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

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13



14 **Abstract**

15

16 Climate change has multiple direct and indirect potentially synergistic effects on Baltic Sea species,
17 organism communities, and on ecosystem functioning, through physical and biogeochemical
18 environmental characteristics of the sea. Associated indirect and secondary effects on species
19 interactions, trophic dynamics and ecosystem function are expected to be significant. Evidence on
20 effects of climate are compiled from and reviewed for field studies, experimental work, as well as
21 modelling studies primarily from published literature after 2010.

22 The responses vary within and between species groups, even between sibling species. Such
23 subtle differences, as well as secondary feedbacks and altered trophic pathways, make projections
24 difficult. Some common patterns arise from the wealth of recent studies, however. It is likely that the
25 combined effects of increased external nutrient loads, stratification and internal loading will improve
26 the conditions for cyanobacterial blooms in large parts of the Baltic. In the northernmost areas the
27 increasing allochthonous DOM may further complicate the picture by increasing heterotrophy and by
28 decreasing food web efficiency. This effect may, however, be counteracted by the intensification of
29 the bacteria-flagellate-microzooplankton-mesozooplankton link, which may change the system from a
30 bottom-up controlled one to a top-down controlled one.

31 In deep benthic communities, continued eutrophication may promote higher sedimentation of
32 organic matter and increase zoobenthic biomasses, but eventually increasing stratification and
33 hypoxia/anoxia will disrupt benthic-pelagic coupling, leading to reduced benthic biomass. In the
34 photic benthic systems warmer winters with less ice and nutrient increase enhances eutrophication.
35 The projected salinity decline suppresses marine species, and temperature increase overgrowth of
36 perennial macroalgae by annual filamentous alga throughout the growing-season, and major changes
37 in the marine entire ecosystem are expected. The changes in environmental conditions probably also
38 lead to increased establishment of non-indigenous species, potentially affecting food web dynamics in
39 large areas of the Baltic Sea.

40 However, several modelling studies have concluded that nutrient reductions according to the
41 Baltic Sea Action Plan of Helsinki Commission may be a stronger driver for ecosystem functions in
42 the Baltic Sea than climate change. Such studies highlight the importance of studying the Baltic Sea
43 as an interlinked socio-ecological system.

44 Knowledge gaps include uncertainties in projecting the future salinity level as well as
45 stratification under different climate forcings. This weakens our ability to project how overall
46 biodiversity, pelagic productivity, fish populations, and macroalgal communities may change in the
47 future. Experimental work must be better integrated into studies of food web dynamics, to get a more
48 comprehensive view of the responses of the pelagic and benthic systems to climate change, from
49 bacteria to fish. Few studies have holistically investigated the shallow water ecosystems holistically.
50 There are complex climate-induced interactions and multiple feedbacks between algae, grazers and



51 their predators, that are poorly known, as are the effects of non-native invasive species. Finally, both
52 2D species distribution models and 3D ecosystem models could benefit from better integration of
53 approaches including physical, chemical and biological parameters.

54

55 **Keywords:** Global climate change, biodiversity, species, communities, food webs, ecosystem
56 functioning, Baltic Sea

57



58 **1. Introduction**

59

60 Climate change has multiple effects on Baltic sea species, communities and ecosystem functioning,
61 through its effects on oceanographic, biogeochemical parameters of the sea, and associated indirect
62 effects on species interactions, trophic dynamics and ecosystem function mechanisms, potentially
63 affecting both the marine biota and human society alike (Paasche et al., 2015; Chen, 2021; Stenseth et
64 al., 2020). Hence, detailed knowledge of these mechanisms and processes are vital for the
65 understanding and management of the Baltic Sea as an ecosystem (Blenckner et al., 2021).

66 These overall effects have been reviewed in two earlier synthesis-studies
67 (The_Bacc_Author_Team, 2008; The_Bacc_Ii_Author_Team, 2015). Since then, a wealth of field-,
68 experimental and modelling studies have shed more light into the complex interactions between
69 ‘climate’ (the large-scale physical drivers) and the Baltic Sea system (Meier et al., 2021). In this
70 paper, we review these effects again, primarily based on literature published after year 2010. Firstly,
71 evidence is compiled from documented responses of species, populations and communities to climate-
72 induced changes in temperature, salinity, ocean acidification as well as other biogeochemical
73 parameters. Secondly, a large number of experimental studies, investigating the same parameters are
74 reviewed. Thirdly, the complex effects of climate change on the marine food webs and food web
75 dynamics are analyzed based on studies where multiple species or trophic levels have been studied.
76 Finally, a number of modelling studies are reviewed. The main challenge when analyzing global
77 climate change-induced effects on ecosystems is the possible synergistic effects between climate and
78 other environmental drivers, such as eutrophication, hypoxia, fishing, habitat modifications, and
79 levels of harmful substances, as all of these may be influenced by changes in temperature, salinity and
80 acidification, which then in turn may have profound impacts on parts of or entire ecosystems and their
81 functioning in time and space (Reusch et al., 2018; Stenseth et al., 2020; Bonsdorff, 2021).

82

83 **2. Effects on species and communities**

84

85 **2.1. Microbial communities**

86

87 The effects of projected ocean acidification on microbes have been studied together with ocean
88 warming (OAW). For the spring bloom microbial communities (example from the sea area around the
89 island Öland in the Baltic Proper), OA alone had a limited impact, but when combined with increased
90 temperature, the communities changed markedly (Lindh et al., 2013). In the southern Baltic Sea (Kiel
91 Bight) the impact of OA was also limited to certain dominant OTUs (operational taxonomic units), as
92 the bacterial community mainly responded to temperature and phytoplankton succession (Bergen et
93 al., 2016).



94 In experiments using a natural summer microplanktonic community, where CO₂ was increased
95 and salinity decreased (from 6 to 3 psu), the biovolume of heterotrophic bacteria declined (Wulff et
96 al., 2018). In experiments with increasing temperature (from 16 to 18-20 degrees °C) and reduced
97 salinity (from 6.9 to 5.9 PSU) in the Baltic Proper (NW Gotland Sea) the microbial community
98 showed mixed responses, i.e., no conclusive evidence of direct climate-induced change. Further
99 evidence of potential change in marine microbial communities were presented by (Berner et al.,
100 2018). At reduced salinity levels, the heterotrophic bacteria community changed drastically and
101 resembled communities at high temperature, indicating synergistic effects of temperature and salinity.
102 It was suggested that the increase in bacterial biomass was caused by the decay of filamentous
103 cyanobacteria (Berner et al., 2018). This highlights the importance of considering food web effects
104 (both bottom-up and top-down) on microbial communities under climate change.

105

106 **2.2. Phytoplankton and Cyanobacteria**

107

108 The growing season of phytoplankton has significantly prolonged with warming temperatures during
109 the past few decades (Kahru et al., 2016). For instance in the western Baltic Sea, it now extends from
110 February to December (Wasmund et al., 2019). The earlier and prolonged spring bloom has been
111 attributed to changes in environmental conditions associated with global change (Groetsch et al.,
112 2016), including more sunshine and less windy conditions (Hjerne et al., 2019). The spring species
113 communities have also shifted from dominance of early blooming diatoms to later blooming
114 dinoflagellates and the autotrophic ciliate *Mesodinium rubrum* (Hjerne et al., 2019; Hällfors et al.,
115 2013; Kuosa et al., 2017; Klais et al., 2011), due to changes in climate and weather patterns, including
116 ice cover and wind conditions (Klais et al., 2013).

117 The amount of Cyanobacteria has increased and the phytoplankton biomass maximum, which
118 in the 1980's was in spring, is now in July-August. This shift has been explained by a complex
119 interaction between warming, eutrophication and increased top-down pressure (Suikkanen et al.,
120 2013). In the Gulf of Bothnia, salinity decline was also an important factor for phytoplankton
121 community change in 1979 to 2012 (Kuosu et al., 2017).

122 Experimental evidence supports findings that climate change can and will drive changes in the
123 pelagic primary production (Sommer et al., 2012), and a thorough review illustrating benthic-pelagic
124 coupling shows ecosystem-wide consequences of altered pelagic primary production (Griffiths et al.,
125 2017), probably also impacting food web dynamics (Kortsch et al., 2021).

126 There is, however, a discrepancy on the relative effects of eutrophication and climate in
127 explaining past changes in phytoplankton biomass and communities. In the long-term data, variable
128 results can be seen, according to area and dominating species group (Wasmund et al., 2011; Groetsch
129 et al., 2016). Certain studies have found evidence of eutrophication effects which have been modified
130 by climate-induced variations in temperature and salinity (Hällfors et al., 2013; Olofsson et al., 2020),



131 and a connection with the Baltic Sea Index has also been demonstrated (Griffiths et al., 2020). Other
132 studies did not find any explanation for the observed change in community composition, and
133 concluded that phytoplankton community in the Baltic Sea is not in a steady state (Olli et al., 2011),
134 or noted that stochastic dynamics at local scales confound any commonalities between phytoplankton
135 groups (Griffiths et al., 2020).

136 The projected increase in precipitation is expected to increase river runoff and nutrient load into
137 the sea, especially in the northern Baltic Sea (Huttunen et al., 2015), and together with increased
138 internal loading of nutrients, several modelling studies project an increased phytoplankton biomass
139 until the end of the century (Meier et al., 2012a; Meier et al., 2012b; Skogen et al., 2014; Ryabchenko
140 et al., 2016). There is also evidence that nutrient reduction in combination with predicted climate
141 change may induce a shift from pelagic to benthic primary production (Lindegren et al., 2012).

142 While ocean acidification (OA) has a negative effect on many organisms, it may enhance
143 phytoplankton productivity due to increased CO₂ concentration in water. E.g. the biomass of southern
144 Baltic autumn phytoplankton, biomass increased in mesocosms simulating OA, also under warm
145 conditions (Sommer et al., 2015). In many experiments, however, OA had little effects on community
146 composition, fatty acid composition or biovolumes of phytoplankton in spring or autumn (Paul et al.,
147 2015; Bermudez et al., 2016; Olofsson et al., 2019). Even when (positive) effects were detected, they
148 were mainly caused by an associated release of grazing by copepod nauplii in low temperature
149 treatments (Paul et al., 2016).

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

156

157 **2.3. Zooplankton**

158

159 Several studies have confirmed that marine copepod species have declined, while euryhaline and
160 limnetic, often small-sized, species increase in abundance (Hänninen et al., 2015; Suikkanen et al.,
161 2013). The decline of marine taxa has been linked to the decline of salinity, while the increase of
162 brackish-water taxa has been, directly or indirectly, positively affected by the temperature increase.
163 (Mäkinen et al., 2017). Species that reside in the upper water layers, such as the copepod *Acartia* spp,
164 are mostly affected by temperature driven increase in food availability, whereas species inhabiting the
165 deep layers, such as older stages of *Pseudocalanus acuspes*, are more dependent on salinity and
166 predation pressure (Ehrnsten, 2020; Otto et al., 2014b; Otto et al., 2014a; Mäkinen et al., 2017).



167 Small-scale impacts on species-level may affect reproductive success, and thus influence both
168 populations and communities (Möller et al., 2015).

169 The effects of climate-driven variations in temperature and ocean acidification (OA) on
170 zooplankton have been studied experimentally. In *Acartia* sp., a dominant copepod in the northern
171 Baltic Sea, warming decreased egg viability, nauplii development and adult survival (Vehmaa et al.,
172 2013), and both warming (Garzke et al., 2015) and OA (Vehmaa et al., 2016) had negative effects on
173 adult female size. This suggests that the projected OAW may affect the populations of these dominant
174 copepods in the coming decades. Subtle effects on zooplankton functional groups, such as a shift to a
175 dominance by cladocerans and rotifers, have also been shown as a result of warming (Jansson et al.,
176 2020), and it seems likely that the zooplankton community will undergo significant change as climate-
177 induced warming and reduced salinity continues.

178

179 **2.4. Macroalgae and vascular plants**

180

181 Long-term changes in Baltic Sea macroalgae and charophytes have mostly been explained by
182 combined or synergistic simultaneous changes in salinity, wind exposure, nutrient availability and
183 water transparency (Gubelit, 2015; Blindow et al., 2016; Rinne and Salovius-Laurén, 2020), as well
184 as biotic interactions (Korpinen et al., 2007). For the brown algae bladderwrack *Fucus* spp., light
185 availability, which may also be indirectly affected by climate-induced increase in nutrients, affects the
186 local coverage (Lappalainen et al., 2019). A documented long-term decrease of water transparency in
187 1936 to 2017 has reduced favorable sea floor areas for *Fucus* spp. by 45% (Sahla et al., 2020). The
188 conclusion for coastal ecosystems has, however, been that eutrophication, whether being caused
189 solely by anthropogenic nutrient loads, or amplified by climate change, has been the most important
190 pressure affecting the shallow coastal water areas of the Baltic Sea (Olsson et al., 2015).

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

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



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

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

223 Similar experiments on climate change effects as done with bladderwrack have also been made
224 with other macroalgae and certain vascular plants. In laboratory and field experiments (in the Gulf of
225 Riga), OA increased the growth of the opportunistic green alga *Ulva intestinalis* (Pajusalu et al., 2013;
226 Pajusalu et al., 2016). This suggests that OA could favour such fast-growing species and induce an
227 overgrowth of *Fucus* by annual green algae. Other studies showed that photosynthesis of charophytes
228 increased under high pCO₂ treatments, whereas the eelgrass *Zostera marina* did not respond to the
229 elevated pCO₂ alone (Pajusalu et al., 2015). Salinity decline is projected to decrease the distributional
230 ranges of *Z. marina* and the red algae *Furcellaria lumbricalis*, whereas temperature increases
231 probably favours charophytes. Charophytes will however not replace other key habitat forming
232 species because they occupy sheltered soft bottom areas (Torn et al., 2020). A study performed for the
233 southernmost Baltic Sea coupled species distribution and biogeochemical modelling to project how
234 projected wind fields, hydrodynamic conditions and nutrient abatement scenarios affect the
235 distribution of eelgrass *Zostera marina* in the future (2062-2066). It was concluded that nutrient
236 reductions that fulfill the Helsinki Commission's Baltic Sea Action Plan (BSAP) will lead to an
237 expansion of eelgrass coverage, despite potentially harmful effects on eelgrass distribution caused by
238 a projected stormier climate (Bobsien et al., 2021). The rapidly changing marine environment in the



239 Baltic Sea however pose an evolutionary risk, especially for populations with specific adaptations,
240 such as relicts, which may be at risk for local extinctions (Johannesson et al., 2011).

241 Overall, observations of past changes, experimental work and modelling studies suggest that
242 climate change can cause complex responses in relation to other environmental factors (e.g.
243 eutrophication) and influence carbon storage in both macroalgae and vascular plants in the Baltic Sea
244 (Jonsson et al., 2018; Takolander et al., 2017a; Röhr et al., 2016; Salo et al., 2020; Bobsien et al.,
245 2021).

246

247 **2.5. Zoobenthos**

248

249 Soft bottom benthic communities are dependent on several biogeochemical variables, and climate
250 change related parameters have been shown to act as drivers for the long-term progression of
251 zoobenthic communities (Rousi et al., 2019; Weigel et al., 2015; Ehrnsten et al., 2020). For instance,
252 in the SW coast of Finland, a drastic community change, where amphipods were replaced by Baltic
253 clam *Limecola balthica* and the non-indigenous polychaete *Marenzelleria* spp., took place. It was best
254 explained by an increase in near-bottom temperature and by fluctuations in salinity and oxygen (Rousi
255 et al., 2013). As for benthic biomass, food availability and oxygen conditions have been the most
256 important factors, but it is also suggested that, in the future, climate-induced changes in salinity,
257 temperature and eutrophication will also be of importance (Timmermann et al., 2012; Ehrnsten et al.,
258 2019a; Ehrnsten et al., 2019b).

259 In the Åland Islands (northern Baltic Sea), zoobenthos variations were associated with salinity
260 decline during 1983-2012 (Snickars et al., 2015), and environmentally driven shifts in the links
261 between zoobenthos and benthic-feeding fish assemblages were recorded. Long-term climate-induced
262 shifts in zoobenthos and other trophic levels have also been described (Törnroos et al., 2019;
263 Forsblom et al., 2021), and in all of these cases, interactions between the physical climate-controlled
264 drivers and secondary impacts (mainly eutrophication and/or hypoxia) have been registered. It is
265 notable that eutrophication-induced hypoxia is by no means limited to the deep basins of the Baltic
266 Sea (Conley et al., 2011). Especially the mosaic archipelagoes of the northern Baltic Sea, which have
267 limited water exchange, are prone to hypoxia (Virtanen et al., 2018a). As climate change will affect
268 such rapidly warming areas, late summer hypoxia may increase especially within the coastal areas of
269 the northern Baltic Sea, and contribute to the “vicious circle of eutrophication” (Vahtera et al., 2007)
270 by enhancing internal loading of phosphorus to the system.

271 The effects of warming on invertebrates are non-linear. In experiments, respiration and growth
272 of the isopod *Idotea balthica* first increased until 20°C, and then decreased at 25°C (Ito et al., 2019).
273 Therefore, heat waves may pose a severe threat to sublittoral invertebrates. Different species show
274 different responses to single and sequential heat waves, however, resulting in a change in community
275 structure (Pansch et al., 2018). Many marine invertebrates will directly and indirectly suffer from



276 decreasing salinity. In experiments simulating projected changes in temperature and salinity, the
277 survival of the isopod *Idotea balthica* decreased, albeit with variations between and within regions
278 (Rugiu et al., 2018c), and a combination of experimental studies and species distribution modelling
279 demonstrated that abundances of *I. balthica* will be significantly reduced, mainly due to the salinity-
280 induced decline of its host macroalgae, *Fucus vesiculosus* (Kotta et al., 2019).

281 Ocean acidification has various effects on benthic invertebrates. The size and time to settlement
282 of pelagic larvae of the Baltic clam *Limecola/Macoma balthica* increased with OA, suggesting a
283 developmental delay (Jansson et al., 2016), while OA had no effects on larvae of the barnacle
284 *Amphibalanus improvisus* (Pansch et al., 2012). Short (12 h) or long-term (2 week) exposures to OA
285 did not have significant effects on the isopod *Saduria entomon* either (Jakubowska et al., 2013).
286 Controversial results were obtained for the isopod *Idotea balthica*, from three different sea areas:
287 North Sea, Kattegat, and the Baltic Sea. The populations from more saline habitats were not
288 significantly affected by OA, while the Baltic Sea population showed 100 % mortality (Wood et al.,
289 2014). It was suggested that the Baltic *I. balthica* had higher levels of oxidative stress, and the
290 combined stress became lethal to them.

291

292 **2.6. Non-indigenous invertebrates**

293

294 It is often suggested that climate change will favour invasions of non-indigenous species worldwide
295 (Jones and Cheung, 2015). It has also been shown that native and non-native species tend to inhabit
296 separate niches in the Baltic Sea. The non-native species typically occur in areas characterized by
297 reduced salinity, high temperatures, high proportion of soft seabed and decreased wave exposure,
298 whereas most native species display an opposite pattern (Jänes et al., 2017). This suggest that the
299 former areas are more prone to further range expansion of non-native species than the latter.

300 Disentangling factors facilitating invasive or non-native species demands long-term surveys, and data
301 from multiple environments in order to distinguish climate-related effects from other ecosystem-level
302 drivers (Bailey et al., 2020), and there is no conclusive evidence that non-indigenous species will gain
303 competitive advantages from climate-induced change, such as heat-waves (Henseler et al., 2021).

304 Modelled scenarios of temperature and salinity have also been used to project how the change in the
305 abiotic environment could affect NIS already present in the Baltic Sea. The analysis suggests an
306 increase of Ponto-Caspian cladocerans in the pelagic community, and an increase in dreissenid
307 bivalves, amphipods and mysids in the coastal benthic areas of the northern Baltic Sea until 2100
308 (Holopainen et al., 2016).

309

310 **2.7. Fish**

311



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

317 Increasing seawater temperature has also made it possible for certain warm water Atlantic
318 species, such as anchovy (Reusch et al., 2018) and sole and turbot (Sparrevojn et al., 2013) to occur
319 more abundantly in Kattegat and the westernmost Baltic Sea. Such northward migrations may be
320 caused by both global climate change and by variations in the North Atlantic Oscillation (NAO), the
321 Atlantic Multidecadal Oscillation (AMO), as well as contraction of the subpolar gyre. It seems
322 evident that fish communities in the Baltic Sea and in the adjacent marine regions may undergo
323 drastic change with increasing temperatures, decreasing salinities and increasing instances of
324 hypoxia/anoxia (Reusch et al., 2018; Stenseth et al., 2020), which in turn may lead to altered food
325 web dynamics (Woods et al., 2021), also in the Baltic Sea (Eero et al., 2021).

326 As for coastal fish, the distribution of pikeperch (*Sander lucioperca*) expanded towards north
327 along the coasts of the Bothnian Sea, apparently due to the warming of waters (Pekcan-Hekim et al.,
328 2011). For many coastal piscivores (perch, pike, pike-perch), as well as cyprinids, the eutrophication
329 status of coastal waters is however an equally or more important factor for distribution than climatic
330 variation (Bergstrom et al., 2016; Snickars et al., 2015). A long-term study (over four decades) made
331 at different coastal areas of the Baltic Sea illustrates that it is hard to disentangle the abiotic and biotic
332 interactions, e.g. between fish and their food-sources (benthos), and climate-related drivers thus
333 appear significant on a multidecadal time-scale across a large spatial scale (Törnroos et al., 2019). The
334 study also highlights possible decoupling of benthic-feeding fish from long-term changes of
335 zoobenthos.

336 Future climatic variations may affect fish in the Baltic Sea through their effects on water
337 temperature, salinity, oxygen and pH, as well as nutrients, which indirectly affect food availability for
338 fish. The responses of cod larvae to ocean acidification (OA), also in combination with warming
339 (OAW), have been studied experimentally. In some studies, no effect of OA or OAW on hatching,
340 survival or development rates of cod larvae was found (Frommel et al., 2013), while in others
341 mortality of cod larvae doubled when treated with high end projections (RCP8.5) of OA. When the
342 projected increase of mortality was included into a stock-recruitment model, recruitment of western
343 Baltic Cod declined to an average of 8 % of the current recruitment (Stiasny et al., 2016). Also,
344 several modelling studies project low abundances of cod towards the end of the century, due to the
345 decrease of 'cod reproductive volume' (Niiranen et al., 2013; Wåhlström et al., 2020), although the
346 large importance of fisheries to the recovery potential of cod stocks has been pointed out (Cardinale
347 and Svedäng, 2011).



348 Climate change may also have positive effects on fish stocks. Increasing spring and summer
349 temperatures have in modelling studies been projected to gradually increase productivity and stocks of
350 sprat (Voss et al., 2011; Mackenzie et al., 2012; Niiranen et al., 2013). For herring the results are more
351 variable: both increase (Bartolino et al., 2014) and a short-term decrease (until 1950) (Niiranen et al.,
352 2013) have been projected.

353

354 **3. Climate change and ecosystem structure and function**

355

356 The marine food webs of the Baltic Sea have been, and are projected to be, impacted by climate
357 change-related variables by altering the physical environment for several species, by impacting micro-
358 evolution of species in the Baltic Sea, and by synergistic effects of climate change and other
359 environmental drivers such as eutrophication and hypoxia (Niiranen et al., 2013; Wikner and
360 Andersson, 2012; Schmidt et al., 2020; Pecuchet et al., 2020; Ehrnsten et al., 2020). It has even been
361 shown that the entire ecosystem may fulfil criteria for becoming a novel system with profoundly
362 altered energy-pathways (Ammar et al., 2021). Below, recent findings regarding specifically climate
363 impacts on trophic structure and functioning on the Baltic Sea ecosystem are summarized.

364

365 **3.1. Climate change and primary production in the pelagial**

366

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

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

380 There are also contrasting results. When pCO₂ was experimentally increased, the production of
381 single-celled cyanobacterium *Cyanothece* increased, while that of *Nodularia* sp. decreased (Eichner et
382 al., 2014). Also, increase of temperature from 16 to 18–20 °C, led to an earlier peak of
383 cyanobacteria, while yields were reduced (Berner et al., 2018). In particular, the biomass of nitrogen-



384 fixer *Dolichospermum* sp. decreased. This suggests that there are species specific responses to climate
385 change and associated oceanographic parameters even within Cyanobacteria. If the biomasses of
386 *Nodularia* asp. and *Dolichospermum* decrease due to increased acidification, nitrogen input into the
387 Baltic Sea as well as carbon export to heterotrophic bacteria via cyanobacteria might decline (Eichner
388 et al., 2014; Berner et al., 2018).

389

390 **3.2. Nutrient recycling, benthic-pelagic coupling and trophic efficiency**

391

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

396 A climate and nutrient load driven model reconstruction of the Baltic Sea state from 1850 to
397 2006 suggest that the shift from spring to summer primary production is accompanied by an
398 intensification of pelagic recycling of organic matter (Gustafsson et al., 2012). In mesocosm studies
399 warming accelerated (southern Baltic Sea) phytoplankton spring bloom and increased carbon specific
400 primary productivity (Sommer and Lewandowska, 2011; Sommer et al., 2012; Paul et al., 2016). The
401 total phytoplankton biomass however decreased due to negative effects of warming on nutrient flux
402 (Lewandowska et al., 2014; Lewandowska et al., 2012).

403 It has also been projected that the flow of dissolved organic matter (DOM) into the northern
404 Baltic Sea increases in the future climate, especially in the northernmost Baltic Sea (Strååt et al.,
405 2018). By using long-term time series from 1994 to 2006, it was indeed shown that climate change
406 brought about increased riverine DOM, which increased the amount of substrate available for bacteria
407 (Wikner and Andersson, 2012). Also experimental studies have demonstrated increased microbial
408 activity and biomass with increasing DOM and temperature (Ducklow et al., 2010). Eventually
409 bacteria compete for nutrients with phytoplankton, and as the brownification of water also reduces
410 light availability, phytoplankton productivity and biomass may decrease. This shifts the carbon flow
411 towards microbial heterotrophy (Wikner and Andersson, 2012).

412 It has also been suggested that climate change may decrease fish productivity, especially in the
413 northernmost Baltic Sea, because when the system towards heterotrophy, the food web efficiency
414 declines, and eventually the fish production may decrease (Berglund et al., 2007; Wikner and
415 Andersson, 2012). In most areas, however, also heterotrophic production through the bacteria-
416 flagellates-ciliates chain may remain high, yielding a high number of copepods, the favourite food of
417 forage fishes (Lefebure et al., 2013), and the consequences of climate change associated changes in
418 trophic efficiency on fish productivity remain unsecure. There is also evidence that ocean warming
419 may lead to increased species turnover in coastal waters of the Baltic, impacting all trophic levels of
420 the system (Hillebrand et al., 2010).



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

434

435 **3.3. Complex food web responses in the microbial loop**

436

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

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

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



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

461 In summary, climate change probably strengthens trophic pathways from phytoplankton and
462 flagellates through ciliates to copepods (Aberle et al., 2015). It has also been suggested, from
463 experimental (mesocosm) evidence, that warming induces a switch from a bottom-up controlled to a
464 mainly top-down controlled system, which may result in increased zooplankton abundance and
465 reduced phytoplankton biomass under warm temperature (Paul et al., 2016). Such results highlight the
466 importance of considering food web effects (both bottom-up and top-down) on microbial
467 communities under climate change.

468

469 **3.4. Food web interactions in the littoral ecosystem**

470

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

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

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

489 If the same takes place in other sea areas of the Baltic Sea as well, warming may promote the
490 growth of filamentous algae and contribute to the decline of bladderwrack. Decline of the
491 bladderwrack habitats will affect other trophic levels in various ways, due to declining availability to
492 habitat, food conditions (Kotta et al., 2019; Takolander et al., 2017a; Jonsson et al., 2018) as well as
493 connectivity between bladderwrack populations as well as organisms inhabiting patches of



494 bladderwrack (Jonsson et al., 2020; Virtanen et al., 2020). These results suggest that both summer
495 heatwaves and cold season warming can induce eutrophication-like effects in the photic zone
496 dominated by macroalgae, even without an increase in nutrient loading, and without major changes in
497 salinity.

498

499 **3.5. Climate change and regime shifts**

500

501 In the 1980's a partly climate induced regime shift took place with drastic changes in the central
502 Baltic food web (Möllmann et al., 2009; Lindegren et al., 2010a). Later studies also confirmed that,
503 during that period declines in suitable habitat and 'reproductive volume' (where cod egg survival is
504 possible) contributed to the decline of cod population (Hinrichsen et al., 2011; Casini et al., 2016;
505 Bartolino et al., 2017), causing the earlier demonstrated (Casini et al., 2008) cascading effects on its
506 main prey, sprat and herring, as well as zooplankton. However, the overall food web complexity in
507 both the coastal and open central Baltic Sea has remained surprisingly stable, in spite of significant
508 changes in both environmental drivers and individual populations, making overall conclusions
509 somewhat uncertain (Yletyinen et al., 2016).

510 The different effects of temperature and salinity on sprat and cod also resulted in a spatial
511 mismatch between these species, which contributed to the increase of sprat stocks (Reusch et al.,
512 2018). Transition to a lower saline Baltic Sea, and associated decline of marine copepods (Hänninen
513 et al., 2015), also induced a halving of (3-year old) herring weight-at-age, from 50–70 g in the late
514 1970s to 25–30 g in 2000s (Dippner et al., 2019). These studies have mostly considered the central
515 and southern Baltic fish stocks. In the Bothnian Bay, the northernmost basin of the Baltic Sea, salinity
516 was the major driver for herring as well, but the species involved were different. Here the decline of
517 spawning-stock biomass observed in 1980–2013 was explained by a simultaneously increased
518 competition for food with vendace, a limnic species that had increased with lowering salinity (Pekcan-
519 Hekim et al., 2016).

520 Recent awareness of marine heatwaves and their potential impact on the ecosystem has also
521 increased our knowledge on how short-term pulses in temperature, as a result of overall warming,
522 may impact littoral, benthic and pelagic communities, indicating that there are numerous levels of
523 ecosystem-responses yet to be explored (Pansch et al., 2018; Saha et al., 2020).

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

529 Different scenarios may yield very different outcomes, however. Medium CO₂ concentrations
530 (RCP4.5), low nutrients and sustainable fisheries resulted in high biodiversity and high numbers of



531 cod and flounder, while high emissions (RCP8.5) and high nutrient loads resulted in diminished
532 biodiversity and high abundance of lower value fish, especially sprat (Bauer et al., 2018; Bauer et al.,
533 2019; Hyytiäinen et al., 2019).

534

535 **4. Knowledge gaps**

536

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

542 Furthermore, regime shifts mostly looked at through food web changes in the central Baltic
543 Sea, using the cod-sprat-herring-zooplankton trophic links as an example. Only recently have the
544 experimental and mesocosm studies on the dynamics of the lower trophic levels, i.e., bacteria,
545 flagellates and microzooplankton started to shed light on the complex dynamics of the microbial loop
546 under different scenarios of DOM, temperature and OA. The conclusions from the experimental work
547 should be integrated into the wider empirical studies of food web dynamics, to get a more
548 comprehensive view of the responses of the pelagic and benthic systems to climate change, from
549 bacteria to fish (Kortsch et al., 2021).

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

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

561

562 **5. Conclusions**

563

564 With escalating environmental change caused by climate-driven and associated factors, the entire
565 marine food webs, from coastal to off-shore, from shallow to deep, from pelagic to benthic
566 (sedimentary) are expected to change as species-distributions are impacted, and key nodes and



567 linkages in the food webs may be altered or lost (Lindegren et al., 2010b; Niiranen et al., 2013;
568 Leidenberger et al., 2015; Griffiths et al., 2017; Kotta et al., 2019; Gårdmark and Huss, 2020).

569 The direct and indirect effects of climate change-related parameters on species, communities
570 and the ecosystem are summarized in Table 1.

571 Climate change induces multiple direct and indirect effects on species and communities and
572 affects nutrient and carbon dynamics of the Baltic Sea ecosystem in the pelagial, deep sea benthos, as
573 well as the photic zone close to the shores. The responses vary from species group to another, and
574 within groups, even between sibling species. While responses of individual species to single
575 parameters may be straightforward, but when more complex systems with several parameters and
576 multiple species or trophic levels are studied, the system responses of the system become difficult to
577 foresee. Species-specific response, many feedbacks, and altered trophic pathways, make projections
578 concerning the state of the ecosystem and trophic effects difficult.

579 The consequences of climate change are difficult to predict, also because research into the long-
580 term dynamics of food webs is still scarce (Kortsch et al., 2021; Pecuchet et al., 2020; Törnroos et al.,
581 2019). Some common patterns arise from the wealth of recent studies, however. It is probable that the
582 combined effects of increased nutrient loads, increased stratification and increased internal loading
583 will improve the conditions for cyanobacterial blooms in the central basins, as well as the Gulf of
584 Finland. In the northernmost areas - Kvarken and the Bothnian Bay – the increasing allochthonous
585 DOM may complicate the picture by increasing heterotrophy and by decreasing food web efficiency.
586 This effect may however be counteracted by the intensification of the reduction of time lags between
587 bacteria, phytoplankton, microzooplankton, suspension feeding cladocerans and microzooplankton-
588 eating copepods, which may change the system from a bottom-up controlled one to top-down
589 controlled one.

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

597 Naturally, climate change is not the only factor determining the fate of the Baltic Sea in the
598 future. Several modelling studies have concluded that nutrient reductions according to HELCOM
599 BSAP will be a stronger driver for ecosystem functions in the Baltic Sea than climate change
600 (Ehrnsten et al., 2019b; Friedland et al., 2012; Niiranen et al., 2013; Pihlainen et al., 2020). In
601 moderate nutrient loading scenarios also climate change will play a role, but under full
602 implementation of BSAP, the environmental state of the Baltic Sea will be significantly improved by
603 the end of the century (Meier et al., 2018; Saraiva et al., 2018, 2019). This also means that extreme



604 cyanobacteria blooms will no longer occur, despite the proceeding climate change (Meier et al.,
605 2019a).

606 These studies further highlight the importance of studying the Baltic Sea as a socio-ecological
607 system, responding to both environmental and societal changes (Bauer et al., 2018; Bauer et al., 2019;
608 Hyttiäinen et al., 2019), and it is important to continue efforts combining long-term monitoring,
609 experimental studies, modelling and dialogue with human society in order to attune to the changes
610 ultimately driven by the Ocean itself (Stenseth et al., 2020).

611

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613

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615

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621

622 Table 1. Summary of research findings and conclusions on the anticipated effects of climate change
 623 (CC) effects in the Baltic Sea. The table only includes studies published in 2011-2021. For earlier
 624 studies, see Dippner et al. (2008) and Viitasalo et al. (2015). Observations, experimental simulations
 625 or modelled projections: T = temperature increase; S = salinity decline; TSO = temperature increase
 626 with salinity decline, also with oxygen decline; OA = CO₂ increase; OAW = CO₂ and temperature
 627 increase; EXP = experimental manipulations /microcosms; MES = experimental manipulations
 628 /mesocosms; LTS = Long-term studies; MOD = modelling studies; FIE = Field data.
 629

Taxonomic group		T	S	TSO	OA	OAW & OAS	Changes in physico-chemical environment	Interactions between trophic levels
Bacterial and microbial communities, including microzooplankton		EXP: Community change ¹ ; MES: Growth rate of microzooplankton increased ⁹⁴	EXP: Drastic change in bacterial communities ²	EXP: Mixed responses; TS change in microbial community ²	EXP: Limited impact ^{1,3} ; MES: No effect on microzooplankton ⁹⁴	EXP; Biovolume of bacterial communities decline with OAS ² ; EXP: Community change with OAW ³		BC increase caused by decaying cyanobacteria ⁴ ; EXP: T increase induced a decline in bacteria, due to increase of bacterivorous flagellates ⁹³ ; MES: Positive effect on ciliate <i>Myrionecta</i> due to increase in food availability ⁹⁵
Phytoplankton		LTS: Prolonged growing season ^{5,6} . Earlier and longer spring bloom ⁶⁻⁸		LTS: Eutrophication effects modified by climate-induced variations in temperature and salinity ^{11,16} and by Baltic Sea Index ¹⁷	MES: Autumn phytoplankton biomass increased ²³ EXP: No/minor effects on community composition, fatty acids or biovolumes of phytoplankton ²⁴⁻²⁶	MES: Autumn phytoplankton biomass increase with OAW ²³	LTS: Shift from diatoms to dinoflagellates due to changes in sunshine, wind and ice conditions ⁹⁻¹³ ; MOD: Increased phytoplankton biomass caused by increase in nutrient	EXP: OAW effects modified by associated diminishing of grazing by copepods ²⁷ ; MES: Warming increases zooplankton grazing on medium-sized algae which releases smaller



							availability ¹⁸⁻²¹ MOD: CC and nutrient reduction lead to a shift from pelagic to benthic primary production ²²	algae from predation ²⁴
Cyano-bacteria and toxic dino-flagellates		EXP: Earlier peak but lower biomass of cyano-bacteria ⁴ ; LT: Increase of cyano-bacteria blooms in summer ¹⁴ . EXP: Toxicity of cyano-bacterium <i>Dolichospermum</i> sp. increases ²⁸⁻²⁹ . EXP: Toxicity of dino-flagellate <i>Alexandrium ostenfeldii</i> increases ³⁰	LTS: community change caused by S decline in the Gulf of Bothnia ¹⁵ ; EXP: Toxicity of cyanobacterium <i>Dolichospermum</i> sp. increases ²⁹		EXP: Production of single-celled cyano-bacterium <i>Cyanothece</i> increases and that of filamentous <i>Nodularia</i> sp. decreases ¹⁰⁴ ; EXP: Decline of nitrogen-fixing cyano-bacteria may induce a decline of nitrogen input into the Baltic Sea ^{4, 103}		MOD: Cyano-bacteria blooms increase ⁹⁷⁻¹⁰²	LTS: Shift to cyano-bacteria dominance also attributed to changes in eutrophication and top-down pressure ¹⁴
Mesozoo-plankton		EXP: Decrease in copepod egg viability and nauplii development ³³ ; Decrease in copepod adult body size and survival ³³⁻³⁴ . A shift to communities dominated by cladocerans and rotifers ³⁶	LTS: Decline of marine copepods due to climate induced decline in S ^{14, 30} ; LTS: Increase of brackish copepods due to decline in S and increase in T ³¹		MES: Decline in body size of adult copepods ³⁵ ;			MOD: Surface-dwelling copepods are favoured by T-induced increase in food availability ³² ; MES: At high T copepods control their micro-zooplankton prey ⁹⁴ ; MES: OA promotes growth of cladocerans possibly



								because of a CO ₂ -driven increase in food availability ⁹⁵ , MES: Warming strengthens the microbial loop ⁹⁶ and induces a switch from bottom-up to top-down controlled system ²⁷
Macroalgae		EXP: At heat wave temperatures, photosynthesis declines, growth ceases and necrosis starts in bladder-wrack ³⁷⁻³⁸	EXP: Sexual reproduction of bladder-wrack ceases ³⁹⁻⁴⁰ MOD: Bladder-wrack distribution will be restricted in the Baltic Sea ⁴⁴⁻⁴⁷ ; MOD: Red alga <i>Furcellaria</i> distribution will be restricted in the Baltic Sea ⁵¹		EXP: Generally small effects on macroalgae ⁴¹⁻⁴² EXP: Increase in growth of green alga <i>Ulva intestinalis</i> ⁴⁸⁻⁴⁹	EXP: OA-induced necrosis in bladder-wrack is worsened in low salinity ³⁸ ; EXP: Upwelling of hypoxic water causes mortality of bladder-wrack germlings under OAW conditions ⁴³		MES: In spring, T increase induces overgrowth of bladder-wrack by epiphytic diatoms ⁸⁴ ; In summer, a heatwave-driven collapse of grazers results in overgrowth of bladder-wrack by filamentous algae; in winter, warming enhances grazing by invertebrates, resulting in decline of bladder-wrack biomass ⁸⁵
Vascular plants		MOD: Charophyte distribution increases ⁵¹	MOD: Eelgrass distribution will be restricted in the Baltic Sea ⁵¹		EXP: No effect on eelgrass <i>Zostera marina</i> ⁵⁰		MOD: Eelgrass distribution will be retained if nutrient abatement is implemented, despite CC effects ⁵²	



Benthic animals		EXP: Non-linear response to T in isopod <i>Idothea balthica</i> ⁵³ ; EXP: Heat waves induce a shift in community structure ⁵⁴ ; FIE: T increase induces a higher biomass of gammarids and snails ⁸⁶	LTS: Salinity decline affected zoobenthos variations in Åland Islands ⁵⁵	LTS: Long-term changes in physico-chemical parameters drive the variations in zoobenthos ⁵⁶⁻⁶⁰ ; LTS: Replacement of amphipods by Baltic clam and <i>Marenzelleria</i> sp. explained by changes in T, S and O ₂ ⁶¹ ; EXP: Survival of isopod <i>Idothea Baltica</i> decreases ⁶²	EXP: Development of Baltic clam larvae slows down ⁶³ ; EXP: No effects on barnacle larvae ⁶⁴ ; EXP: No effects on isopod <i>Saduria entomon</i> ⁶⁵ ; EXP: No effects on isopod <i>Idothea balthica</i> in Kattegat ⁶⁶ , but strong effects in the Baltic Sea ⁶⁶		MOD: Climate-induced changes in physical and biogeochemical parameters will modify the response of zoobenthos to availability of food and oxygen ⁶⁷⁻⁶⁹	MOD: Abundance of isopod <i>Idothea balthica</i> will decline due to salinity-induced decline in bladderwrack ⁷⁰
Non-indigenous invertebrates		FIE: T increase induced higher biomass of gastropod <i>Potamo-pyrghus</i> ⁸⁶		FIE: NIS establish in areas with high T and low S ⁷¹ ; MOD: Projected increase of Ponto-Caspian bivalves, amphipods and mysids in the coastal benthic areas ⁷²				
Fish		LTS: Sprat has benefited from increasing T ⁷³⁻⁷⁵ ; LTS: Warm water Atlantic species (e.g. anchovy, sole and turbot) occur in the	LT: Salinity decline and associated decline of marine copepods induced a halving of herring weight-at-age ⁸⁸ ; LTS/MOD: Different effects of T and S on	MOD: Climate effects most obvious on a multidecadal scale, across a large spatial scale ⁶¹ ; MOD: Cod reproductive volume diminishes towards the	EXP: No effect on cod larvae ⁷⁹ ; EXP: Mortality of cod larvae doubles when treated with RCP8.5 scenarios ⁸⁰	EXP: No effect on cod larvae with OAW ⁷⁹		MOD: Abiotic and biotic interactions are mixed ⁶¹ ; MOD: Climate-induced decoupling of benthic feeding fish from their food source ⁶¹ ;



		western Baltic ⁷⁶⁻⁷⁷ ; MOD: Sprat productivity will increase with increasing temperatures ^{73-74, 64} ; MOD: Herring stocks will increase ⁸³ ; LTS: Pike-perch more abundant in the northernmost Baltic Sea ⁷⁸	sprat and cod caused a spatial mismatch between these species ⁷⁶ ; LTS: Decline in S increased resource competition between herring and vendace in the Bothnian Bay ⁹²	end of the century ⁸¹⁻⁸²				MOD: Herring stocks decrease in short term ⁸¹ ; FIE: Perch shift from feeding on small fish to gammarid crustaceans, which releases grazing from filamentous algae ⁸⁷ ; LTS/MOD: Partly climate induced decline in cod stock caused a cascading effect on sprat, herring and zooplankton ⁸⁹⁻⁹¹
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632 ¹ Bergen et al. 2016; ² Wulff et al. 2018; ³ Lindh et al. 2013; ⁴ Berner et al. 2018; ⁵ Kahru et al. 2016; ⁶
 633 Wasmund et al. 2019; ⁷ Sommer et al. 2012; ⁸ Groetsch et al. 2016; ⁹ Klais et al. 2011; ¹⁰ Klais et al.
 634 2013; ¹¹ Hällfors et al. 2013; ¹² Kuosa et al. 2017; ¹³ Hjerne et al. 2019; ¹⁴ Suikkanen et al. 2013; ¹⁵
 635 Kuosa et al. 2017; ¹⁶ Olofsson et al. 2020; ¹⁷ Griffiths et al. 2020; ¹⁸ Meier et al. 2012a; ¹⁹ Meier et al.
 636 2012b; ²⁰ Skogen et al. 2014; ²¹ Ryabchenko et al. 2016; ²² Lindegren et al. 2012; ²³ Sommer et al.
 637 2015; ²⁴ Paul et al. 2015; ²⁵ Bermudez et al. 2016; ²⁶ Olofsson et al. 2019; ²⁷ Paul et al. 2016; ²⁸
 638 Brutemark et al. 2015; ²⁹ Wulff et al. 2018; ³⁰ Hänninen et al. 2015; ³¹ Mäkinen et al. 2017; ³² Otto et
 639 al.2014a; ³³ Vehmaa et al. 2013; ³⁴ Garzke et al. 2015; ³⁵ Vehmaa et al. 2016; ³⁶ Jansson et al. 2020; ³⁷
 640 Graiff et al. 2017; ³⁸ Takolander et al. 2017b; ³⁹ Rothäusler et al. 2018; ⁴⁰ Rothäusler et al. 2019; ⁴¹ Al-
 641 Janabi et al. 2016a; ⁴² Wahl et al. 2019; ⁴³ Al-Janabi et al. 2016b; ⁴⁴ Vuorinen et al. 2015; ⁴⁵ Takolander
 642 et al. 2017a; ⁴⁶ Jonsson et al. 2018; ⁴⁷ Kotta et al. 2019; ⁴⁸ Pajusalu et al. 2013; ⁴⁹ Pajusalu et al. 2016;
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