathways of carbon through the microbial food web increased because copepods switched to feed more on ciliates instead of phytoplankton. Decrease of ciliates in turn increased amount of ~~, which probably releases~~ heterotrophic nanoflagellates grazing on bacteria. Decrease of bacteria may reduce remineralization and ~~also~~ thus decrease availability of nutrients for phytoplankton (Lewandowska et al., 2014). On the other hand, decreaseing of bacteria would also ~~diminish~~decrease competition for nutrients between bacteria and phytoplankton, which could counteract the negative effects of diminishing remineralisation on phytoplankton.

It has also been projected that, in addition to nutrients, the flow of dissolved organic matter (DOM) into the Baltic Sea will increase in the future climate (Voss et al., 2011a; Strååt et al., 2018). Precipitation will increase especially in the northern areas~~,~~ and, by using long-term time series from 1994 to 2006, it was shown that climate change has increased discharge of terrestrial DOM into the ~~Bothnian Bay~~middle part of the Gulf of Bothnia. This

Kommentoinut [VM10]: R2:
r.970-973. If flagellate pressure is released bacterioplankton would increase. Please match with the scenario proposed in the last sentence.
Also, “loop” preferably changed to “food web”.

provided additional substrate for bacteria, which maintained bacterial biomass production despite reduced phytoplankton production~~increased accordingly~~ (Wikner and Andersson, 2012). This suggests that increased humic-rich river inflow may counteract climate change induced eutrophication in the coastal waters (Andersson et al., 2013).

Kommentoinut [VM11]: R2: r. 979. More correctly expressed "… maintained bacterial biomass production despite reduced phytoplankton production…".

Experimental studies have also demonstrated increased microbial activity and biomass with increasing DOM and temperature (Ducklow et al., 2010), although different bacteria taxa respond differently to the simultaneous increase of DOM and temperature (Lindh et al., 2015). Increase of DOM and bacteria may be detrimental to primary production as bacteria compete for nutrients with phytoplankton, and as the brownification of water reduces light availability. Consequently, the carbon flow shifts towards microbial heterotrophy, which may induce a decrease in both phytoplankton productivity and biomass and lead to a promotion of the microbial food web and other heterotrophic organisms (Wikner and Andersson, 2012; Andersson et al., 2013). Especially if stratification increases, cycling of carbon through the microbial ~~loop~~ food web increases pelagic recycling and may also decrease vertical flux of organic matter to zoobenthos (Ehrnsten et al., 2020).

It has been suggested that climate change may also decrease fish productivity. In areas where climate change increases the supply of allochtonous DOM into the system, and where increasing stratification reduces the transport of nutrients from deeper waters, phytoplankton production may decline and the trophic pathways from bacteria and flagellates through ciliates to copepods may strengthen (Aberle et al., 2015). When the system shifts towards heterotrophy, the food web efficiency declines (Båmstedt and Wikner, 2016), and if zooplankton also becomes dominated by smaller sized plankton (Dahlgren et al., 2011; Suikkanen et al., 2013; Jansson et al., 2020), there will be less suitable food available for planktivorous fish. If also sedimentation of organic matter will be reduced, zoobenthos production will decrease and there will be less food for benthic-eating fish. Eventually the total fish production may decrease.

Results of experimental studies have not equivocally confirmed this hypothesis. A study performed in a large biotest area artificially heated by the cooling waters of the Forsmark nuclear power plant, southern Bothnian Sea, found that warming of water may lead to increased species turnover, and in decreased compositional stability of diatom, macrophyte and invertebrate communities (Hillebrand et al., 2010). Certain mesocosm studies, simulating effects of climate change in the pelagic ecosystem, have also found that the production and biomass of both copepods and fish (three-spined sticklebacks) can remain high, because the positive effects of increasing temperature and increasing availability of DOC ~~on copepod~~

~~production~~ override the negative effects of decreasing food web efficiency on copepod production (Lefébure et al., 2013).

Furthermore, many Baltic Sea copepods are omnivorous and can opportunistically switch between suspension feeding on flagellates and raptorial feeding on ciliates (Kiørboe et al., 1996). Such a flexible feeding strategy stabilizes the system and can sustain copepod production even under lower phytoplankton production. This flexibility, and the fact that heterotrophic production increases with high DOC availability, suggests that fish production may be supported even also when relatively more carbon flows through the microbial ~~loop~~ food web (Lefébure et al., 2013).~~.~~

To sum up, a reorganisation of pathways of carbon is possible in the Baltic Sea due to the climate change. The system is complex, however, due to several counter- and interacting processes and large uncertainties in key processes, such as stratification and nutrient loads from land and the sediments (Meier et al., 2019c; Saraiva et al., 2019), and both increases and decreases of secondary producers have been demonstrated in field, experimental and modelling studies. The complexity of the system has been highlighted by a thorough review which illustrated how changes in benthic-pelagic coupling may induce ecosystem-wide consequences, via increasing sedimentation of organic matter inducing hypoxic conditions and internal loading of nutrients (Griffiths et al., 2017).

5.3. Food web interactions in the sublittoral ecosystem

If the climate change induces an increase in allochtonous nutrient loads, consequences can be expected in the communities of algae and vascular plants in the shallow photic zone. The shallow water food webs based on macroalgae and seagrasses may also be affected by the indirect effects of climate change, mediated through interactions between algae and their grazers.

The effects of late summer heatwaves on algae and invertebrates living amongst bladderwrack *Fucus vesiculosus* have been studied by outdoor mesocosm experiments (Werner et al., 2016). A heatwave resulted in a collapse of invertebrate grazers, such as isopods and amphipods, which in turn released grazing on filamentous algae and resulted in overgrowth of *Fucus* by epiphytic algae. In the autumn and winter, when the biomass of epiphytes was lower, the process was reversed: warming resulted in intensified grazing on bladderwrack. 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, where the biomass of the non-native gastropod grazer *Potamopyrgus*, gammarids and the snail *Theodoxus* was much higher than in the adjacent non-heated area. 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 similar cascades take place in other coastal sea areas of the Baltic Sea as well, warming may promote the growth of filamentous algae and contribute to the decline of bladderwrack.

Decline of bladderwrack will affect other species ~~trophic levels in various ways,~~ due to declining availability to habitat and food (Takolander et al., 2017a; Jonsson et al., 2018; Kotta et al., 2019). Connectivity between bladderwrack populations as well as organisms inhabiting patches of bladderwrack may also decline (Jonsson et al., 2020; Virtanen et al., 2020). However, perhaps due to the complex biotic interactions in the sublittoral ecosystem, there are very few modelling studies that have attempted to project the fate of the algal and invertebrate communities inhabiting the shallow photic zone of the Baltic Sea. Only one study has used a combination of experimental work and modelling to study the effects of climate change on invertebrates. A decline of the isopod *Idothea baltica*, the main grazer of *Fucus* spp., was projected due to the decline of bladderwrack (Kotta et al., 2019).

To sum up, temperature and salinity changes have been projected to affect species interactions in hard and soft bottoms in the sublittoral zone. Both summer heatwaves and cold season warming can induce novel trophic interactions that produce eutrophication-like effects, e.g., overgrowth of bladderwrack by epiphytes, in the photic zone dominated by macroalgae, even without an increase in nutrient loading. However, as macroalgae are very much dependent on water clarity, the future level of eutrophication will also affect the fate of the shallow water communities in the Baltic Sea. The complexity of the system, uncertainty of the oceanographic projections, and unknown adaptation capabilities of species, make it challenging to project the future food web interactions in the sublittoral ecosystem.

5.4. Regime shifts

In the 1980's a partly climate induced regime shift was recorded with drastic changes in the central Baltic food web, including phytoplankton, zooplankton and pelagic planktivores and their main predator, Baltic cod (Möllmann et al., 2009; Lindegren et al., 2010a). In 1980-2000, a decline in 'reproductive volume' (RV), contributed to the decline of cod population (Hinrichsen et al., 2011; Casini et al., 2016; Bartolino et al., 2017) and induced cascading effects on planktivorous fish as well as zooplankton (Casini et al., 2008). The different effects of temperature and salinity on sprat and cod (see above) also resulted in a spatial mismatch between these species, which further released sprat from cod predation and contributed to the increase of sprat stocks in the central Baltic Sea (Eero et al., 2012; Reusch et al., 2018). As herring is an inferior competitor for food, and food availability per individual declined, the condition of herring declined (Möllmann et al., 2003; Casini et al., 2010). Transition to a lower saline Baltic Sea, and associated decline of marine copepods (Hänninen et al., 2015), also contributed to the observed halving of (3-year old) herring weight-at-age, from 50–70 g in the late 1970s to 25–30 g in the 2000s (Dippner et al., 2019). The described regime shift has also been partly questioned, as the descriptions of the shift did not cover the entire food web (Yletyinen et al., 2016).

A factor that has been less often considered when studying reasons of cod decline is the interaction with another benthic predator, flounder. Flounder may be both prey for larger cod and a competitor for the small and juvenile ones. Now that cod size has declined, cod predation on flounder has decreased, releasing competition for benthic food again. This has caused more spatial overlap between flounder populations and the remaining small sized cod, and created more intense competition between flounder and the small sized cod, further contributing to the decline in body condition of cod (Orio et al., 2020).

Multi-species modelling studies have 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 change proceeds as projected (according to the intermediate-high A2 scenario), cod goes extinct in two models out of seven, even with present low fishing effort (Gårdmark et al., 2013). Different combinations of climate change and eutrophication scenarios may yield very different outcomes, however. Medium CO_2 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 clupeids, especially sprat (Bauer et al., 2018; Bauer et al., 2019; Hyytiäinen et al., 2019).

The above studies have mostly considered the ecosystem of the central Baltic. In other basins, the associated processes and species interactions may be different. E.g., in the Bothnian Bay, salinity was also a major driver for changes in populations of planktivorous fish, but the species involved were different. Here the decline of spawning-stock biomass of herring, observed in 1980-2013, was explained by a simultaneously increased competition with vendace, a limnic species that had increased with lowering salinity (Pekcan-Hekim et al., 2016).

In Kattegat, the western Baltic Sea, where the ecosystem is more oceanic than in the other parts of the Baltic Sea, a regime shift was detected in mid 1990s. Here the shift was explained by both global climate change, cyclic climate phenomena, and by human intervention. First, a reduction of anthropogenic nutrient loading led into a shift from a eutrophic ecosystem state to an ecosystem characterized by decreasing phytoplankton and zooplankton biomass, dominance by small sized fish in the pelagial, an increase of macroalgae and filter-feeding molluscs on hard bottoms and other benthic animals in the soft sediments (Lindegren et al., 2012). Second, the positive phases of NAO and BSI enabled an inflow of oxygenized water from the North Sea, which improved conditions for zoobenthos, including the commercially important Norway lobster. A climate induced increase of sea surface temperatures contributed to the improved flatfish growth and survival in the shallow nursery areas (Lindegren et al., 2012). Decreasing fishing may also have contributed to the increase of gadoid and flatfish populations, but its relative importance is difficult to distinguish from other co-occurring effects.

To sum up, regime shifts are usually a result of several environmental, climatic, and anthropogenic effects acting synergistically on the entire ecosystem. The climate driven changes in temperature and salinity have been identified as key drivers for the significant rise of ‘novelty’ in both abiotic conditions and biotic assemblages in several basins of the Baltic Sea (Ammar et al., 2021), but also human contribution, i.e., anthropogenic eutrophication or its alleviation have also contributed (Reusch et al., 2018). The recent research confirms that climate change induces multiple direct and indirect effects on species and communities and affects nutrient and carbon dynamics of the Baltic Sea ecosystem. However, despite the major structural changes, the overall food web complexity in the central Baltic Sea has remained surprisingly stable (Yletyinen et al., 2016). The relatively small changes may be explained by the fact that responses to climate change are not uniform or unidirectional, but vary from species group to another, within groups, and even between sibling species. Species-specific responses, many feedbacks, altered trophic pathways, and possibility of species level adaptation, make projections concerning the state of the ecosystem and trophic effects challenging.

6. Knowledge gaps

The main challenge when analysing effects of climate change on ~~ecosystems~~ the Baltic Sea is the possible synergistic effects of climate with other environmental drivers, such as eutrophication, harmful substances, and introduction of non-indigenous species, which also may have profound impacts on ecosystems and their functioning (Reusch et al., 2018; Stenseth et al., 2020; Bonsdorff, 2021). Consequently there are numerous knowledge gaps, bottlenecks and issues of dissensus that weaken our ability to project the future biological processes, such as primary and secondary productivity, benthic-pelagic coupling and hypoxia, interactions between phytoplankton, zooplankton and fish populations, as well as geographic shifts in macroalgal and invertebrate communities.

Attribution of the observed phenomena to climate change is challenging because of the collinear, intertwined and interacting processes. Especially difficult is to distinguish the effects of anthropogenic global climate change from those of quasi-cyclic phenomena, such as the NAO or BSI, or from other more stochastic variations in climate. This is partly due to the slow pace of climatic variations and time lags between physical and chemical variations and ecosystem responses. Quite few studies have investigated a period long enough to cover any larger number of NAO periods. Especially research into the long-term dynamics of the food webs is still scarce (Törnroos et al., 2019; Pecuchet et al., 2020; Kortsch et al., 2021).

Field studies have ended up with different conclusions concerning past and present changes of the environment and the biota, and their causes, depending on time periods and data scrutinized. For instance, certain studies note that cyanobacteria have increased (Suikkanen et al., 2013; Kuosa et al., 2017), while others do not find proof for such a phenomenon (Griffiths et al., 2020; Olofsson et al., 2020). Different periods studied, sparse sampling, varying species responses, and changes in phenology rather than total biomass, may explain some of the discrepancies between studies. The tendency of filamentous cyanobacteria to float during calm weather may also bias our view on the total biomass cyanobacteria in the sea, especially if low wind periods become more frequent.

Experimental studies are useful in pinpointing causative relationships, but their small spatial scales, short duration and simple food webs make upscaling of results to natural systems difficult. Experiments usually only last for a few days or weeks and study one or few species at a time. Reproducing natural patterns of environmental variability is also challenging. When mesocosms of hundreds of litres and natural communities are used, it may be difficult to simulate seasonal processes extending over several life cycles of the studied organisms. Even the most sophisticated multi-stressor experiments, which use levels of environmental stressors projected by modelling studies, tend to use constant stress levels.

~~Only~~ A few mesocosm studies ~~that~~ have exposed the communities to near-natural environmental conditions and have been able to shed light on the complex dynamics of the Baltic Sea ecosystem, e.g., the ~~functions~~ responses of the microbial ~~loop~~ food web to ~~under~~ changes of environmental variables affected by the climate change~~, variable levels of DOM, temperature, salinity and ocean acidification~~. In studies made in the Gulf of Bothnia, bacterial, phytoplankton and zooplankton production increased with additions of inorganic carbon, and the systems remained net autotrophic. In contrast, when both nutrients and DOC was increased, only bacterial and zooplankton production increased, driving the system to net heterotrophy (Andersson et al., 2013; Båmstedt and Wikner, 2016) ~~(Lindh et al., 2015; Bergen et al., 2016)~~. Increased heterotrophy led to a decreased fatty acid content and lower individual weight in the zooplankton (Dahlgren et al., 2011). With the combined treatment of elevated temperature and terrestrial nutrient loads, also fish production (of three-spined sticklebacks) increased, with terrestrial and not autotrophic carbon being the main energy source (Lefébure et al., 2013). The complex responses ~~observed in such experiments~~ indicate that, t~~T~~o provide useful inferences about physiological and population-level responses of organisms to climate change, experimental work should use full communities, apply naturalistic exposure regimes, and investigate effects of stress at spatial and temporal scales appropriate to the species studied (Gunderson et al., 2016).

Kommentoinut [VM12]: R2:
r. 1182-1185 There are more valuable mesocosm studies so a “(e,g, Lindh et al. 2015….)” would be appropriate or better adding some more examples covering larger parts of the food web (some suggested below).

Ecosystem modelling using coupled oceanographic-biogeochemical models has advanced greatly in the past 15 years, but significant challenges remain. Projections of sea surface temperature and ice conditions can be held relatively reliable, but there are still large uncertainties in projecting salinity, stratification, hypoxia and, hence, the rate of internal loading (Meier et al., 2022a). Also, natural variability is a larger source of uncertainty in future projections of hypoxia than previously understood (Meier et al., 2021). Because salinity, stratification and oxygen strongly affect many Baltic Sea organisms, it is difficult to project the fate of plankton and benthos communities with certainty. This uncertainty concerns especially marine species, such as cod, bladderwrack, eelgrass, and blue mussel, which in many studies have been projected to decrease in the northern basins of the Baltic

Sea. Further, uncertainties are imposed by complex biogeochemical processes in the terrestrial and freshwater ecosystems, as well as by unknown development of national economies and farming practices (Huttunen et al., 2015), especially in coastal areas strongly affected by nutrient loading.

Ecosystem models rarely consider complex biological interactions and feedback effects, caused, e.g., by multi-species predatory or intraguild relationships. Inclusion of such effects would require parameterizing the 3D ecosystem models with experiments and results from multi-species food web models, that operate on the level populations rather than carbon flows. Also, models cannot at present consider potential adaptation capabilities of species, as little is known on them. Several recent studies have however pointed out that, e.g., macroalgae (Rothäusler et al., 2018; Rugiu et al., 2018a) and zooplankton (Karlsson and Winder, 2020) have phenotypic plasticity and potential for adaptation against gradual changes in the abiotic environment.

Food web models offer useful tools for assessing the relative effects of climate, eutrophication, and other human impacts, including fisheries, on the structure of the Baltic Sea ecosystem. They could potentially take into account characteristics of species and their responses to changes in the environment. The current models however mostly concern the pelagic ecosystems (e.g. cod-sprat-herring-zooplankton food web) and there are major gaps for key trophic groups, such as macrophytes and macrozoobenthos (Korpinen et al., 2022) as well as the microbial food web.

Kommentoinut [VM13]: R2:
r. 1216 Please add " , microbial food web….". Typically overlooked in current models.

3D ecosystem models, food web models and 2D spatial modelling would benefit from integration. Species distribution models (SDMs) can be produced at a fine spatial scale, even a few tens of meters (Virtanen et al., 2018b), and in climate change studies they can be parametrized with 3D model results (Jonsson et al., 2018; Kotta et al., 2019). In the future, food web models involving relevant coastal taxa could also be used to fill in the missing links between the large scale (3D) processes and detailed spatial patterns identified by the 2D models.

Assessing climate effects in a smaller spatial scale would be useful, because shallow and sheltered bays, lagoons and estuaries may be more susceptible to climate change effects than deeper offshore areas, and may appear as 'climate change hotspots', where climate change drives the ecosystem towards a new state (Queiros et al., 2021). The existing coupled oceanographic-biogeochemical modelling studies however typically have a horizontal resolution of 1 or 2 nautical miles (ca. 2 or 4 km) and thus cannot easily be used for projecting local variations in temperature, salinity and stratification within the archipelago or inside estuaries. A bottleneck for high-resolution 3D models is the poor availability of high-resolution pan-Baltic bathymetries and forcing data (e.g. wind fields). For the SDMs, in turn, a major constraint is in many areas the poor availability of detailed species and habitat mapping data, as well as availability of high-resolution data on benthic substrates. Considering population level effects on spatial patterns of species would also require estimation of connectivity between sea areas, a research field that is also under-developed in the Baltic Sea (Berglund et al., 2012; Jonsson et al., 2020; Virtanen et al., 2020). Consequently no study this far has considered how the climate change affects microclimatic patterns in the Baltic Sea, and how different species and habitats may respond to such local variations.

Due to the above challenges, there are certain discrepancies concerning our view on the effects of climate change on the structure and function of the Baltic Sea ecosystem. Some of these issues are highlighted below.

Increased primary production and phytoplankton biomass (measured in chlorophyll a) have been projected by several modelling studies (Meier et al., 2012a; Skogen et al., 2014; Ryabchenko et al., 2016). Experimental studies however show that responses of phytoplankton to climate induced changes in temperature, salinity and pH are variable and can be modified by simultaneous changes in biogeochemical processes and zooplankton grazers (Paul et al., 2015; Sommer et al., 2015). Also, strengthening of stratification and simultaneous increase in riverine DOM loads may induce a decrease in phytoplankton production, at least in sea areas where rivers carry large DOM loads (Wikner and Andersson, 2012). Presently it is not clear which of these processes determine primary production in different sea areas, or whether there are transition areas where the two processes balance each other, leading to no net change in primary production.

Several ecosystem models also predict an increase of cyanobacteria. As cyanobacteria blooms are favoured by warm, stabile and conditions and low N:P ratio (Munkes et al., 2021), increase of vigorous blooms and an increase in nitrogen fixation, could be expected. However, there are large differences in model projections, due to the unclear relationship between excess phosphorus and cyanobacteria growth, and the relation between bloom intensity and nitrogen fixation (Munkes et al., 2021). Cyanobacteria are also not a uniform group. Some cyanobacteria species benefit from increased temperature and acidification, whereas others suffer from them (Eichner et al., 2014; Berner et al., 2018; Paul et al., 2018). Further uncertainty is caused by unknown biological factors, such as stoichiometric elasticity, impact of viruses and grazers. Thus it is still challenging to project how biomasses of cyanobacteria and nitrogen fixation will develop in the future.

Recent awareness of marine heatwaves and their potential impacts on the marine ecosystem has increased our knowledge on how climate change may impact pelagic, benthic, and littoral communities in the ocean (Pansch et al., 2018; Saha et al., 2020). More studies on the responses of pelagic and benthic organisms of the Baltic Sea to heat waves would increase our understanding of the population level consequences of short term variability in environmental parameters. Research on effects of climate change would also benefit from methodological diversity. E.g., more extensive use of biochemical and genetic methods, such as biomarkers (Turja et al., 2014; Turja et al., 2015; Villnäs et al., 2019), stable isotopes (Voss et al., 2000; Gorokhova et al., 2005; Morkune et al., 2016; Lienart et al., 2021), compound-specific isotope analyses (Ek et al., 2018; Weber et al., 2021) or metabarcoding (Leray and Knowlton, 2015; Bucklin et al., 2016; Klunder et al., 2021), as well as development of remote sensing methods (Huber et al., 2021), could yield novel information on stress levels experienced by organisms and environmental niches preferred by species. Such information would allow validation of the biogeochemical models under different environmental and climate scenarios.

There is some bias in the focus organisms and habitats studied. While experiments on planktonic organisms and soft bottom animals are relatively abundant, experiments on macroalgae, vascular plants and invertebrates inhabiting hard bottoms are less abundant, and ~~combined experiments~~ studies focusing on the entire food web are scarce. In general, empirical and modelling studies focusing on climate effects on shallow photic habitats are less abundant than those on the pelagic and deep benthic habitats (Tedesco et al., 2016). Very few studies have investigated the shallow water ecosystems holistically, including macro- and microalgae, invertebrates and fish at the same time. Those that have done so, have revealed complex interactions and multiple feedbacks between species and ecosystem components (Svensson et al., 2017; Salo et al., 2020). Also, while there are ample monitoring data on pelagic and deep benthic communities, similar long-term records are very sporadic for communities associated with key habitat-forming species such as bladderwrack, eelgrass, blue mussel on hard bottoms, and vascular plants growing on soft sediments. This lack of empirical data and subsequent modelling studies hampers our understanding of the long-term responses of sublittoral communities to climate change.

Furthermore, there is a large body of literature published on sea ice algae and sea ice ecology in the Baltic Sea (Granskog et al., 2006; Tedesco et al., 2017; Thomas et al., 2017), and all of them are relevant for studying winter ecology. However, few of them have directly assessed the effects of climate change on ice ecology in the Baltic Sea. More empirical and modelling studies including quantitative projections on the effect of diminishing sea ice to biodiversity and functioning of the Baltic Sea ecosystem in winter and spring would therefore be desirable.

To sum up, there are still several significant knowledge gaps and issues of dissensus in our understanding of the effects of climate change on the Baltic Sea ecosystem. To fill these gaps, the results and conclusions from the experimental work should be better integrated into the wider empirical and modelling studies of food web dynamics, and more emphasis should be placed on studying effects of climate change on less studied environments, such as ~~whole~~ the microbial food web, sea ice communities, and the sublittoral ~~communities~~ecosystem. Such studies would provide a more comprehensive view of the responses of the pelagic and benthic systems to climate change in both the open sea and the benthic system, from bacteria to fish (Kortsch et al., 2021). Also, continuation of both spatial mapping programs and long term ecological studies ~~is also~~ will be crucial for validating experimental results and for developing ~~statistical~~ ecosystem models, ~~and will~~ advanc~~e~~ing our understanding of environmental and meteorological drivers of the Baltic Sea ecosystem on large spatial and temporal scales.

Kommentoinut [VM14]: R2:
r. 1308 I suggest to add: “Continuation and expansion of long term ecological studies in collaboration with environmental monitoring programs is also crucial for validating experimental results and advance our knowledge of environmental and meteorological drivers on large spatial and temporal scales.”

7. Conclusions

Climate change has an obvious potential to affect entire marine food webs, from coastal to offshore areas, from shallow to deep, as well as from pelagic to benthic systems. Climate change can also induce changes in species distributions and proportions, and key nodes and linkages in the food webs may be altered or lost (Lindegren et al., 2010b; Niiranen et al., 2013; Leidenberger et al., 2015; Griffiths et al., 2017; Kotta et al., 2019; Gårdmark and Huss, 2020). As many ecosystem services are dependent on the state of the entire ecosystem (Hyytiäinen et al., 2019), a long-term decline in provision of ecosystem services to humans is possible. It is therefore indispensable to increase our understanding of the consequences of climate change on the socio-ecological system of the Baltic Sea and its surrounding marine regions (Stenseth et al., 2020).

The direct and indirect effects of climate change-related parameters on species, communities and the ecosystem are summarized in Table 1, based on research done since 2010. While results are variable, some conclusions can be drawn from the evidence this far.

As for the eutrophication status of the Baltic Sea it can be concluded that the ecological status of the Baltic Sea has not significantly improved despite a decrease in anthropogenic nutrient loading since the 1980s (Fleming-Lehtinen et al., 2015; Andersen et al., 2017), largely due to the pervasive internal loading (Murray et al., 2019; Stigebrandt and Anderson, 2020). Success of nutrient abatement largely determines the future state of the Baltic Sea (Hyytiäinen et al., 2019; Ehrnsten et al., 2020), but climate change may delay, or even counter the improvement of the ecosystem state (Bonsdorff, 2021).

Climate induced increase of nutrient loading and enhancing of internal loading of phosphorus have been hypothesized to promote phytoplankton and cyanobacteria production, and to maintain the ‘vicious circle of eutrophication’ (Vahtera et al., 2007), and several modelling studies indeed project an increase in both total phytoplankton biomass and cyanobacteria blooms in the future (Meier et al., 2011a; Funkey et al., 2014).

Eutrophication process may however be counteracted by various factors. Increase of DOM flowing via the rivers may decrease both primary and secondary production, at least in the ~~Bothnian Bay~~ Gulf of Bothnia (Wikner and Andersson, 2012; Andersson et al., 2013), and certain cyanobacteria may be negatively affected by increased temperature and ocean acidification (Paul et al., 2018). Thus, changes in structure and functioning of phytoplankton and cyanobacteria communities are probable, but the narrative that the global climate change will inevitably increase phytoplankton biomass and cyanobacteria blooms, and inevitably amplify the eutrophication of the Baltic Sea, may be too simplistic and needs to be refined by reconsidering the climate effects on food web processes and nutrient and carbon dynamics.

Also for the deep benthic communities, climate change effects are not straightforward. If salinity declines, the most marine species will suffer, but according to the latest analyses undisputable evidence is lacking for a future decline in the salinity of the Baltic Sea (Lehmann et al., 2022; Meier et al., 2022b). Improvement of oxygen conditions may first promote higher zoobenthos biomasses but, eventually, increasing stratification will weaken benthic-pelagic coupling and reduce food availability for benthic organisms. If also nutrient abatement proceeds favourably, biomass of zoobenthos will start to decline (Ehrnsten et al., 2020).

In the shallower photic benthic systems, nutrient increase probably enhances eutrophication, and, if salinity also declines, habitat-forming marine species, such as

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bladderwrack, eelgrass and blue mussel, probably decline in the northern Baltic Sea (Vuorinen et al., 2015; Jonsson et al., 2018; Kotta et al., 2019). As both eutrophication and increasing temperature favour filamentous algae, continued major changes in the sublittoral communities can be expected, including negative effects of such algal aggregations (Arroyo and Bonsdorff, 2016). Of particular concern is the potential loss from rocky substrates of the habitat forming bladderwrack and red macroalgae. Freshwater vascular plants will be favoured by freshening of the Baltic Sea, but they cannot replace the marine macroalgae on rocky sublittoral, because they only grow on soft substrates. On the other hand, salinity projections are still uncertain (Lehmann et al., 2022), and even if salinity declined, *Fucus vesiculosus* may be able to adapt to salinity changes (Rothäusler et al., 2018).

As for fish, responses also depend on species. Salinity decline and hypoxia increase will most probably have negative consequences on cod stocks (Gårdmark et al., 2013), whereas the increasing temperature has been projected to favour sprat (Mackenzie et al., 2012) and certain coastal fish (Bergström et al., 2016). Again, as projections for salinity, stratification and oxygen levels are uncertain, the future fate of fish populations cannot be projected with certainty.

The global climate change induces many environmental changes that may favour establishment of NIS in the Baltic Sea. Opportunistic and thermophilic species occupying soft sediments are the most probable winners. It is notable that it is extremely difficult to eradicate a marine NIS after it has found a suitable niche in the Baltic Sea. As the effects of NIS on both the ecosystem and the society are usually negative, their spreading should be prevented already before they enter the Baltic Sea, by effectively eradicating NIS from ballast waters of ships and other possible vectors.

Climate change is obviously not the only factor determining the fate of the Baltic Sea in the future. Several modelling studies have concluded that nutrient reductions 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; Meier et al., 2021). 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 is projected to become significantly improved and hypoxia reduced by the end of the century (Meier et al., 2018; Saraiva et al., 2018, 2019; Meier et al., 2021). Despite the many uncertainties concerning the effects of climate and eutrophication on the state of the Baltic Sea (Munkes et al., 2021), it can be stated that continued abatement of anthropogenic nutrient loading, combined with sustainable fisheries, seem~~s~~ to be the most reliable, albeit slow, measures to solve the grand challenges of the Baltic Sea (Meier et al., 2018; Murray et al., 2019).

Several studies have focused on studying the effects of climate change on the future state of the Baltic Sea, and especially the ecosystem modelling studies already provide valuable results that are directly usable in decision making concerning mitigation of eutrophication under climate change. In contrast, studies concerning effects of climate change on biodiversity of the Baltic Sea are lagging behind, and are hampered by model uncertainties (e.g. for salinity) and by the current inability of models to consider the complex interactions between species and multiple feedbacks between trophic levels. Especially long-term and modelling studies focusing on shallow photic environments, which harbour the highest biodiversity in the Baltic Sea, are sparse. This is a major drawback in a situation where all major environmental policies, including UN Convention on Biological Diversity and EU Biodiversity Strategy for 2030, urge for halting the ongoing biodiversity loss. To designate effective measures to safeguard biodiversity, including a climate smart expansion of the protected area network, a better understanding of the effects of climate change on the sublittoral ecosystem is urgently needed.

Knowledge of the mechanisms and processes governing Baltic Sea ecosystem under climate change have recently accumulated and already provide information that can be used to design adaptation tools and mitigation measures for the Baltic Sea (Reusch et al., 2018). It is necessary to continue 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), and to continue the dialogue with human society, in order to attune to the future changes ultimately driven by the Ocean itself (Stenseth et al., 2020).

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Competing interests. The authors declare that they have no conflict of interest.

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Table 1. Summary of research findings and conclusions on the anticipated effects of climate change (CC) effects in the Baltic Sea for selected variables. The table only ~~includes~~ shows studies published in 2011-2021 and a part of studies referred to in the text are not included. For earlier studies, see Dippner et al. (2008) and Viitasalo et al. (2015). Observations, experimental simulations, or modelled projections: T = temperature increase; S = salinity decline; TSO_2 = temperature increase, salinity decline and/or oxygen decline; A = acidification; AT = acidification and temperature increase; AS = acidification increase and salinity decline; DOM = dissolved organic matter. EXP = experimental manipulations /microcosms; MES = experimental manipulations /mesocosms; LTS = Long-term studies; MOD = modelling studies; FIE = Field data. Empty fields indicate knowledge gaps.

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r. 1427 I suggest to specify "…in the Baltic Sea for selected test variables". Several studies referred to in the text, and some covering other test variables, are omitted.

Taxonomic group	**T**	**S**	**TSO_2**	**A**	**AT & AS**	**Other changes in physico-chemical environment**	**Interactions between trophic levels**
Bacterial communities	EXP: Bacteria community changes under T (Bergen et al. 2016)	EXP: Drastic change in bacterial communities (Wulff et al. 2018)	EXP: Mixed responses to TS change in microbial community (Wulff et al. 2018)	EXP: Limited impact of A on bacteria (Bergen et al. 2016; Lindh et al. 2013)	EXP: Community change with AT (Lindh et al. 2013); EXP: Biovolume of bacterial communities decline with AS (Wulff et al. 2018)	MES: Different responses for increase of DOM and T in different bacteria taxa (Lindh et al. 2015); MES: Bacteria increase with DOC addition (Andersson et al. 2013)	EXP: T induced a decline in bacteria, due to increase of flagellates (Nydahl et al. 2013); EXP: Bacteria increase caused by decaying cyanobacteria (Berner et al. 2018)
Phytoplankton	LTS: Prolonged growing season under T (Kahru et al. 2016; Wasmund et al. 2019). Earlier and longer spring bloom (Sommer et al. 2012; Groetsch et al. 2016;	EXP: Growth rates of *A. ostenfeldii* declined at lowered S (Kremp et a. 2016) Toxicity of *A. ostenfeldii* may increase or decrease, depending on strain, under S	LTS: Eutrophication effects modified by climate-induced variations in T and S (Hällfors et al. 2013; Olofsson et al. 2020) and by Baltic Sea Index (Griffiths et al. 2020)	MES: Autumn phytoplankton biomass increased Sommer et al. 2015); EXP: No/minor effects on community composition, fatty acids or biovolumes of	MES: Autumn phytoplankton biomass increase with AT (Sommer et al. 2015); EXP: Growth and saxitoxing concentration of *Alexandrium ostenfeldii* increases	LTS: Shift from diatoms to dinoflagellates due to changes in sunshine, wind and ice conditions (Klais et al.2011, 2013;Hällfors et al. 2013; Spilling et al. 2013; Kuosa et al.	MES: Phytoplankton increases with increasing inorganic nutrients but not when also DOC is added (Andersson et al. 2013). MES: Warming increases zooplankton grazing on

	Wasmund et al. 2016) EXP: Growth of dinoflagellate *Alexandrium ostenfeldii* decreased under T (Kremp et al. 2016) EXP: Toxicity of *A. ostenfeldii* may increase or decrease, depending on strain, under T (Kremp et al. 2016) Germination of *A. ostenfeldii* resting cysts is unaffected by T (Jerney et al. 2019)	(Kremp et al. 2016) Germination of *A. ostenfeldii* resting cysts is unaffected by T (Jerney et al. 2019)		phytoplankton (Paul et al. 2015; Bermudez et al.2016; Olofsson et al. 2019)	with AT (Kremp et al. 2012)	2017; Hjerne et al. 2019) MOD: Increased phytoplankton biomass caused by increase in nutrient availability (Meier et al. 2012a,b; Skogen et al. 2014; Ryabchenko et al. 2016); MOD: CC and nutrient reduction lead to a shift from pelagic to benthic primary production (Lindegren et al. 2012)	medium-sized algae which releases smaller algae from predation (Paul et al. 2015); EXP: Effects of AT modified by diminishing of grazing by copepods (Paul et al. 2016)
Cyanobacteria	EXP: Earlier peak but lower biomass of cyanobacteria (Berner et al. 2018); LTS: Increase of cyanobacteria blooms in summer (Suikkanen et al. 2013); EXP: Toxicity of *Dolichospermum* sp. increases with T (Brutemark et al. 2015; Wulff et al. 2018)	LTS: community change caused by S decline in the Gulf of Bothnia (Kuosa et al. 2017); EXP: Toxicity of *Dolichospermum* sp. increases at low salinity (3-6 psu) (Wulff et al. 2018)		EXP: Production of single-celled cyanobacterium *Cyanothece* increases and that of filamentous *Nodularia* decreases under A (Eichner et al. 2014); EXP: Decline of cyanobacteria may induce a decline of nitrogen fixation (Eichner et al. 2014; Berner et al. 2018)	MES: AT has a negative impact on *Nodularia* biomass (Paul et al. 2018); EXP: Only T affects biovolume and photosynthetic activity of *Nodularia* and *Aphanizomenon* (Karlberg & Wulff 2013)	MOD: Cyanobacteria blooms will increase in the warmer and more stratified future (Meier et al. 2011a,b; Neumann et al. 2012; Chust et al. 2014; Funkey et al. 2014; Lessin et al. 2014; Andersson et al. 2015)	LTS: Shift to cyanobacteria dominance also attributed to changes in eutrophication and top-down pressure (Suikkanen et al. 2013)
Microzooplankton	MES: Growth rate			MES: No effect on	EXP: Community		MES: Positive

	of microzooplankton increased (Horn et al. 2016)			microzooplankton (Horn et al. 2016)	change with AT (Lindh et al. 2013); EXP: Biovolume of cilates decline with AS (Wulff et al. 2018)		effect from A on the mixotrophic ciliate *Myrionecta* (*Mesodinium*) due to increase in food availability (Lischka et al. 2017)
Mesozooplankton	EXP: Decrease in copepod egg viability and nauplii development under T (Vehmaa et al. 2013); Decrease in copepod adult body size and survival (Vehmaa et al. 2013; Garzke et al. 2015); LTS: T favours cladocerans and rotifers (Jansson et al. 2020); EXP: Southern populations of copepod *Eurytemora affinis* can adapt to T (Karlsson & Winder 2020)	EXP: Respiration of copepod *Acartia longiremis* increases and feeding rate decreases at S below 7 psu (Dutz & Christensen 2018)	LTS: Decline of marine copepods due to S (Suikkanen et al. 2013; Hänninen et al. 2015); LTS: Increase of brackish copepods due to S and T (Mäkinen et al. 2017)	MES: A-induced decline in body size of adult copepods (Vehmaa et al. 2016);			MOD: Surface-dwelling copepods are favoured by T-induced increase in food (Otto et al. 2014a); MES: T induces a grazer-driven change to smaller-sized phytoplankton (Klauschies et al. 2012; Paul et al. 2015); MES: At T copepods control micro-zooplankton (Horn et al. 2016); MES: T strengthens ~~microbial loop~~ hetero-trophic pathways of carbon through protozoo-plankton to copepods (Aberle et al. 2015) and induces a switch from bottom-up to top-down

							control (Paul et al. 2016); MES: Growth of cladocerans increases under A because of increase in food (Lischka et al. 2017) MES: Mesozooplankton production is maintained both with autotrophic and heterotrophic production (Andersson et al. 2013; Lefébure et al. 2013)
Macroalgae	EXP: At heat wave temperatures, photosynthesis declines, growth ceases and necrosis starts in bladderwrack (Graiff et al. 2017; Takolander et al. 2017b); MES: T is beneficial for *Fucus* in early and late summer, but harmful in mid-summer (Wahl et al. 2021)	EXP: Sexual reproduction of bladderwrack ceases at S (Rothäusler et al. 2018, 2019); MOD: Bladderwrack distribution will be restricted in the Baltic Sea (Vuorinen et al. 2015; Takolander et al. 2017a; Jonsson et al. 2018; Kotta et al. 2019); MOD: Red alga *Furcellaria* distribution will be restricted (Torn et al. 2020);		EXP: Generally small effects on macroalgae (Al-Janabi et al. 2016a; Wahl et al. 2019); EXP: Increase in growth of green alga *Ulva intestinalis* due to A (Pajusalu et al. 2013, 2016)	EXP: A-induced necrosis in bladderwrack is worsened by S (Takolander et al. 2017b); EXP: Upwelling of hypoxic water causes mortality of bladderwrack germlings under AT Al-Janabi et al. 2016b)		MES: In spring, T induces overgrowth of bladderwrack by epiphytic diatoms (Werner & Matthiessen 2017); In summer, heatwave collapses grazers and results in overgrowth of bladderwrack by filametous algae; in winter, T enhances grazing by invertebrates, resulting in decline of bladderwrack (Werner et al. 2016)

		EXP: Populations of *F. vesiculosus* show different responses to S (Kinnby et al. 2020)					
Vascular plants	MOD: Charophyte distribution increases under T (Torn et al. 2020); MES: Springtime heatwaves cause high mortality in eelgrass (Sawall et al. 2021)	MOD: Eelgrass distribution will be restricted by S (Torn et al. 2021)		EXP: No effect of A on eelgrass *Zostera marina* (Pajusalu et al. 2015)		MOD: Eelgrass distribution will be retained if nutrient abatement is implemented, despite CC effects (Bobsien et al. 2021)	
Benthic animals	EXP: Non-linear response to T in isopod *Idothea balthica* (Ito et al. 2019); EXP: Heat waves induce a shift in community structure (Pansch et al. 2018); LTS: T increase induces a higher biomass ofgammarids and snails (Salo et al. 2020)	LTS: Salinity decline affected zoobenthos variations in Åland Islands (Snickars et al. 2015)	LTS: Long-term changes in physico-chemical parameters drive the variations in zoobenthos (Weigel et al.2015; Rousi et al. 2019; Törnroos et al. 2019; Ehrnsten et al. 2020; Forsblom et al. 2021); LTS: Replacement of amphipods by Baltic clam and *Marenzelleria* sp. explained by TSO (Rousi et al. 2013); EXP: Survival of isopod *Idothea Baltica* decreases	EXP: Development of Baltic clam larvae slows down under A (Jansson et al. 2016); EXP: No effects of A on barnacle larvae (Pansch et al. 2012); EXP: No effects of A on isopod *Saduria entomon* (Jakubowska et al. 2013); EXP: No effect of A on isopod *Idothea balthica* in Kattegat but strong effects in the other parts of the Baltic Sea (Wood et al. 2014)		MOD: Climate-induced changes in physical and biogeochemical parameters will modify the response of zoobenthos to availability of food and oxygen (Timmermann et al. 2012; Ehrnsten et al. 2019a,b)	MOD: Abundance of isopod *Idothea baltica* will decline due to salinity-induced decline in bladderwrack (Kotta et al. 2019)

			(Rugiu et al. 2018c); MOD: Biomass of Saduria entomon increases due to S (Gogina et al. 2020)				
Non-indigenous invertebrates	FIE: T induced higher biomass of gastropod *Potamopyrgus* (Salo et al. 2020)		MOD: Ponto-Caspian bivalves, amphipods and mysids will increase under TS in the coastal benthic areas (Holopainen et al. 2016); FIE: NIS establish in areas with high T and low S (Jänes et al. 2017)				
Fish	LTS: Sprat has benefited from T (Voss et al. 2011; MacKenzie et al. 2012; Eero et al. 2016); LTS: Warm water Atlantic species (e.g. anchovy, sole and turbot) occur in the western Baltic (Alheit 2012; Sparrevohn et al. 2013); MOD: Sprat productivity will increase with T (Voss et al. 2011; MacKenzie	LT: S and associated decline of marine copepods induced a halving of herring weight-at-age (Dippner et al. 2019); LTS/MOD: Different effects of T and S on sprat and cod cause a spatial mismatch between these species (Eero et al. 2012); LTS: Decline in S intensified resource competition between herring and	MOD: Cod reproductive volume will diminish towards the end of the century due to TSO (Niiranen et al. 2013; Wåhlström et al. 2020); FIELD, EXP & MOD: Digestion, food consump-tion, growth and maximum length of cod declines in low O conditions (Limburg et al. 2019; Brander et al. 2020;	EXP: No effect of A on cod larvae (Frommel et al. 2013); EXP: Mortality of cod larvae doubles when treated with RCP8.5 scenarios (Stiasny et al. 2016)	EXP: No effect on cod larvae with AT (Frommel et al. 2013)	LTS/MOD: cod declined due to the climate- and human-induced decrease of 'reproductive volume' (Gårdmark et al., 2013; Niiranen et al., 2013; Wåhlström et al., 2020).	MES: Stickleback production is maintained with elevated temperature and increased DOC loads (Lefébure et al. 2013); MOD: Climate-induced decoupling of benthic feeding fish from their food source (Törnroos et al. 2019); MOD: Herring stocks decrease in short term Niiranen et a. 2013); FIE: Perch

	et al. 2012; Pansch et al. 2012); MOD: Herring stocks will increase due to T (Bartolino et al., 2014); LTS: Pike-perch more abundant in the northern-most Baltic Sea due to T (Peckan-Hekim et al.2011)	vendace in the Bothnian Bay (Pekcan-Hekim et al. 2012)	Orio et al. 2021)				shift from feeding on small fish to gammarids, which releases grazing from filamentous algae (Svensson et al. 2017); LTS/MOD: Partly climate induced decline in cod stock caused a cascading effect on sprat, herring and zooplankton (Hinrichsen et al. 2011; Casini et al. 2016; Bartolino et al. 2017)

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