Manuscript "Global climate change and the Baltic Sea ecosystem: direct and indirect effects on species, communities and ecosystem functioning"
by Markku Viitasalo and Erik Bonsdorff, submitted to Earth System Dynamics.

Author comments for reviewer no. 1 (esd-2021-73-RC1.pdf).

All author replies to reviewer comments in red font.

Anonymous reviewer #1

This review by Viitasalo and Bonsdorff offers a timely overview of the scientific evidence for effects of climate change on the ecosystems of the Baltic Sea. Both authors are in a good position to deliver a comprehensive review of this complex field, and Erik Bonsdorff is probably the researcher with the broadest knowledge on Baltic ecosystems. The review covers most ecosystem components except for marine birds and mammals. With 177 included references the coverage is impressive.

The authors give a balanced account of the wide range of studies applying many different approaches including observational, experimental and modelling studies. The emerging picture is complex where ecosystem components show different sensitivity to ongoing and anticipated climate-change effects. This review also highlights the great challenges involved in the interpretation of effects on the ecosystem from studies on the species level considering feedbacks and indirect effects through biological interactions like trophic links, cascading effect and the potential capacity for plastic acclimation and adaptation. The review honestly points out the great difficulty in predicting major changes in ecosystem functions with possible regime shifts. This is also viewed in the perspective of the uncertainties involved in climate model projections of how the climate may change across this century.

This review should be a very useful introduction to the field of climate-change effects on the ecosystem to many researchers as well as in higher education.

The review is well-written and concise. It may be argued that the review is a bit short considering the scope, but this may be an advantage if the aim is to offer a brief summary of the current knowledge together with an extensive collection of relevant literature. I only have a few comments below.

We are thankful for the constructive comments.

Major Comment

The only major comment is that the section on "Knowledge gaps" could be more extensive. There are questions how to best approach climate-change effects through experimental studies. There may be a lack of experimental infrastructure of sufficient scale in terms of the ability to control multiple environmental factors, sufficient replication, and not least technical staff to maintain also long-term studies. There is the question of more extensive habitat-mapping and also the development of more advanced Species Distribution Models (partly mentioned), e.g. the inclusion of biological interactions, plasticity and capacity for adaptation. A major knowledge gap (likely deserving a different paper) is also how to interpret the present, rather sprawling, knowledge about climate-change effects into Marine Spatial Planning and conservation efforts, e.g. the design of Marine Protected Areas.

Very valid points, thank you. We have now expanded the chapter Knowledge gaps significantly and also point out methodological challenges.

Minor Comments

Page 4, line 63. Climate change may also affect the opportunities for freshwater biota, e.g. vegetation.

Modified as suggested. Edited text: "…potentially affecting the marine and freshwater biota inhabiting the Baltic Sea, as well as the human society"

Page 5, line 112. More sunlight because of less cloudy conditions?

Yes, it is probable that the proximate reason for more sunlight is decreased cloudiness in spring. Hjerne et al. (2019) states: "The less windy and *less cloudy springs* observed after 1990 are linked to a negative trend in the North Atlantic Oscillation Index (p = 0.01, Mann–Kendall) and is most likely only a temporary shift in the long-term climate development." We edit the text and add a notion on the potential attribution to NAO and global climate change, and the uncertainties associated with projections.

New text: "Some studies have attributed these shifts to changes in environmental conditions associated with global change (Groetsch et al., 2016), while others have indicated a connection with the North Atlantic Oscillation (NAO); a decline in the intensity of NAO in the 1990s caused less cloudy conditions (more irradiance), and less windy conditions induced stronger stratification of surface water (Hjerne et al., 2019). Such shifts, if caused by variations in NAO, may be temporary and reversable, whereas shifts caused by global climate change may be more enduring. It has 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, but this development may be counteracted by increasing windiness and cloudiness, which have been projected by earlier modelling studies (Hjerne et al., 2019). However, more recent models have suggested that, while the winter conditions will most probably become more cloudy and windy, the projections for future conditions in spring and summer are more uncertain (Christensen et al., 2021). Therefore, while it is obvious that the projected warming will induce shifts in the structure of spring phytoplankton communities in the next 60 to 80 years, the exact nature of the changes cannot be projected with certainty."

Page 5, line 114. Mesodinium should be considered mixotrophic (e.g. Stoecker DK, Hansen PJ, Caron DA, Mitra A. 2017. Mixotrophy in the Marine Plankton. Annual Review of Marine Science 9: 311-335).

Modified as suggested. Edited text: "…mixotrophic ciliate *Mesodinium rubrum*…"

Page 5, line 119. A change in N/P ratio? with more P favouring the N-fixing Cyanobacteria?

A good point. We include a notion on the N/P ratio and add a more thorough analysis of the development in the Bothnian Sea, where the N/P ratio has also declined.

New text: "Also, in the Gulf of Bothnia, changes in phytoplankton and cyanobacteria communities have been observed in a study covering period 1979 to 2017. In both Bothnian Sea and Bothnian Bay diatoms have decreased while chrysophytes, prasinophytes, and prymnesiophytes have increased. In the Bothnian sea, also concentration of chlorophyll *a* has increased in summer, along with the increase of the autotrophic ciliate *Mesodinium rubrum* and cyanobacteria blooms. have increased (Kuosa et al., 2017). The observed increase of Cyanobacteria blooms in the Bothnian Sea have been attributed to an increased freshwater flow and, since 2000, to an increased intrusion of more saline Baltic Proper water into the Bothnian Sea. These changes have increased stratification, lowered oxygen conditions and a led to decline in N:P ratio of the Bothnian Sea, which have favoured the development of Cyanobacteria blooms in the area (Rolff and Elfwing, 2015; Ahlgren et al., 2017; Kuosa et al., 2017)."

Page 6, line 140. So what is causing that nutrient reduction? This sentence links poorly to the previous sentence about increased nutrient loading.

Here, "nutrient reduction" refers to measures to reduce anthropogenic nutrient loading. The text is now clarified.

New/edited text: "On the other hand, it has been projected that reduction of anthropogenic nutrient loading according to HELCOM Baltic Sea Action Plan will, in the long run, counteract the increased nutrient loading caused by climate change and lead to decreased eutrophication (Ehrnsten et al., 2019b;

Pihlainen et al., 2020). This has also been seen in Kattegatt, where reduction of nutrient loading led in mid 1990s to a shift from a highly eutrophic state characterized by small phytoplankton species and low water transparency to increasing share of diatoms, decreasing overall phytoplankton biomass and increase of water transparency (Lindegren et al., 2012)."

Page 6, line 155. What competitive advantage? Higher levels of toxins that defend against predation?

Yes, we refer to toxic effects, and this is now clarified and backed up by references.
New/edited text: "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 unpalatable cyanobacteria may get a competitive advantage against diatoms in a future Baltic Sea."

Page 7, line 173. There is an experimental study "Karlsson K, Winder M. 2020. Adaptation potential of the copepod Eurytemora affinis to a future warmer Baltic Sea, Ecology and Evolution 10: 5135-5151". This Experimental study suggests that copepod populations from warmer environments can at present adapt to a future warmer Baltic Sea, whereas populations from colder areas show reduced adaptation potential to high temperatures.

A good suggestion. Text amended and reference added.
New text: "On the other hand, some capability to temperature adaptation has been demonstrated experimentally for the Baltic Sea copepod *Eurytemora affinis* (Karlsson and Winder, 2020). Interestingly, the adaptability was better in populations reared in warm temperatures (≥17°C), which suggests that (*i*) southern populations can better cope with increasing temperatures than the northern ones, and (*ii*) the adaptation capability of all (surviving) populations may improve with proceeding climate change."

Page 8, line 216. There is a recent study by "Kinnby A, Jonsson PR, Ortega-Martinez O, Töpel M, Pavia H, Pereyra RT, Johannesson K. 2020. Combining an ecological experiment and a genome scan show Idiosyncratic responses to salinity stress in local populations of a seaweed. Frontiers in Marine Science. 7: 470". This study shows the possible presence of locally adapted populations of Fucus vesiculosus in the Baltic with different tolerance to salinity and with different genetic backgrounds.

A good suggestion. Text amended and reference added.
New text: "Especially if populations are genetically separated, they may have very different adaptation capabilities. In a study performed in the Danish Straits, certain populations of *Fucus vesiculosus* were only slightly affected by a salinity decline, while others displayed clear responses, and one population showed severe stress symptoms and stopped growing (Kinnby et al., 2020)."

Page 8, line 230. A typo: "algae" should read "alga".

Corrected.

Page 9, line 239. It may be pointed out that Zostera in the Baltic proper may consist of some few clones making the total genetic diversity low with less capacity for adaptation to a changing environment, although it has been found that somatic mutations may increase overall diversity (Yu et al. 2020. Nature Ecology & Evolution 4: 952).

Good point. Text amended with a notion to low genetic differentiation in Baltic *Zostera*.
Edited text: "The rapidly changing marine environment in the Baltic Sea however pose an evolutionary risk, especially for populations with specific adaptations, such as relicts, which may be at risk for local extinctions (Johannesson et al., 2011), and for populations that live close to the limits of their geographical ranges and may have low genetic differentiation, such as eelgrass *Zostera marina* (Billingham et al., 2003). Indeed, mesocosm studies have indicated that Baltic Sea eelgrass populations suffer from heatwaves in summer (Ehlers et al., 2008) and elevated temperatures in winter-spring period (Sawall et al., 2021)."

Page 9, line 241. A particular concern is the potential loss of marine, canopy-forming macroalgae (Fucus, Furcellaria). There is here no freshwater vascular plants that can replace that type of vegetation on hard substrata.

Important point. New text (in Conclusions): "Of particular concern is the potential loss from rocky substrates of marine canopy-forming brown and red macroalgae. Freshwater vascular plants only grow on soft substrates and therefore they cannot replace the ecological functions of marine macroalgae, even though they would be favoured by freshening of the surface waters."

Page 9, line 273. In the paper "Meier et al. 2020. Future projections of record-breaking sea surface temperature and cyanobacteria bloom events in the Baltic Sea. Ambio 48: 1362-1376", they showed how the frequency of heatwaves may dramatically increase under some climate change scenarios.

Yes, we agree. (The paper is from 2019, though.)

Edited text: "Therefore, heat waves, which have been projected to increase in frequency (Meier et al., 2019), may pose a severe threat to sublittoral invertebrates."

Page 12, line 369. "Ipcc" should read "IPCC".

Corrected.

Page 12, line 375. The previous sentence states a projected increase in stratification, while this sentence refers to enhanced mixing. I guess that this enhanced mixing is caused by more intense wind speeds during the spring when the thermocline is weak. Please, rephrase to avoid confusion here.

The paragraph is now clarified.

Edited text: "Several studies using coupled oceanographic-biogeochemical ecosystem models have projected more phytoplankton and especially cyanobacteria in the warmer future Baltic Sea. In the central Baltic Sea, increased water temperature causes, together with increased irradiation and enhanced wind-induced mixing of the surface-layer, an earlier but less intense spring bloom, while in summer, enhanced thermal stratification favours more intense cyanobacteria blooms (Meier et al., 2011a; Andersson et al., 2015; Neumann et al., 2012; Chust et al., 2014). Intensified blooms of cyanobacteria are expected especially if hypoxia will prevail and internal loading will increase supply of phosphorus from anoxic sediments into the surface layer, decreasing the N:P ratio (Meier et al., 2011b; Funkey et al., 2014). However, the magnitude of changes and their consequences for biogeochemical processes, e.g. for nitrogen fixation, differ greatly between models (Munkes et al., 2021)."

Page 12, line 378. Do you know what is the projected P/N ratio for the external loading?

Good point. We do not find direct references, but from Huttunen et al. 2015, their Figs 6 and 7, something can be deduced.

New text: "Phytoplankton communities will also be affected by anthropogenic nutrient loading. It has been projected that, due to climate change, the total phosphorus loading into the Finnish sea area will increase relatively more than that of nitrogen (Huttunen et al., 2015), suggesting a decreased N:P ratio of the external loading. The future nutrient ratios of the external loading are, however, hard to be predicted, as they are affected by several factors, including agricultural adaptation, and biogeochemical processes in the soil, lakes and rivers."

Page 13, line 386. Species names should appear in italic.

Corrected.

Page 13, line 386. Note that also Cyanothece (supposed to increase) is a nitrogen fixer.

Good point. New text: "This could however be balanced by potential increase of *Cyanothece*, which is also a nitrogen fixer."

Page 13, line 401. What is the mechanism behind this negative effect on flux? Stratification?

Yes, but also trophic effects. Edited text: "The total phytoplankton biomass however decreased because increased stratification decreased nutrient flux to the surface layer (Lewandowska et al., 2014; Lewandowska et al., 2012). Furthermore, in stratified conditions the relative importance of the microbial loop increased because copepods switched to feed more on ciliates instead of phytoplankton, which probably releases heterotrophic nanoflagellate grazing on bacteria, which may reduce remineralization and decrease availability of nutrients for phytoplankton (Lewandowska et al., 2014)."

Page 13, line 410. What may be the consequence of this shift apart from lower food web efficiency? Lower export to benthic biota?

Yes. Edited text: "This shifts the carbon flow towards microbial heterotrophy (Wikner and Andersson, 2012), which may also decrease vertical flux of organic matter to zoobenthos (Ehrnsten et al., 2020)."

The whole chapter is now thoroughly rewritten to encompass all different aspects of this phenomenon.

Page 14, line 449. A detail: Myrionecta is regarded as a junior synonym to Mesodinium (and not the other way around). Also, Mesodinium rubrum is now considered a complex of several species.

Yes, we now use the form *Mesodinium* sp. (although Lischka et al. 2017 use *M. rubra*).
Edited text: "…and the abundance of the mixotrophic ciliate *Mesodinium* sp. even increased in mesocosms with OA,…"

Page 14, line 450. Note that Dinophyta (e.g. Dinophysis acuminata) is a PREDATOR on M. rubrum.

We agree and omit "Dinophyta". Edited text: "…the abundance of the mixotrophic ciliate *Mesodinium* sp. even increased in mesocosms with OA, because of increase of its food, e.g. picoeukaryotes, at higher CO_2 levels…"

Page 17, line 542. The word "through" should be omitted.

Corrected.

Page 17, line 558. A bottle-neck for high-resolution 3D circulation models is the availability of high-resolution pan-Baltic bathymetries, and forcing data (e.g. wind fields).
For species distribution models (SDM) a major constraint is the poor habitat mapping in many areas (with exceptions in Finland and Estonia). There is also a need for the inclusion of biological interactions (e.g. predator-prey) into SDMs.

Good suggestions. New text: "A bottleneck for high-resolution 3D circulation models is however the availability of high-resolution pan-Baltic bathymetries and forcing data (e.g. wind fields). For pan-Baltic species distribution models (SDMs), in turn, a major constraint is – in many areas – the poor availability of detailed species and habitat mapping data."
New text: "Statistical models, both 3D ecosystem models and 2D SDMs, rarely include biological interactions into the models, nor can they fully incorporate the more complex effects of multi-species predatory or intraguild relationships. Inclusion of such complex food web effects would require merging of 3D and 2D models with multi-species food web models that operate on the level populations rather than carbon flows (ecosystem models) or species coverages (SDMs)."

Page 18, line 574. The word "While" can be omitted.

Omitted.

Page 18, line 581. Better start this sentence with "However, some common…".

Edited as suggested.

AC1 references

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