

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

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1 Abstract

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

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

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

26 In deep benthic communities, continued eutrophication promotes high sedimentation
27 and keeps food conditions for zoobenthos good. If nutrient abatement proceeds, improving
28 oxygen conditions will first increase zoobenthos biomass but the subsequent decrease of
29 sedimenting matter will disrupt the pelagic-benthic coupling and lead to a decreased
30 zoobenthos biomass. In the shallower photic systems, heatwaves may produce
31 eutrophication-like effects, e.g., overgrowth of bladderwrack by epiphytes, due to a trophic
32 cascade. If salinity also declines, marine species such as bladderwrack, eelgrass and blue
33 mussel may decline. Freshwater vascular plants will be favoured but they cannot replace
34 macroalgae on rocky substrates. Consequently also invertebrates and fish benefiting from
35 macroalgal belts may suffer. Climate induced changes in the environment also favour
36 establishment of non-indigenous species, potentially affecting food web dynamics in the
37 Baltic Sea. As for fish, salinity decline and continuing of hypoxia is projected to keep cod
38 stocks low, whereas the increasing temperature has been projected to favour sprat and certain
39 coastal fish. Regime shifts and cascading effects have been observed in both pelagic and
40 benthic systems, as a result of several climatic and environmental effects acting
41 synergistically.

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

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

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

59

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

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64 **1. Introduction**

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

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

81 The effects of climate change on the Baltic Sea ecosystem may differ from those
82 projected for the oceanic areas as the Baltic Sea differs in many respects from the oceans and
83 even from the coastal ecosystems surrounding the other regional seas and oceans. The
84 communities of the Baltic Sea are formed of a peculiar combination of marine, limnetic and
85 brackishwater taxa. The long winter and the strong seasonal cycle give the area sub-arctic
86 properties, especially in the northern areas. The Baltic Sea has also been shown to warm up
87 faster than most other sea areas of the world (Belkin, 2009; Sherman et al., 2009), albeit with
88 large differences between sub-basins (Kniebusch et al., 2019; Dutheil et al., 2021). The Baltic
89 Sea is also strongly affected by its watershed, which is more than four times larger than its

90 surface area and is inhabited by ca. 85 million people (Omran and Negm, 2020). The marine
91 ecosystem therefore receives excess nutrients and other elements and contaminants from the
92 land via rivers, through the air, and by leaking from the sediments of the Baltic Sea.

93 Furthermore, the irregular inflows of more saline and oxic North Sea water, which at specific
94 basin-wide weather conditions enter the Baltic sea through the Danish Straits (Matthäus and
95 Schinke, 1994; Lehmann et al., 2022) influence the state and functioning of the Baltic Sea.

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

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

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

116 In this paper, we review research on climate change effects on the Baltic Sea species,
117 habitats, and ecosystem functioning, primarily based on research published in 2010—2021.
118 We include both studies investigating direct effects of climate related parameters on
119 organisms, as well as studies that investigate the more indirect processes affecting the
120 structure and functioning of the Baltic Sea ecosystem through biogeochemistry and food web
121 interactions. Evidence is compiled from empirical field studies that show past changes and
122 responses of species, populations, and communities to climate-affected parameters such as
123 temperature, salinity, oxygen, and pH. Then a large number of experimental studies,

124 investigating species responses to the same parameters in micro- or mesocosms, are
125 reviewed. Studies investigating the complex effects of climate change on the interactions
126 between species and trophic groups, i.e., phytoplankton, bacteria, cyanobacteria,
127 zooplankton, and fish, as well as algae or vascular plants and invertebrates grazing on them,
128 are also analysed. Modelling studies, based on coupled oceanographic-biogeochemical
129 models or other types of species-level or food web models, are reviewed. Based on the
130 published research we draw conclusions about the role of climate driven environmental
131 variables on shaping the structure and functioning of the Baltic Sea ecosystem and identify
132 knowledge gaps and current issues of dissensus. Areas in need of more research are
133 recommended.

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136 **2. Definitions**

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

143 By *global climate change* we refer to the past and contemporary increase in global
144 temperature, caused by anthropogenic emissions of CO₂ and other greenhouse gases, and its
145 effects on various climatic as well as oceanographic and biogeochemical parameters. By
146 *climate change*, in turn, we refer to a large-scale shift in climatic parameters affecting the
147 Baltic Sea region, that may be caused either by global climate change, by cyclic climate
148 fluctuations (such as North Atlantic Oscillation, NAO) or by irregular or stochastic variation
149 in climate parameters. We are not referring to short-term or seasonal weather patterns, but
150 mainly consider longer term (several years) variability in climate.

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

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

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

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169 **3. Review methods**

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

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

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

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

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199

200 **4. Effects on species and communities**

201

202 **4.1. Phytoplankton**

203

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

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

221 The spring species communities have also shifted from dominance of early blooming
222 diatoms to later blooming dinoflagellates and the mixotrophic ciliate *Mesodinium rubrum*
223 (Klais et al., 2011; Hällfors et al., 2013; Kuosa et al., 2017; Hjerne et al., 2019), probably due

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

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

242 It has also been suggested that, in the future climate, higher temperatures and less ice
243 will cause an earlier bloom of both diatoms and dinoflagellates, with increased dinoflagellate
244 dominance (Hjerne et al., 2019). Experimental (mesocosm) evidence supports findings that
245 warming up of water and changes in light conditions will accelerate the spring bloom, induce
246 a decline in peak biomass and favour small size cells, either directly or via increased grazing
247 by copepods (Sommer et al., 2012). On the other hand, this development may be
248 counteracted by increasing windiness and cloudiness, which have also been projected by
249 certain modelling studies (Hjerne et al., 2019). Recent studies have however indicated that
250 the projections for spring and summer wind and radiation are uncertain (Christensen et al.,
251 2022), and future weather changes and associated spring bloom dynamics therefore remain
252 obscure.

253 Climate change effects, i.e., temperature increase, salinity decline and acidification
254 have been shown to have variable results on the toxic dinoflagellate *Alexandrium ostenfeldii*.
255 Generally, the growth rates, as well as saxitoxin production, increased with increased
256 temperature and elevated pCO₂, but the responses were variable between strains (Kremp et

257 al., 2012; Kremp et al., 2016). In contrast, temperature or salinity changes do not seem to
258 have a significant effect on cyst germination of this species (Jerney et al., 2019).

259 Climate change also increases concentration of water carbon dioxide, a compound
260 necessary for primary production, and ocean acidification (OA) could therefore enhance
261 productivity of phytoplankton. The results of experimental studies investigating effects of
262 pCO₂ on phytoplankton are variable, however. The biomass of southern Baltic autumn
263 phytoplankton (kept in 1400-L indoor mesocosms for 21 days) increased when pCO₂ was
264 increased from 439 ppm to 1040 ppm, also under warm conditions (Sommer et al., 2015). In
265 other experiments, OA had little effects on community composition, fatty acid composition or
266 biovolumes of phytoplankton in spring or autumn (Paul et al., 2015; Bermudez et al., 2016;
267 Olofsson et al., 2019). Even when (positive) effects were detected, they were mainly caused
268 by an associated decrease of grazing by copepod nauplii in low temperature treatments (Paul
269 et al., 2016).

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

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

285 It is obvious that climatic influences are intertwined with other processes and
286 parameters affecting phytoplankton, especially anthropogenic nutrient loading from land and
287 internal loading of nutrients from the sediments. There is however a discrepancy on the
288 relative effects of eutrophication, climate change and other environmental and anthropogenic
289 factors in explaining past variations in phytoplankton communities and biomass. Also,

290 several studies have identified complex variations in phytoplankton communities that cannot
291 be easily explained by any of the studied factors or environmental parameters.

292 A study comparing historic phytoplankton communities from 1903-1911 with the
293 present ones (1993-2005) in the northern Baltic Proper and the Gulf of Finland observed an
294 undefined “period effect”, characterized by a decline of diatoms and increase of
295 dinoflagellates, that was not well explained by the available environmental variables
296 (temperature, salinity, and general regional climatological data). Although data on
297 biogeochemical parameters was not available for the period 103-1911, the authors interpreted
298 the observed community change as evidence of the direct and/or indirect influence of
299 eutrophication (Hällfors et al., 2013).

300 A study investigating summer phytoplankton time series (HELCOM monitoring 1979-
301 2012) across the Baltic Sea found that there were no common interannual patterns. Instead,
302 the class trends, e.g. that of cryptophytes, may be affected by anomalies in the BSI, although
303 a mechanistic explanation for the relationship could not be found (Griffiths et al., 2020).
304 Other studies did not find any explanation for the observed changes in the biovolumes of
305 different taxa, e.g. decrease of diatoms and increase of certain dinoflagellate taxa, and
306 concluded that phytoplankton community in the Baltic Sea is not in a steady state (Olli et al.,
307 2011), or noted that stochastic dynamics at local scales confound any commonalities between
308 phytoplankton groups (Griffiths et al., 2020).

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

315

316 **4.2. Cyanobacteria**

317

318 Filamentous diazotrophic cyanobacteria benefit from warm temperatures and stratified water,
319 as they tend to bloom during the hottest and calmest periods of summer (Munkes et al.,
320 2021). Several modelling studies suggest that the climate induced increase in stratification
321 (Liblik and Lips, 2019), together with potentially increasing hypoxia, and consequent release
322 of phosphorus from the anoxic sediments, will increase cyanobacteria blooms in the Baltic

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

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

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

340 It has also been suggested that the various drivers of climate change may contribute to
341 increase blooms and toxicity of species such as the dinoflagellate *Alexandrium ostenfeldii*
342 (Kremp et al., 2012; Kremp et al., 2016; Jerney et al., 2019). Also, the intracellular toxin
343 concentration of the Baltic cyanobacterium *Dolichospermum* sp. may increase with elevated
344 temperature (+4°C) (Brutemark et al., 2015; Wulff et al., 2018) and with decreased salinity
345 (from 6 to 3) (Wulff et al., 2018). As toxins of both dinoflagellates (Sopanen et al., 2011) and
346 cyanobacteria (Karjalainen et al., 2006; Karjalainen et al., 2007; Engström-Öst et al., 2017)
347 can accumulate in Baltic Sea zooplankton and induce lower grazing rates and higher
348 mortality, these studies suggest that toxic dinoflagellates and filamentous cyanobacteria may
349 get, due to their toxic effects and unpalatability, a competitive advantage over diatoms and
350 other phytoplankton in a future Baltic Sea.

351 A few long-term studies have not found an increase in cyanobacteria during the past.
352 Two recent studies compiling monitoring data from the Baltic Sea countries for 1979-2012
353 (Griffiths et al., 2020) and 1979-2017 (Olofsson et al., 2020) did not find any evidence for an
354 overall increase of diatzotrophic filamentous cyanobacteria during this period. Biovolume of
355 the hepatotoxic *Nodularia spumigena* did not change, and that of the non-toxic
356 *Aphanizomenon* sp. increased in the north and declined in the south (Olofsson et al., 2020).

357 Also, a study that compared years 1903-1911 and 1993-2005 concluded that cyanophyte
358 biomass has not increased in summer and have decreased in spring and autumn (Hällfors et
359 al., 2013). It has been suggested that, although cyanobacteria do prefer warmer temperatures,
360 the effect of ongoing warming can better be seen in changes in phenology of cyanobacteria
361 rather than as an increase of biomass (Griffiths et al., 2020). Also, a connection between the
362 amount of cyanobacteria and the Baltic Sea Index has been identified (Griffiths et al., 2020).

363 Hypothetically, ocean acidification could benefit cyanobacteria through increased
364 availability of carbon dioxide in water. The available studies do not give a definitive answer,
365 however. When pCO₂ was experimentally increased, the production of single-celled
366 cyanobacterium *Cyanothece* increased, while that of *Nodularia* sp. decreased (Eichner et al.,
367 2014). Also, increase of temperature from 16 to 18—20 °C, led to an earlier peak of
368 cyanobacteria, while the biomass of cyanobacteria, especially that of nitrogen-fixer
369 *Dolichospermum* sp. was reduced (Berner et al., 2018). Further, in mesocosm studies an
370 increase of pCO₂ (from 360 to 2030 µatm) coupled with an increase in water temperature
371 (from 16.6 to 22.4 °C) had a *negative* impact on the biomass of the diatzotrophic
372 cyanobacteria *Nodularia spumigena* (in 1400-L mesocosms, 28 days) (Paul et al., 2018).
373 Another experimental study (using 75 ml cell culture flasks), investigating the effects of
374 increased temperature (from 12 to 16 °C), decreased salinity (from 7 to 4) and elevated pCO₂
375 (from 380 to 960 ppm), found that only temperature had an effect on biovolume and
376 photosynthetic activity of *Nodularia spumigena* and *Aphanizomenon* sp. (Karlberg and
377 Wulff, 2013). The two species however had antagonistic effects on each other: biovolumes
378 were lower when grown together than when grown separately, indicating species interactions.

379 If the biomasses of *Nodularia* sp. and *Dolichospermum* decrease due to increased
380 acidification, nitrogen input into the Baltic Sea as well as carbon export to heterotrophic
381 bacteria via cyanobacteria might decline (Eichner et al., 2014; Berner et al., 2018). This could
382 however be balanced by the potential increase of *Cyanothece*, which is also a nitrogen-fixer
383 (Eichner et al., 2014).

384 To sum up, there are species specific responses to climate change and associated
385 oceanographic parameters within cyanobacteria. Several field and modelling studies suggest
386 that the climate induced increase in stratification, together with increasing hypoxia and
387 release of phosphorus from the sediments, has increased cyanobacteria biomass and will
388 continue to favour cyanobacteria blooms also in the future . However, the results of certain
389 empirical and experimental studies give a more multifaceted picture of cyanobacteria
390 response to climate change. The past increase of cyanobacteria is not as obvious as might be

391 expected, responses vary from species to species, and processes affecting amount of
392 cyanobacteria in the Baltic Sea can be modified, counteracted, or amplified by various
393 environmental processes and food web interactions.

394

395 **4.3. Zooplankton**

396

397 The Baltic Sea mesozooplankton species originate either from marine or freshwater
398 environments, and some are typically brackishwater. It is therefore plausible that they
399 respond to long-term variations in oceanographic parameters. Several field studies have
400 confirmed that marine copepod species (e.g., *Pseudocalanus* spp. and *Temora longicornis*)
401 declined during the 1980s and 1990s, while euryhaline and limnetic, smaller-sized copepod
402 species (*Acartia* spp. and *Eurytemora* spp.) increased in abundance (Suikkanen et al., 2013;
403 Hänninen et al., 2015), and the decline of marine taxa has usually been proposed to be linked
404 to a decrease of salinity (Suikkanen et al., 2013; Hänninen et al., 2015). It has also been
405 experimentally shown that close to the physiological tolerance limit for salinity (below 7
406 psu), respiration of copepods (*Acartia longiremis*) increases and feeding rate decreases (in
407 610 ml bottles, 24 h experiments), indicating a disruption of the energetic balance under low
408 salinity (Dutz and Christensen, 2018).

409 Environmental impacts on the physiology of the more sensitive species may also affect
410 the reproductive success of zooplankton (Möller et al., 2015). The increase of euryhaline taxa
411 has been, directly or indirectly, attributed to the temperature increase (Mäkinen et al., 2017).
412 It has also been suggested that species that reside in the upper water layers, such as the
413 copepod *Acartia* sp., are mostly affected by temperature driven increase in food availability,
414 whereas species inhabiting the deep layers, such as older stages of *Pseudocalanus acuspes*,
415 are more dependent on salinity and predation pressure (Otto et al., 2014a; Otto et al., 2014b;
416 Mäkinen et al., 2017).

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

424 Changes in zooplankton functional groups, such as a shift from raptorially and
425 suspension-feeding copepods and cladocerans to a dominance by small filter-feeding rotifers
426 and cladocerans, have also been shown as results of warming (Suikkanen et al., 2013;
427 Jansson et al., 2020). OA also promoted the growth of suspension-feeding cladocerans,
428 because of a CO₂-driven increase of cyanobacteria (Lischka et al., 2017).

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

443 Sufficient supply of essential compounds such as amino acids (AA) produced by
444 phytoplankton and cyanobacteria is essential for the growth and productivity of zooplankton
445 grazers. A field study performed in the Baltic Proper shows that, during a warm summer,
446 thermophilic rotifers and cladocerans (e.g. *Bosmina* spp.) acquired ample AA through filter
447 feeding on the abundant diazotrophic cyanobacteria, whereas the temperate copepods (e.g.
448 copepods *Temora longicornis* and *Pseudocalanus* spp.) avoided the warm surface layer and
449 acquired AA mainly through sinking organic matter and/or via grazing on chemoautotroph
450 based microbial food web in the suboxic zone (Eglite et al., 2018). This may imply that
451 thermophilic zooplankton species, such as rotifers and certain cladocerans gain more AA than
452 copepods in a future warmer and more stratified Baltic Sea.

453 Little is known on the adaptation capabilities of zooplankton against physicochemical
454 stress, but some degree of temperature adaptation has been demonstrated experimentally for
455 the copepod *Eurytemora affinis* (Karlsson and Winder, 2020). Interestingly, the adaptability
456 was better in populations reared in warm temperatures ($\geq 17^{\circ}\text{C}$), which suggests that southern
457 populations can better cope with increasing temperatures than the northern ones, and that the

458 adaptation capability of all (surviving) populations may improve with proceeding climate
459 change.

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

466

467 **4.4. Bacteria and the microbial loop**

468

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

474 The effects of climate induced changes in environmental factors to pelagic bacteria and
475 the other components of the microbial loop have been studied experimentally. The effects of
476 projected ocean acidification (OA) on bacteria have been studied alone and also in
477 combination with with other abiotic variables, such as temperature (OAW) and salinity
478 (OAS). OA alone had a limited impact on spring bloom microbial communities (sampled
479 from the sea area around the island Öland in the Baltic Proper and kept in 100-liter
480 mesocosms for 21 days), but when combined with increased temperature, certain bacterial
481 phylotypes, such as betaproterobacteria, increased. It was suggested that synergistic effects of
482 increased temperature and acidification selectively promote growth of specific bacterial
483 populations (Lindh et al., 2013). In the southern Baltic Sea (Kiel Bight) the impact of OA
484 was studied in 1400-liter indoor mesocosms for 21-24 days. Acidification only affected few
485 operational taxonomic units (OTUs), such as *Bacteroidetes* 'NS3a marine group', as the
486 bacterial community mainly responded to temperature and phytoplankton succession.
487 Depending on studied season and temperature treatment, Cyanobacteria, *Bacteroidetes*,
488 Alphaproterobacteria and/or Gammaproterobacteria increased under OA (Bergen et al.,
489 2016).

490 In an OAS experiment (4-liter aquaria, 12 days) using a natural summer
491 microplanktonic community, the biovolume of heterotrophic bacteria declined when pCO₂

492 was increased (from 380 to 960 μatm) and salinity was decreased (from 6 to 3 psu) (Wulff et
493 al., 2018). In experiments done in the Baltic Proper (NW Gotland Sea, 25-liter microcosms
494 for 23 days), where temperature was increased (from 16 to 18-20 $^{\circ}\text{C}$) and salinity reduced
495 (from 6.9 to 5.9 PSU), the microbial community showed mixed responses. No conclusive
496 evidence of direct climate-induced change could be detected (Berner et al., 2018). At reduced
497 salinity levels, certain Actinobacteria and *Bacteroidetes* OTUs increased, and the
498 heterotrophic bacteria community resembled communities at high temperature, indicating
499 synergistic effects of temperature and salinity. Biotic interactions were more dominant than
500 abiotic ones, however. The largest increase in heterotrophic bacterial biomass was detected
501 when filamentous cyanobacteria started to decay, regardless of temperature or salinity. It was
502 suggested that this indirect coupling between heterotrophic bacteria and filamentous
503 cyanobacteria is more important for bacterial communities than the direct effects of climate
504 induced changes in temperature or salinity (Berner et al., 2018).

505 Experimental studies have demonstrated that complex food web responses to climate
506 change may also arise. In Kvarken, the Gulf of Bothnia, increase of dissolved organic matter
507 (DOM) enhanced respiration and abundance of bacteria, whereas an increase of temperature
508 (from 12 to 15 $^{\circ}\text{C}$) induced a decrease of bacteria, probably due to an increase in
509 bacterivorous flagellates (Nydahl et al., 2013). A complex response to warming was also
510 demonstrated for different size classes of heterotrophic flagellates (HF). There was a
511 succession from flagellates feeding on bacteria to omnivorous nanoflagellates preying upon
512 other HF. This intraguild predation pattern probably dampened the response to experimental
513 treatments (Moustaka-Gouni et al., 2016).

514 As for microzooplankton (MZP), the effects of OA and warming seem to be mostly
515 beneficial. OA does not have a negative effect on MZP, probably because estuarine MZP are
516 adapted to a large natural variability in pCO_2 (Horn et al., 2016). The abundance of the
517 mixotrophic ciliate *Mesodinium* sp. even increased in mesocosms with OA, because of
518 increase of its prey and food, e.g. picoeukaryotes, at higher CO_2 levels (Lischka et al., 2017).
519 In addition, warming improved the growth rate of MZP, and their biomass peaked earlier in
520 warm mesocosm treatments. This led to a reduced time-lag between MZP and phytoplankton
521 peaks, inducing a better food supply to microzooplankton in warm conditions (Horn et al.,
522 2016). The same applied to the MZP-copepod link: at low temperatures MZP escaped from
523 predation by slower growing copepods, whereas at higher temperatures especially small-sized
524 ciliates were more strongly controlled by copepod predation.

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

532

533 **4.5. Macroalgae and vascular plants**

534

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

539 For the brown alga bladderwrack *Fucus* spp., light availability, which may also be
540 affected by partly climate-driven changes in eutrophication, affects their local coverage
541 (Lappalainen et al., 2019). A documented long-term decrease of water transparency in 1936
542 to 2017 has reduced favourable sea floor areas for *Fucus* spp. by 45% (Sahla et al., 2020),
543 and resulted in a halving of the depth range of *F. vesiculosus* in the Åland Islands (Eveleens
544 Maarse et al., 2020). For many shallow coastal ecosystems of the Baltic Sea, it has been
545 concluded that eutrophication is the most important pressure affecting the ecosystem
546 structure and functioning (Olsson et al., 2015). This is plausible, because of the strong
547 influence of anthropogenic nutrient loading in coastal areas (Vigouroux et al., 2021),
548 especially those that are prone to hypoxia due to complex topography (Virtanen et al.,
549 2018a), and which often are affected by internal loading of phosphorus from the sediment
550 (Puttonen et al., 2014; Puttonen et al., 2016). The effects of anthropogenic eutrophication on
551 macroalgae may however be amplified or counteracted by climate induced changes in
552 environmental parameters. Such interactions are reviewed below.

553 The direct effects of climate induced changes in temperature, salinity, and ocean
554 acidification (OA) on bladderwrack *Fucus vesiculosus* have been investigated by a number of
555 experimental studies. OA appears to have a relatively small effect on macroalgae (Al-Janabi
556 et al., 2016a; Wahl et al., 2019), while temperature effects may be significant. The impacts of
557 increasing temperature are not linear, however. Growth or photosynthesis is not impaired
558 under temperatures of 15 to 17.5 °C but at extreme temperatures, simulating heat waves of 27

559 to 29 °C, photosynthesis declines, growth ceases and necrosis starts (Graiff et al., 2015;
560 Takolander et al., 2017b). Necrosis is also enhanced by low salinity (4 PSU) (Takolander et
561 al., 2017b), and under very low salinity (2.5 PSU) the sexual reproduction of *F. vesiculosus*
562 ceases (Rothäusler et al., 2018; Rothäusler et al., 2019).

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

570 Ocean acidification combined with warming (OAW) may also act in concert with
571 hypoxia, in areas where upwellings bring hypoxic water close to the surface. In a three-day
572 experiment simulating an upwelling event, hypoxic water caused severe mortality of *Fucus*
573 germlings if they were already stressed by OAW (Al-Janabi et al., 2016b).

574 Climate induced decline in salinity may affect communities via its direct effect on the
575 physiology of individual populations and species. A retreat towards the south/south-west has
576 been predicted for marine species such as bladderwrack and eelgrass, and for species
577 affiliated to them (Vuorinen et al., 2015). Species distribution modelling studies have
578 confirmed that this mainly salinity-induced decrease of bladderwrack will cause habitat
579 fragmentation with large effects on the biodiversity and ecosystem functioning of the shallow
580 water communities of the northern Baltic Sea (Takolander et al., 2017a; Jonsson et al., 2018;
581 Kotta et al., 2019).

582 It is not certain to what degree *Fucus vesiculosus* can adapt to the anticipated changes.
583 It has been suggested that Baltic marine species have, due to local adaptation, isolation and
584 genetic endemism, diminished potential for adaptation and therefore, an increased risk of
585 local extinction (Johannesson et al., 2011). E.g., *F. vesiculosus* has long generation time and
586 relatively restricted dispersal, and therefore the dispersal rate of locally adapted genotypes
587 may not keep pace with the projected velocity of salinity decline (Jonsson et al., 2018).
588 However, a growing body of evidence from experimental studies show that *F. vesiculosus*
589 has phenotypic plasticity and tolerance against salinity change (Rothäusler et al., 2018; Rugiu
590 et al., 2018a, b), and genetic studies show that different sibling groups of *F. vesiculosus* have
591 different responses to environmental change, e.g. OAW (Al-Janabi et al., 2016a; Al-Janabi et
592 al., 2016b). There may also be population-specific responses to different stressors, especially

593 if populations are genetically isolated. In a study performed in the Danish Straits, certain
594 populations of *F. vesiculosus* were only slightly affected by a salinity decline, while others
595 displayed clearer responses; one population even showed severe stress symptoms and stopped
596 growing (Kinnby et al., 2020).

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

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

612 Salinity decline is projected to decrease the distributional ranges of eelgrass *Zostera*
613 *marina* and the red alga *Furcellaria lumbricalis* (Torn et al., 2020) The changing
614 environment poses an evolutionary risk for populations that live close to the limits of their
615 geographical ranges (Johannesson et al., 2011), including *Z. marina* (Billingham et al., 2003).
616 Indeed, mesocosm studies have indicated that, while OA has little effect on the eelgrass
617 *Zostera marina* (Pajusalu et al., 2015), they suffer from heatwaves in summer (Ehlers et al.,
618 2008) and elevated temperatures in winter-spring period (Sawall et al., 2021). On the other
619 hand, the viability of eelgrass beds also strongly depends on water clarity. A study performed
620 for the southernmost Baltic Sea coupled species distribution and biogeochemical modelling
621 to assess how projected wind fields, hydrodynamic conditions and nutrient abatement
622 scenarios affect the distribution of eelgrass *Z. marina* in the future (2062-2066). It was
623 concluded that nutrient reductions that fulfil the Baltic Sea Action Plan of the Helsinki
624 Commission (HELCOM BSAP) will lead to an expansion of eelgrass coverage, despite
625 potentially harmful effects on eelgrass distribution caused by the climate change (Bobsien et
626 al., 2021).

627 Certain species may be favoured by the projected climate change. Lowering of salinity
628 generally favours vascular plants originating from freshwater, and temperature increase
629 favours thermophilic species, such as charophytes (Torn et al., 2020). In mesocosm studies
630 made in Kõiguste Bay, photosynthesis of charophytes (*Chara aspera*, *C. tomentosa* and *C.*
631 *horrida*) increased under high pCO₂ treatments (Pajusalu et al., 2015) which suggest that they
632 may also be favoured by ocean acidification.

633 To sum up, recent studies suggest that changes in species composition of macroalgae
634 and vascular plants are likely, due to temperature, pH, and salinity changes. Climate change,
635 in conjunction with other environmental changes (especially eutrophication) may also
636 influence carbon storage in both macroalgae and vascular plants in the Baltic Sea (Röhr et al.,
637 2016; Takolander et al., 2017a; Jonsson et al., 2018; Salo et al., 2020; Bobsien et al., 2021). It
638 has been projected that macroalgae will decline in hard bottoms and vascular plants increase
639 in the more sheltered soft bottom areas (Torn et al., 2020). Because algae and plants mostly
640 occupy different habitats, the possible increase of vascular plants or charophytes cannot
641 counteract the negative effects of the disappearance of macroalgae. Consequently also the
642 invertebrates, fish and birds benefiting from habitats formed by macroalgae will suffer from
643 the climate change.

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

650

651 **4.6. Benthic invertebrates**

652

653 Soft bottom benthic communities are dependent on several hydrographic and biogeochemical
654 variables, and parameters that change with climatic variations have been shown to drive the
655 long-term progression of zoobenthic communities (Weigel et al., 2015; Rousi et al., 2019;
656 Ehrnsten, 2020). In the SW coast of Finland, a drastic community change took place, with
657 amphipods being replaced by Baltic clam *Limecola balthica* and the non-indigenous
658 polychaete *Marenzelleria* spp. This major community change was explained by an increase in
659 near-bottom temperature and by fluctuations in salinity and oxygen (Rousi et al., 2013). In
660 the Åland Islands (northern Baltic Sea), zoobenthos variations in 1983-2012 were associated

661 with salinity decline, and environmentally driven shifts in the links between zoobenthos and
662 benthic-feeding fish assemblages were recorded (Snickars et al., 2015). Long-term climate-
663 induced shifts in zoobenthos and other trophic levels have also been described in various
664 parts of the Baltic Sea (Törnroos et al., 2019; Forsblom et al., 2021). In all these cases,
665 interactions between the physico-chemical climate-affected parameters and secondary
666 impacts (mainly eutrophication and/or hypoxia) have been identified.

667 Many marine invertebrates will directly and indirectly suffer from decreasing salinity.
668 In experiments simulating projected changes in temperature and salinity, the survival of the
669 isopod *Idotea balthica* decreased, albeit with differences between and within regions (Rugiu
670 et al., 2018c). Also, effects of warming on invertebrates are often non-linear, with stress
671 effects being manifested after a certain threshold. In experiments, respiration and growth of
672 the isopod *Idotea balthica* first increased until 20°C and then decreased at 25°C (Ito et al.,
673 2019). Heat waves, which have been projected to increase in frequency (Meier et al., 2019a),
674 may therefore pose a severe threat to sublittoral invertebrates (Pansch et al., 2018). Different
675 species show different responses to single and sequential heat waves, however, resulting in a
676 change in community structure. E.g., the bivalve *Limecola balthica* suffered from repeated
677 heat waves, whereas the sessile amphipod *Corophium* sp. benefited from them. The
678 polychaete *Polydora cornuta* seemed to get acclimated to heat waves when they were
679 repeated, showing some signs of adaptation. In general, heat waves favoured crawling or
680 burrowing predators and suspension feeders, while the abundance of detritivores decreased,
681 suggesting a climate-induced change in dominant zoobenthic traits (Pansch et al., 2018).

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

694 Several modelling studies have suggested that climate-induced changes in temperature,
695 salinity and eutrophication (affecting both oxygen levels and food availability), drive the
696 development of benthic communities and their biomass in the future (Ehrnsten et al., 2019a;
697 Ehrnsten et al., 2019b). A physiological fauna model linked to a 3D coupled hydrodynamic–
698 ecological model projected that, in areas previously burdened by hypoxia, benthic biomass
699 will increase (until year 2100) by up to 200 % after re-oxygenating bottom waters, whereas in
700 permanently oxygenated areas the macrofauna biomass will decrease by 35 %, due to
701 lowered food supply to the benthic ecosystem (Timmermann et al., 2012). In another
702 modelling study, zoobenthic production decreased in the coastal zones, and gradually also in
703 the more offshore areas, with increasing temperature and declining salinity and bottom
704 oxygen, regardless of the nutrient load scenarios (Weigel et al., 2015). The fate of zoobenthos
705 also depends on human intervention, i.e., success of nutrient reduction schemes. For instance,
706 it has been projected that, if the HELCOM BSAP will be implemented, the biomass of
707 benthic animals, and hence food for benthic-eating fish, will first increase and then decrease
708 (Ehrnsten et al., 2020).

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

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

725 It is notable that hypoxia, which is a key factor affecting zoobenthos, is by no means
726 limited to the deep basins of the Baltic Sea (Conley et al., 2011). Especially the archipelagos
727 of the northern Baltic Sea are, due to their complex topography and limited water exchange,

728 prone to hypoxia (Virtanen et al., 2018a). Increasing sea surface temperature will strengthen
729 stratification and enhance mineralization of organic matter by microbes, which may increase
730 the release of phosphorus from sediments (Puttonen et al., 2016) and lead to a “vicious circle
731 of eutrophication” (Vahtera et al., 2007). The sheltered archipelago areas and enclosed bays
732 may therefore become “climate change hotspots” (Queiros et al., 2021), where also
733 zoobenthic communities are most drastically changed.

734 To sum up, zoobenthic communities are affected by all environmental parameters that
735 are projected to change with climate change, i.e., temperature, salinity, pH, oxygen, and
736 benthic-pelagic coupling. However, the effects are not unidirectional and several processes
737 may amplify or counteract the possible changes. The magnitude of the future salinity decline
738 is unclear, and other factors, such as decreasing ice cover and changes in future wind
739 conditions (of which no consensus exists) may also affect nutrient and oxygen dynamics of
740 the Baltic Sea. Also, there may be feedback effects on sediment oxygen levels, as different
741 benthic species have different bioirrigation activities (Norkko et al., 2012; Guy-Haim et al.,
742 2018). Such processes, that are dependent of traits of a few species, may be of particular
743 importance in low-diversity systems such as the northern Baltic Sea (Gladstone-Gallagher et
744 al., 2021).

745

746 **4.7. Non-indigenous invertebrates**

747

748 It is often suggested that global climate change favours invasions of non-indigenous species
749 (NIS) worldwide (Jones and Cheung, 2015). This is plausible, because increase of
750 temperature will open new niches and induce a poleward shift of the ranges of species
751 inhabiting tropical and temperate sea areas. In the Baltic Sea, it has been shown that non-
752 native species typically occur in areas characterized by high temperatures, reduced salinity,
753 high proportion of soft seabed, and decreased wave exposure, whereas most native species
754 display an opposite pattern (Jänes et al., 2017). This suggest that the former areas are more
755 prone to climate induced range expansion of non-native species than the latter. This is
756 consistent with the hypothesis of climate change hotspots, which suggests that some coastal
757 areas may be more susceptible to effects of climate change than others (Queiros et al., 2021).

758 Modelled scenarios of temperature and salinity have been used to project how changes
759 in the abiotic environment could affect NIS already present in the Baltic Sea. One modelling
760 study suggests an increase of Ponto-Caspian cladocerans in the pelagic community, and an

761 increase in dreissenid bivalves, amphipods and mysids in the coastal benthic areas of the
762 northern Baltic Sea until 2100 (Holopainen et al., 2016).

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

772

773 **4.8. Fish**

774

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

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

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

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

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

805 A thorough review including long-term data and modelling demonstrated how
806 predation, fishing, eutrophication, and climate have sequentially affected eastern Baltic cod
807 during the past century (Eero et al., 2011). In the early decades of the 20th century, cod
808 reproduction was successful but seal predation and food availability kept the size of cod stock
809 at a moderate level. From the 1940s, fishing replaced seal predation in controlling cod
810 population, whereas the slowly increasing eutrophication had a minor positive influence on
811 cod spawning stock biomass in 1950s to 1970s. In the late 1970s, a series of large saline
812 inflows increased the salinity of the Baltic Sea and kept oxygen conditions in the deep basins
813 favourable for cod. Consequently, reproduction peaked in 1978-1982 and, as also fishing
814 pressure was temporarily low, the spawning stock biomass increased to a record-breaking
815 level of ca. 700,000 tonnes in 1980-1984 (Eero et al., 2011). After this peak period, cod stock
816 started to decline, due to a drastic reduction of the ‘cod reproductive volume’ (RV), water
817 layer sufficiently saline and oxic for survival of cod eggs and larvae. The decline of RV was
818 associated to a stagnation period with low oxygen, caused by a combination of anthropogenic
819 eutrophication and climate-induced paucity of major saline inflows. The productivity of cod
820 stocks has remained low (Eero et al., 2020), and also the average maximum length of cod
821 individuals has been constantly declining (Orio et al., 2021). The reason for low growth may
822 have been the low availability of both benthic and pelagic food (Neuenfeldt et al., 2020).
823 Alternatively, a long-term exposure to low oxygen conditions may affect body chemistry
824 (Limburg and Casini, 2019) and decrease digestion rate and food consumption of cod
825 (Brander, 2020). The physiological hypothesis is strengthened by the observed increase in
826 depth distribution of cod and consequent dwelling of cod in low oxygen water (Casini et al.,
827 2021).

828 Several studies project low abundances of cod towards the end of the century, due to
829 the climate and eutrophication induced decrease of RV (Eero et al., 2011; Gårdmark et al.,
830 2013; Niiranen et al., 2013; Eero et al., 2020; Wåhlström et al., 2020). It has also been
831 speculated that seal predation could contribute to keeping cod stocks low but, although seal
832 predation can cause damage to cod fisheries in coastal areas (Blomquist and Waldo, 2021), it
833 has been concluded that the increased seal predation is a less important factor for the future
834 size of fish stocks in the Baltic Sea than climate, eutrophication and fisheries (Mackenzie et
835 al., 2011; Tomczak et al., 2021).

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

846 Increasing seawater temperature has also made it possible for certain warm water
847 Atlantic species, such as anchovy (Alheit et al., 2012) and sole and turbot (Sparrevohn et al.,
848 2013) to occur more abundantly in Kattegat and the southernmost Baltic Sea. Such north- and
849 eastward migrations of these warm-water species may be caused by both global climate
850 change and by variations in the Northern Hemisphere temperature Anomalies (NHA), North
851 Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO), as well as
852 contraction of the subpolar gyre (Alheit et al., 2012; Sparrevohn et al., 2013).

853 As for coastal fish, the distribution of pikeperch (*Sander lucioperca*) expanded towards
854 north along the coasts of the Bothnian Sea, apparently due to the warming of waters (Pekcan-
855 Hekim et al., 2011). For many coastal piscivores (perch, pike, pike-perch) and cyprinids,
856 eutrophication status of coastal waters is however a more important factor for distribution
857 than climatic variation (Snickars et al., 2015; Bergström et al., 2016). A long-term study
858 covering four decades (1970s to 2010s), made at different coastal areas of the Baltic Sea,
859 illustrated that it is hard to disentangle the effects of abiotic factors from biotic interactions
860 affecting fish and their benthic food-sources (Törnroos et al., 2019).

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

868

869

870 **5. Climate change and ecosystem structure and function**

871

872 As seen from the above studies, the Baltic Sea ecosystem is impacted by climate induced
873 changes in the physical and biogeochemical environment in various ways. Climatic changes
874 affect species and populations directly and indirectly, also impacting micro-evolution of
875 species and having synergistic effects on other environmental drivers such as eutrophication
876 and hypoxia (Wikner and Andersson, 2012; Niiranen et al., 2013; Ehrnsten et al., 2020;
877 Pecuchet et al., 2020; Schmidt et al., 2020). In synergy, these impacts have already boosted
878 the emergence of ‘novelty’ in the system and profoundly altered pathways of energy (Ammar
879 et al., 2021). This development will probably continue, at least if the environmental
880 conditions of the Baltic Sea will continue to change as projected by modelling studies.

881 Below, recent relevant findings regarding climate impacts on structure and functioning on the
882 Baltic Sea ecosystem are summarized.

883

884 **5.1. Projections of primary production and eutrophication**

885

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

892 In the Baltic Sea, changes in ice conditions, water temperature, density stratification,
893 and especially supply of nutrients through rivers and from the sediment, affect the nutrient
894 dynamics and primary productivity in both coastal areas and the open sea. Different species

895 however respond in different ways to changes in the environmental parameters, and both
896 increases and decreases in primary production have been reported and projected along with
897 climate induced changes in the environment.

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

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

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

927 Interacting effects of nutrient abatement and climate were observed in Kattegat already
928 in mid 1990s. Reduction of nutrient loading led to a shift from a highly eutrophic state,

929 characterized by small phytoplankton species and low water transparency, to an improved
930 state, with a larger share of diatoms, decreased phytoplankton biomass and increase of water
931 transparency (Lindegren et al., 2012). An opposing trend has taken place in the Bothnian Sea.
932 Because of the lack of halocline and lower anthropogenic nutrient loading, the Bothnian Sea
933 has this far remained in a relatively good condition. However, since year 2000 also the
934 Bothnian Sea has shown symptoms of eutrophication (Kuosa et al., 2017), and also open sea
935 cyanobacteria blooms have in recent years become more common, due to a “leaking” of
936 phosphorus rich water from the central Baltic Sea through the Åland Sea (Rolff and Elfving,
937 2015; Ahlgren et al., 2017). The connection of this process to climate change is not certain.
938 Rather, the severe hypoxia of the central Baltic Sea has brought the anoxic layer so close to
939 the sill separating the Baltic Proper from the Åland Sea that flow of nutrient rich water across
940 the Åland Sea is at times possible. Whether or not the proceeding climate change will amplify
941 the ongoing eutrophication of the Bothnian Sea remains to be seen, but if temperature
942 stratification will increase and N:P ratio continues to decline, this will create conditions that
943 are favourable for cyanobacteria blooms also in this relatively pristine sea area.

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

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

956

957 **5.2. Trophic efficiency and consequences to the secondary production**

958

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

962 A climate and nutrient load driven model reconstruction of the Baltic Sea state from
963 1850 to 2006 suggest that the shift from spring to summer primary production is
964 accompanied by an intensification of pelagic recycling of organic matter (Gustafsson et al.,
965 2012). In mesocosm studies warming accelerated (southern Baltic Sea) phytoplankton spring
966 bloom and increased carbon specific primary productivity (Sommer and Lewandowska,
967 2011; Sommer et al., 2012; Paul et al., 2016). The total phytoplankton biomass decreased,
968 because increased stratification decreased nutrient flux to the surface layer, however
969 (Lewandowska et al., 2012; Lewandowska et al., 2014). Furthermore, in stratified conditions
970 the relative importance of the microbial loop increased because copepods switched to feed
971 more on ciliates instead of phytoplankton, which probably releases heterotrophic
972 nanoflagellate grazing on bacteria. Decrease of bacteria may reduce remineralization and also
973 decrease availability of nutrients for phytoplankton (Lewandowska et al., 2014).

974 It has also been projected that, in addition to nutrients, the flow of dissolved organic
975 matter (DOM) into the Baltic Sea will increase in the future climate (Voss et al., 2011a;
976 Strååt et al., 2018). Precipitation will increase especially in the northern areas, and, by using
977 long-term time series from 1994 to 2006, it was shown that climate change increased supply
978 of terrestrial DOM into the Bothnian Bay. This provided additional substrate for bacteria,
979 which increased accordingly (Wikner and Andersson, 2012).

980 Experimental studies have also demonstrated increased microbial activity and biomass
981 with increasing DOM and temperature (Ducklow et al., 2010), although different bacteria
982 taxa respond differently to the simultaneous increase of DOM and temperature (Lindh et al.,
983 2015). Increase of DOM and bacteria may be detrimental to primary production as bacteria
984 compete for nutrients with phytoplankton, and as the brownification of water reduces light
985 availability. Consequently, the carbon flow shifts towards microbial heterotrophy, which may
986 induce a decrease in both phytoplankton productivity and biomass (Wikner and Andersson,
987 2012). Especially if stratification increases, cycling of carbon through the microbial loop
988 increases pelagic recycling and may also decrease vertical flux of organic matter to
989 zoobenthos (Ehrnsten et al., 2020).

990 It has been suggested that climate change may decrease fish productivity. In areas
991 where climate change increases the supply of allochthonous DOM into the system, and where
992 increasing stratification reduces the transport of nutrients from deeper waters, phytoplankton
993 production may decline and the trophic pathways from bacteria and flagellates through
994 ciliates to copepods may strengthen (Aberle et al., 2015). When the system shifts towards
995 heterotrophy, the food web efficiency declines, and if zooplankton also becomes dominated

996 by smaller sized plankton (Suikkanen et al., 2013; Jansson et al., 2020), there will be less
997 suitable food available for planktivorous fish. If also sedimentation of organic matter will be
998 reduced, zoobenthos production will decrease and there will be less food for benthic-eating
999 fish. Eventually the total fish production may decrease (Berglund et al., 2007; Wikner and
1000 Andersson, 2012).

1001 Results of experimental studies have not equivocally confirmed this hypothesis. A
1002 study performed in a large biotest area artificially heated by the cooling waters of the
1003 Forsmark nuclear power plant, southern Bothnian Sea, found that warming of water may lead
1004 to increased species turnover, and in decreased compositional stability of diatom, macrophyte
1005 and invertebrate communities (Hillebrand et al., 2010). Certain mesocosm studies, simulating
1006 effects of climate change in the pelagic ecosystem, have also found that the production and
1007 biomass of copepods can remain high, because the positive effects of increasing temperature
1008 on copepod production override the negative effects of decreasing food web efficiency
1009 (Lefebure et al., 2013).

1010 Furthermore, many Baltic Sea copepods are omnivorous and can opportunistically
1011 switch between suspension feeding on flagellates and raptorial feeding on ciliates (Kiørboe et
1012 al., 1996). Such a flexible feeding strategy stabilizes the system and can sustain copepod
1013 production even under lower phytoplankton production. This suggests that fish production
1014 may be supported even also when relatively more carbon flows through the microbial loop
1015 (Lefebure et al., 2013).

1016 To sum up, a reorganisation of pathways of carbon is possible in the Baltic Sea due to
1017 the climate change. The system is complex, however, due to several counter- and interacting
1018 processes and large uncertainties in key processes, such as stratification and nutrient loads
1019 from land and the sediments (Meier et al., 2019c; Saraiva et al., 2019). The complexity of the
1020 system has been highlighted by a thorough review which illustrated how changes in benthic-
1021 pelagic coupling may induce ecosystem-wide consequences, via increasing sedimentation of
1022 organic matter inducing hypoxic conditions and internal loading of nutrients (Griffiths et al.,
1023 2017).

1024

1025 **5.3. Food web interactions in the sublittoral ecosystem**

1026

1027 If the climate change induces an increase in allochthonous nutrient loads, consequences can be
1028 expected in the communities of algae and vascular plants in the shallow photic zone. The
1029 shallow water food webs based on macroalgae and seagrasses may also be affected via the

1030 indirect effects of climate change, mediated through interactions between algae and their
1031 grazers.

1032 The effects of late summer heatwaves on algae and invertebrates living amongst
1033 bladderwrack *Fucus vesiculosus* have been studied by outdoor mesocosm experiments
1034 (Werner et al., 2016). A heatwave resulted in a collapse of invertebrate grazers, such as
1035 isopods and amphipods, which in turn released grazing on filamentous algae and resulted in
1036 overgrowth of *Fucus* by epiphytic algae. In the autumn and winter, when the biomass of
1037 epiphytes was lower, the process was reversed: warming resulted in intensified grazing on
1038 bladderwrack. Again, a significant reduction of *Fucus* biomass resulted (Werner et al., 2016).
1039 As for the microalgae (diatoms), growing on *Fucus* in spring, temperature effects were
1040 stronger than grazing effects, suggesting a positive overall effect of climate change on
1041 microalgae (Werner and Matthiessen, 2017).

1042 Similar results were obtained in an artificially heated biotest basin (Forsmark nuclear
1043 power plant) in the Gulf of Bothnia, where the biomass of the non-native gastropod grazer
1044 *Potamopyrgus*, gammarids and the snail *Theodoxus* was much higher than in the adjacent
1045 non-heated area. The community shift was mainly driven by direct temperature effects on
1046 invertebrates and by indirect effects of changes in vegetation cover (Salo et al., 2020).
1047 Cascading effects are also possible. In the same biotest basin, perch shifted from feeding on
1048 small fish to gammarid crustaceans, which released grazing pressure from filamentous algae
1049 (Svensson et al., 2017). If similar cascades take place in other coastal sea areas of the Baltic
1050 Sea as well, warming may promote the growth of filamentous algae and contribute to the
1051 decline of bladderwrack.

1052 Decline of bladderwrack will affect other trophic levels in various ways, due to
1053 declining availability to habitat and food (Takolander et al., 2017a; Jonsson et al., 2018;
1054 Kotta et al., 2019). Also, connectivity between bladderwrack populations as well as
1055 organisms inhabiting patches of bladderwrack may decline (Jonsson et al., 2020; Virtanen et
1056 al., 2020). However, perhaps due to the complex biotic interactions in the sublittoral
1057 ecosystem, there are very few modelling studies that have attempted to project the fate of the
1058 algal and invertebrate communities inhabiting the shallow photic zone of the Baltic Sea. Only
1059 one study has used a combination of experimental work and modelling to study the effects of
1060 climate change on invertebrates. A decline of the isopod *Idothea baltica*, the main grazer of
1061 *Fucus* spp., was projected due to the decline of bladderwrack (Kotta et al., 2019).

1062 To sum up, temperature and salinity changes have been projected to affect species
1063 interactions in both hard and soft bottoms in the sublittoral zone, Both summer heatwaves

1064 and cold season warming can induce novel trophic interactions that produce eutrophication-
1065 like effects, e.g., overgrowth of bladderwrack by epiphytes, in the photic zone dominated by
1066 macroalgae, even without an increase in nutrient loading. However, as macroalgae are very
1067 much dependent on water clarity, the future level of eutrophication will also affect the fate of
1068 the shallow water communities in the Baltic Sea. The complexity of the system, and unknown
1069 adaptation capabilities, make it challenging to project the future food web interactions in the
1070 sublittoral ecosystem.

1071

1072 **5.4. Regime shifts**

1073

1074 In the 1980's a partly climate induced regime shift was recorded with drastic changes in the
1075 central Baltic food web, including phytoplankton, zooplankton and pelagic planktivores and
1076 their main predator, Baltic cod (Möllmann et al., 2009; Lindegren et al., 2010a). In 1980-
1077 2000, a decline in 'reproductive volume' (RV), contributed to the decline of cod population
1078 (Hinrichsen et al., 2011; Casini et al., 2016; Bartolino et al., 2017) and induced cascading
1079 effects on planktivorous fish as well as zooplankton (Casini et al., 2008). The different effects
1080 of temperature and salinity on sprat and cod (see above) also resulted in a spatial mismatch
1081 between these species, which further released sprat from cod predation and contributed to the
1082 increase of sprat stocks in the central Baltic Sea (Eero et al., 2012; Reusch et al., 2018). As
1083 herring is an inferior competitor for food, and food availability per individual declined, the
1084 condition of herring declined (Möllmann et al., 2003; Casini et al., 2010). Transition to a
1085 lower saline Baltic Sea, and associated decline of marine copepods (Hänninen et al., 2015),
1086 also contributed to the observed halving of (3-year old) herring weight-at-age, from 50–70 g
1087 in the late 1970s to 25–30 g in the 2000s (Dippner et al., 2019). The described regime shift
1088 has also been partly questioned, as the descriptions of the shift did not cover the entire food
1089 web (Yletyinen et al., 2016).

1090 A factor that has been less often considered when studying reasons of cod decline is the
1091 interaction with another benthic predator, flounder. Flounder may be both prey for larger cod
1092 and a competitor for the small and juvenile ones. Now that cod size has declined, cod
1093 predation on flounder has decreased, releasing competition for benthic food again. This has
1094 caused more spatial overlap between flounder populations and the remaining small sized cod,
1095 and created more intense competition between flounder and the small sized cod, further
1096 contributing to the decline in body condition of cod (Orio et al., 2020).

1097 Multi-species modelling studies have concluded that both fishing and climate strongly
1098 affects the size of cod stocks. If fishing is intense but climate remains unchanged, cod
1099 declines, but not very dramatically, while if climate change proceeds as projected (according
1100 to the intermediate-high A2 scenario), cod goes extinct in two models out of seven, even with
1101 present low fishing effort (Gårdmark et al., 2013). Different combinations of climate change
1102 and eutrophication scenarios may yield very different outcomes, however. Medium CO₂
1103 concentrations (RCP4.5), low nutrients and sustainable fisheries resulted in high biodiversity
1104 and high numbers of cod and flounder, while high emissions (RCP8.5) and high nutrient
1105 loads resulted in diminished biodiversity and high abundance of clupeids, especially sprat
1106 (Bauer et al., 2018; Bauer et al., 2019; Hyytiäinen et al., 2019).

1107 The above studies have mostly considered the ecosystem of the central Baltic. In other
1108 basins, the associated processes and species interactions may be different. E.g., in the
1109 Bothnian Bay, salinity was also a major driver for changes in populations of planktivorous
1110 fish, but the species involved were different. Here the decline of spawning-stock biomass of
1111 herring, observed in 1980-2013, was explained by a simultaneously increased competition
1112 with vendace, a limnic species that had increased with lowering salinity (Pekcan-Hekim et
1113 al., 2016).

1114 In Kattegat, the western Baltic Sea, where the ecosystem is more oceanic than in the
1115 other parts of the Baltic Sea, a regime shift was detected in mid 1990s. Here the shift was
1116 explained by both global climate change, cyclic climate phenomena, and by human
1117 intervention. First, a reduction of anthropogenic nutrient loading led into a shift from a
1118 eutrophic ecosystem state to an ecosystem characterized by decreasing phytoplankton and
1119 zooplankton biomass, dominance by small sized fish in the pelagial, an increase of
1120 macroalgae and filter-feeding molluscs on hard bottoms and other benthic animals in the soft
1121 sediments (Lindegren et al., 2012). Second, the positive phases of NAO and BSI enabled an
1122 inflow of oxygenized water from the North Sea, which improved conditions for zoobenthos,
1123 including the commercially important Norway lobster. A climate induced increase of sea
1124 surface temperatures contributed to the improved flatfish growth and survival in the shallow
1125 nursery areas (Lindegren et al., 2012). Decreasing fishing may also have contributed to the
1126 increase of gadoid and flatfish populations, but its relative importance is difficult to
1127 distinguish from other co-occurring effects.

1128 To sum up, regime shifts are usually a result of several environmental, climatic, and
1129 anthropogenic effects acting synergistically on the entire ecosystem. The climate driven
1130 changes in temperature and salinity have been identified as key drivers for the significant rise

1131 of ‘novelty’ in both abiotic conditions and biotic assemblages in several basins of the Baltic
1132 Sea (Ammar et al., 2021), but also human contribution, i.e., anthropogenic eutrophication or
1133 its alleviation have also contributed (Reusch et al., 2018). The recent research confirms that
1134 climate change induces multiple direct and indirect effects on species and communities and
1135 affects nutrient and carbon dynamics of the Baltic Sea ecosystem. However, despite the
1136 major structural changes, the overall food web complexity in the central Baltic Sea has
1137 remained surprisingly stable (Yletyinen et al., 2016). The relatively small changes may be
1138 explained by the fact that responses to climate change are not uniform or unidirectional, but
1139 vary from species group to another, within groups, and even between sibling species.
1140 Species-specific responses, many feedbacks, altered trophic pathways, and possibility of
1141 species level adaptation, make projections concerning the state of the ecosystem and trophic
1142 effects challenging.

1143

1144

1145 **6. Knowledge gaps**

1146

1147 The main challenge when analysing effects of climate change on ecosystems is the possible
1148 synergistic effects of climate with other environmental drivers, such as eutrophication,
1149 harmful substances, and introduction of non-indigenous species, which also may have
1150 profound impacts on ecosystems and their functioning (Reusch et al., 2018; Stenseth et al.,
1151 2020; Bonsdorff, 2021). Consequently, in the literature concerning effects of climate change
1152 on the Baltic Sea ecosystem there are numerous knowledge gaps, bottlenecks and issues of
1153 dissensus that weaken our ability to project the future biological processes, such as primary
1154 and secondary productivity, benthic-pelagic coupling and hypoxia, or the interactions
1155 between phytoplankton, zooplankton and fish populations, as well as geographic shifts in
1156 macroalgal and invertebrate communities.

1157 Attribution of the observed phenomena to climate change is challenging because of the
1158 collinear, intertwined and interacting processes. Especially difficult is to distinguish the
1159 effects of anthropogenic global climate change from those of quasi-cyclic phenomena, such
1160 as the NAO or BSI, or from the more stochastic climatic variations. This is partly due to the
1161 slow pace of climatic variations and time lags between physical and chemical variations and
1162 ecosystem responses. Quite few studies have investigated a period long enough to cover any
1163 larger number of NAO periods. Especially research into the long-term dynamics of the food
1164 webs is still scarce (Törnroos et al., 2019; Pecuchet et al., 2020; Kortsch et al., 2021).

1165 Field studies have ended up with different conclusions concerning past and present
1166 changes of the environment and the biota, and their causes, depending on time periods and
1167 data scrutinized. For instance, certain studies note that cyanobacteria have increased
1168 (Suikkanen et al., 2013; Kuosa et al., 2017), while others do not find proof for such a
1169 phenomenon (Griffiths et al., 2020; Olofsson et al., 2020). Different periods studied, sparse
1170 sampling, varying species responses, and changes in phenology rather than total biomass,
1171 may explain some of the discrepancies between studies. The tendency of filamentous
1172 cyanobacteria to float during calm weather may also bias our view on the total biomass
1173 cyanobacteria in the sea, especially if low wind periods become more frequent.

1174 Experimental studies are useful in pinpointing causative relationships, but their small
1175 spatial scales, short duration and simple food webs make upscaling of results to natural
1176 systems difficult. Experiments usually only last for a few weeks and study one or few species
1177 at a time. Reproducing natural patterns of environmental variability is also challenging in
1178 experiments. Even when mesocosms of hundreds of litres and natural communities are used,
1179 it may be difficult to simulate seasonal processes extending over several life cycles of the
1180 studied organisms. Even the most sophisticated multi-stressor experiments, which use levels
1181 of environmental stressors projected by modelling studies, tend to use constant stress levels.
1182 Only few mesocosm studies that have exposed the communities to near-natural
1183 environmental conditions have been able to shed light on the complex dynamics of the Baltic
1184 Sea ecosystem, e.g., the functions of the microbial loop under variable levels of DOM,
1185 temperature, salinity and ocean acidification (Lindh et al., 2015; Bergen et al., 2016). To
1186 provide useful inferences about physiological responses of organisms to climate change,
1187 experimental work should use full communities, apply naturalistic exposure regimes, and
1188 investigate effects of stress at spatial and temporal scales appropriate to the species studied
1189 (Gunderson et al., 2016).

1190 Ecosystem modelling using coupled oceanographic-biogeochemical models has
1191 advanced greatly in the past 15 years, but significant challenges remain. Projections of sea
1192 surface temperature and ice conditions can be held relatively reliable, but there are still large
1193 uncertainties in projecting salinity, stratification, hypoxia and, hence, the rate of internal
1194 loading (Meier et al., 2022a). Because salinity, stratification and oxygen strongly affect many
1195 Baltic Sea organisms, it is difficult to project the fate of plankton and benthos communities
1196 with certainty. This uncertainty concerns especially marine species, such as cod,
1197 bladderwrack, eelgrass, and blue mussel, which in many studies have been projected to
1198 decrease in the northern basins of the Baltic Sea. Further, uncertainties are imposed by

1199 complex biogeochemical processes in the terrestrial and freshwater ecosystems, as well as by
1200 unknown development of national economies and farming practices (Huttunen et al., 2015),
1201 especially in coastal areas strongly affected by nutrient loading.

1202 Ecosystem models rarely consider complex biological interactions and feedback
1203 effects, caused, e.g., by multi-species predatory or intraguild relationships. Inclusion of such
1204 effects would require parameterizing the 3D ecosystem models with experiments and results
1205 from multi-species food web models, that operate on the level populations rather than carbon
1206 flows. Also, models cannot at present consider potential adaptation capabilities of species, as
1207 little is known on them. Several recent studies have however pointed out that, e.g.,
1208 macroalgae (Rothäusler et al., 2018; Rugiu et al., 2018a) and zooplankton (Karlsson and
1209 Winder, 2020) have phenotypic plasticity and potential for adaptation against gradual
1210 changes in the abiotic environment.

1211 Food web models offer useful tools for assessing the relative effects of climate,
1212 eutrophication, and other human impacts, including fisheries, on the structure of the Baltic
1213 Sea ecosystem. They could potentially better consider characteristics of species and their
1214 responses to changes in the environment. The current models however mostly concern the
1215 pelagic ecosystems (e.g. cod-sprat-herring-zooplankton food web) and there are major gaps
1216 for key trophic groups, such as macrophytes and macrozoobenthos (Korpinen et al., 2022).

1217 3D ecosystem models, food web models and 2D spatial modelling would benefit from
1218 integration. Species distribution models (SDMs) can be produced at a fine spatial scale, even
1219 a few tens of meters (Virtanen et al., 2018b), and in climate change studies they can be
1220 parametrized with 3D model results (Jonsson et al., 2018; Kotta et al., 2019). In the future,
1221 food web models involving relevant coastal taxa could also be used to fill in the missing links
1222 between the large scale (3D) processes and detailed spatial patterns identified by the 2D
1223 models.

1224 Assessing climate effects in a smaller spatial scale would be useful, because shallow
1225 and sheltered bays, lagoons and estuaries may be more susceptible to climate change effects
1226 than deeper offshore areas, and may appear as ‘climate change hotspots’, where climate
1227 change drives the ecosystem towards a new state (Queiros et al., 2021). The existing coupled
1228 oceanographic-biogeochemical modelling studies however typically have a horizontal
1229 resolution of 1 or 2 nautical miles (ca. 2 or 4 km) and thus cannot easily be used for
1230 projecting local variations in temperature, salinity and stratification with the archipelago or
1231 inside estuaries. A bottleneck for high-resolution 3D models is the poor availability of high-
1232 resolution pan-Baltic bathymetries and forcing data (e.g. wind fields). For the SDMs, in turn,

1233 a major constraint is in many areas the poor availability of detailed species and habitat
1234 mapping data, as well as availability of high-resolution data on benthic substrates.
1235 Considering population level effects on spatial patterns of species would also require
1236 estimation of connectivity between sea areas, a research field that is also under-developed in
1237 the Baltic Sea (Berglund et al., 2012; Jonsson et al., 2020; Virtanen et al., 2020).
1238 Consequently no study this far has considered how the climate change affects microclimatic
1239 patterns in the Baltic Sea, and how different species and habitats may respond to such local
1240 variations.

1241 Due to the above challenges, there are certain discrepancies concerning our view on
1242 the effects of climate change on the structure and function of the Baltic Sea ecosystem. Some
1243 of these issues are highlighted below.

1244 Increased primary production and phytoplankton biomass (measured in chlorophyll a)
1245 have been projected by several modelling studies (Meier et al., 2012a; Skogen et al., 2014;
1246 Ryabchenko et al., 2016). Experimental studies however show that responses of
1247 phytoplankton to climate induced changes in temperature, salinity and pH are variable and
1248 can be modified by simultaneous changes in biogeochemical processes and zooplankton
1249 grazers (Paul et al., 2015; Sommer et al., 2015). Also, strengthening of stratification and
1250 simultaneous increase in riverine DOM loads may induce a decrease in phytoplankton
1251 production, at least in sea areas where rivers carry large DOM loads (Wikner and Andersson,
1252 2012). Presently it is not clear which of these processes determine primary production in
1253 different sea areas, or whether there are transition areas where the two processes balance each
1254 other, leading to no net change in primary production.

1255 Several ecosystem models also predict an increase of cyanobacteria. As cyanobacteria
1256 blooms are favoured by warm, stable conditions and low N:P ratio (Munkes et al.,
1257 2021), increase of vigorous blooms and an increase in nitrogen fixation, could be expected.
1258 However, there are large differences in model projections, due to the unclear relationship
1259 between excess phosphorus and cyanobacteria growth, and the relation between bloom
1260 intensity and nitrogen fixation (Munkes et al., 2021). Cyanobacteria are also not a uniform
1261 group. Some cyanobacteria species benefit from increased temperature and acidification,
1262 whereas others suffer from them (Eichner et al., 2014; Berner et al., 2018; Paul et al., 2018).
1263 Further uncertainty is caused by unknown biological factors, such as stoichiometric elasticity,
1264 impact of viruses and grazers. Thus it is still challenging to project how biomasses of
1265 cyanobacteria and nitrogen fixation will develop in the future.

1266 Recent awareness of marine heatwaves and their potential impacts on the marine
1267 ecosystem has increased our knowledge on how climate change may impact pelagic, benthic,
1268 and littoral communities in the ocean (Pansch et al., 2018; Saha et al., 2020). More studies on
1269 the responses of pelagic and benthic organisms of the Baltic Sea to heat waves would
1270 increase our understanding of the population level consequences of short term variability in
1271 environmental parameters. Research on effects of climate change would also benefit from
1272 methodological diversity. E.g., more extensive use of biochemical and genetic methods, such
1273 as biomarkers (Turja et al., 2014; Turja et al., 2015; Villnäs et al., 2019), stable isotopes
1274 (Voss et al., 2000; Gorokhova et al., 2005; Morkune et al., 2016; Lienart et al., 2021),
1275 compound-specific isotope analyses (Ek et al., 2018; Weber et al., 2021) or metabarcoding
1276 (Leray and Knowlton, 2015; Bucklin et al., 2016; Klunder et al., 2021), as well as
1277 development of remote sensing methods (Huber et al., 2021), could yield novel information
1278 on stress levels experienced by organisms and environmental niches preferred by species.
1279 Such information would allow validation of the biogeochemical models under different
1280 environmental and climate scenarios.

1281 There is some bias in the focus organisms and habitats studied. While experiments on
1282 planktonic organisms and soft bottom animals are relatively abundant, experiments on
1283 macroalgae, vascular plants and invertebrates inhabiting hard bottoms are less abundant, and
1284 combined experiments are scarce. In general, empirical and modelling studies focusing on
1285 climate effects on shallow photic habitats are less abundant than those on the pelagic and
1286 deep benthic habitats (Tedesco et al., 2016). Very few studies have investigated the shallow
1287 water ecosystems holistically, including macro- and microalgae, invertebrates and fish at the
1288 same time. Those that have done so, have revealed complex interactions and multiple
1289 feedbacks between species and ecosystem components (Svensson et al., 2017; Salo et al.,
1290 2020). Furthermore, while there are ample monitoring data on pelagic and deep benthic
1291 communities, similar long-term records are very sporadic for communities associated with
1292 key habitat-forming species such as bladderwrack, eelgrass, blue mussel on hard bottoms,
1293 and vascular plants growing on soft sediments. This lack of empirical data and subsequent
1294 modelling studies hampers our understanding of the long-term responses of sublittoral
1295 communities to climate change. Furthermore, there is a large body of literature published on
1296 sea ice algae and sea ice ecology in the Baltic Sea (Granskog et al., 2006; Tedesco et al.,
1297 2017; Thomas et al., 2017), and all of them are relevant for studying winter ecology.
1298 However, few of them have directly assessed the effects of climate change on ice ecology in
1299 the Baltic Sea. More empirical and modelling studies including quantitative projections on

1300 the effect of diminishing sea ice to biodiversity and functioning of the Baltic Sea ecosystem
1301 in winter and spring would therefore be desirable.

1302 To sum up, there are still several significant knowledge gaps and issues of dissensus in
1303 our understanding of the effects of climate change on the Baltic Sea ecosystem. To fill these
1304 gaps, the results and conclusions from the experimental work should be better integrated into
1305 the wider empirical and modelling studies of food web dynamics, and more emphasis should
1306 be placed on studying effects of climate change on whole sublittoral communities. Such
1307 studies would provide a more comprehensive view of the responses of the pelagic and benthic
1308 systems to climate change, from bacteria to fish (Kortsch et al., 2021).

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1311 **7. Conclusions**

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1313 Climate change has an obvious potential to affect entire marine food webs, from coastal to
1314 offshore areas, from shallow to deep, as well as from pelagic to benthic systems. Climate
1315 change can also induce changes in species distributions and proportions, and key nodes and
1316 linkages in the food webs may be altered or lost (Lindegren et al., 2010b; Niiranen et al.,
1317 2013; Leidenberger et al., 2015; Griffiths et al., 2017; Kotta et al., 2019; Gårdmark and Huss,
1318 2020). As many ecosystem services are dependent on the state of the entire ecosystem
1319 (Hyttiäinen et al., 2019), a long-term decline in provision of ecosystem services to humans is
1320 possible. It is therefore indispensable to increase our understanding of the consequences of
1321 climate change on the socio-ecological system of the Baltic Sea and its surrounding marine
1322 regions (Stenseth et al., 2020).

1323 The direct and indirect effects of climate change-related parameters on species,
1324 communities and the ecosystem are summarized in Table 1, based on research done since
1325 2010. While results are variable, some conclusions can be drawn from the evidence this far.

1326 As for the eutrophication status of the Baltic Sea it can be concluded that the ecological
1327 status of the Baltic Sea has not significantly improved despite a decrease in anthropogenic
1328 nutrient loading since the 1980s (Fleming-Lehtinen et al., 2015; Andersen et al., 2017),
1329 largely due to the pervasive internal loading (Murray et al., 2019; Stigebrandt and Anderson,
1330 2020). Success of nutrient abatement largely determines the future state of the Baltic Sea
1331 (Hyttiäinen et al., 2019; Ehrnsten et al., 2020), but climate change may delay, or even
1332 counter the improvement of the ecosystem state (Bonsdorff, 2021).

1333 Climate induced increase of nutrient loading and enhancing of internal loading of
1334 phosphorus have been hypothesized to promote phytoplankton and cyanobacteria production,
1335 and to maintain the ‘vicious circle of eutrophication’ (Vahtera et al., 2007), and several
1336 modelling studies indeed project an increase in both total phytoplankton biomass and
1337 cyanobacteria blooms in the future (Meier et al., 2011a; Funkey et al., 2014).

1338 Eutrophication process may however be counteracted by various factors. Increase of
1339 DOC flowing via the rivers may decrease both primary and secondary production, at least in
1340 the Bothnian Bay (Wikner and Andersson, 2012), and certain cyanobacteria may be
1341 negatively affected by increased temperature and ocean acidification (Paul et al., 2018). Thus,
1342 changes in structure and functioning of phytoplankton and cyanobacteria communities are
1343 probable, but the narrative that the global climate change will increase phytoplankton
1344 biomass and cyanobacteria blooms, and inevitably amplify the eutrophication of the Baltic
1345 Sea, may be too simplistic and needs to be refined by reconsidering the climate effects on
1346 food web processes and nutrient and carbon dynamics.

1347 Also for the deep benthic communities, climate change effects are not straightforward.
1348 If salinity declines, the most marine species will suffer, but according to the latest analyses
1349 undisputable evidence is lacking for a future decline in the salinity of the Baltic Sea
1350 (Lehmann et al., 2022; Meier et al., 2022b). Improvement of oxygen conditions may first
1351 promote higher zoobenthos biomasses but, eventually, increasing stratification will weaken
1352 benthic-pelagic coupling and reduce food availability for benthic organisms. If also nutrient
1353 abatement proceeds favourably, biomass of zoobenthos will start to decline (Ehrnsten et al.,
1354 2020).

1355 In the shallower photic benthic systems, nutrient increase probably enhances
1356 eutrophication, and, if salinity also declines, habitat-forming marine species, such as
1357 bladderwrack, eelgrass and blue mussel, probably decline in the northern Baltic Sea
1358 (Vuorinen et al., 2015; Jonsson et al., 2018; Kotta et al., 2019). As both eutrophication and
1359 increasing temperature favour filamentous algae, continued major changes in the sublittoral
1360 communities can be expected, including negative effects of such algal aggregations (Arroyo
1361 and Bonsdorff, 2016). Of particular concern is the potential loss from rocky substrates of the
1362 habitat forming bladderwrack and red macroalgae. Freshwater vascular plants will be
1363 favoured by freshening of the Baltic Sea, but they cannot replace the marine macroalgae on
1364 rocky sublittoral, because they only grow on soft substrates. On the other hand, salinity
1365 projections are still uncertain (Lehmann et al., 2022), and even if salinity declined, *Fucus*
1366 *vesiculosus* may be able to adapt to salinity changes (Rothäusler et al., 2018).

1367 As for fish, responses also depend on species. Salinity decline and hypoxia increase
1368 will most probably have negative consequences on cod stocks (Gårdmark et al., 2013),
1369 whereas the increasing temperature has been projected to favour sprat (Mackenzie et al.,
1370 2012) and certain coastal fish (Bergström et al., 2016). Again, as projections for salinity,
1371 stratification and oxygen levels are uncertain, the future fate of fish populations cannot be
1372 projected with certainty.

1373 The global climate change induces many environmental changes that may favour
1374 establishment of NIS in the Baltic Sea. Opportunistic and thermophilic species occupying
1375 soft sediments are the most probable winners. It is notable that it is extremely difficult to
1376 eradicate a marine NIS after it has found a suitable niche in the Baltic Sea. As the effects of
1377 NIS on both the ecosystem and the society are usually negative, their spreading should be
1378 prevented already before they enter the Baltic Sea, by applying effective measures to
1379 eradicate NIS from ballast waters of ships and other possible vectors.

1380 Climate change is obviously not the only factor determining the fate of the Baltic Sea in
1381 the future. Several modelling studies have concluded that nutrient reductions will be a
1382 stronger driver for ecosystem functions in the Baltic Sea than climate change (Friedland et
1383 al., 2012; Niiranen et al., 2013; Ehrnsten et al., 2019b; Pihlainen et al., 2020). In moderate
1384 nutrient loading scenarios also climate change will play a role, but under full implementation
1385 of BSAP, the environmental state of the Baltic Sea is projected to become significantly
1386 improved by the end of the century (Meier et al., 2018; Saraiva et al., 2018, 2019). Despite
1387 the many uncertainties concerning the effects of climate and eutrophication on the state of the
1388 Baltic Sea (Munkes et al., 2021), it can be stated that continued abatement of anthropogenic
1389 nutrient loading seems to be the most reliable, albeit slow, measure to solve the grand
1390 challenges of the Baltic Sea (Meier et al., 2018; Murray et al., 2019).

1391 Several studies have focused on studying the effects of climate change on the future
1392 state of the Baltic Sea, and especially the ecosystem modelling studies already provide
1393 valuable results that are directly usable in decision making concerning mitigation of
1394 eutrophication under climate change. In contrast, studies concerning effects of climate change
1395 on biodiversity of the Baltic Sea are lagging behind, and are hampered by model uncertainties
1396 (e.g. for salinity) and by the current inability of models to consider the complex interactions
1397 between species and trophic levels. Especially long-term and modelling studies focusing on
1398 shallow photic environments, which harbour the highest biodiversity in the Baltic Sea, are
1399 sparse. This is a major drawback in a situation where all major environmental policies,
1400 including UN Convention on Biological Diversity and EU Biodiversity Strategy for 2030,

1401 urge for halting the ongoing biodiversity loss. To designate effective measures to safeguard
1402 biodiversity, including a climate smart expansion of the protected area network, a better
1403 understanding of the effects of climate change on the sublittoral ecosystem is urgently
1404 needed.

1405 Knowledge of the mechanisms and processes governing Baltic Sea ecosystem under
1406 climate change have recently accumulated and already provide information that can be used
1407 to design adaptation tools and mitigation measures for the Baltic Sea (Reusch et al., 2018). It
1408 is necessary to continue studying the Baltic Sea as a socio-ecological system, responding to
1409 both environmental and societal changes (Bauer et al., 2018; Bauer et al., 2019; Hyytiäinen et
1410 al., 2019), and to continue the dialogue with human society, in order to attune to the future
1411 changes ultimately driven by the Ocean itself (Stenseth et al., 2020).

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1414 **Author contributions.** MV prepared the manuscript with contributions from EB.

1415

1416 **Competing interests.** The authors declare that they have no conflict of interest.

1417

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1426 Table 1. Summary of research findings and conclusions on the anticipated effects of climate

1427 change (CC) effects in the Baltic Sea. The table only includes studies published in 2011-

1428 2021. For earlier studies, see Dippner et al. (2008) and Viitasalo et al. (2015). Observations,

1429 experimental simulations, or modelled projections: T = temperature increase; S = salinity

1430 decline; TSO₂ = temperature increase, salinity decline and/or oxygen decline; A =

1431 acidification; AT = acidification and temperature increase; AS = acidification increase and

1432 salinity decline; DOM = dissolved organic matter. EXP = experimental manipulations

1433 /microcosms; MES = experimental manipulations /mesocosms; LTS = Long-term studies;

1434 MOD = modelling studies; FIE = Field data. Empty fields indicate knowledge gaps.

1435

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)	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; Wasmund et al. 2016)	EXP: Growth rates of <i>A. ostentfeldii</i> declined at lowered S (Kremp et al. 2016) Toxicity of <i>A. ostentfeldii</i> may increase or decrease, depending on strain, under S (Kremp et al. 2016)	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 phytoplankton (Paul et	MES: Autumn phytoplankton biomass increase with AT (Sommer et al. 2015); EXP: Growth and saxitoxin concentration of <i>Alexandrium ostentfeldii</i> increases with AT	LTS: Shift from diatoms to dino-flagellates 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. 2017;	MES: Warming increases zooplankton grazing on medium-sized algae which releases smaller algae from predation (Paul et al. 2015); EXP: Effects of AT modified by diminishing

	<p>EXP: Growth of dino-flagellate <i>Alexandrium ostenfeldii</i> decreased under T (Kremp et al. 2016)</p> <p>EXP: Toxicity of <i>A. ostenfeldii</i> may increase or decrease, depending on strain, under T (Kremp et al. 2016)</p> <p>Germination of <i>A. ostenfeldii</i> resting cysts is unaffected by T (Jerney et al. 2019)</p>	<p>Germination of <i>A. ostenfeldii</i> resting cysts is unaffected by T (Jerney et al. 2019)</p>		<p>al. 2015; Bermudez et al. 2016; Olofsson et al. 2019)</p>	<p>(Kremp et al. 2012)</p>	<p>Hjerne et al. 2019)</p> <p>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)</p>	<p>of grazing by copepods (Paul et al. 2016)</p>
Cyano-bacteria	<p>EXP: Earlier peak but lower biomass of cyano-bacteria (Berner et al. 2018); LTS: Increase of cyano-bacteria blooms in summer (Suikkanen et al. 2013); EXP: Toxicity of <i>Dolichospermum</i> sp. increases with T (Brutemark et al. 2015; Wulff et al. 2018)</p>	<p>LTS: community change caused by S decline in the Gulf of Bothnia (Kuosa et al. 2017); EXP: Toxicity of <i>Dolichospermum</i> sp. increases at low salinity (3-6 psu) (Wulff et al. 2018)</p>		<p>EXP: Production of single-celled cyano-bacterium <i>Cyanothece</i> increases and that of filamentous <i>Nodularia</i> decreases under A (Eichner et al. 2014); EXP: Decline of cyano-bacteria may induce a decline of nitrogen fixation (Eichner et al. 2014; Berner et al. 2018)</p>	<p>MES: AT has a negative impact on <i>Nodularia</i> biomass (Paul et al. 2018); EXP: Only T affects biovolume and photosynthetic activity of <i>Nodularia</i> and <i>Aphanizomenon</i> (Karlberg & Wulff 2013)</p>	<p>MOD: Cyano-bacteria 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)</p>	<p>LTS: Shift to cyano-bacteria dominance also attributed to changes in eutrophication and top-down pressure (Suikkanen et al. 2013)</p>
Microzooplankton	<p>MES: Growth rate of microzooplankton</p>			<p>MES: No effect on microzooplankton</p>	<p>EXP: Community change with</p>		<p>MES: Positive effect from A on the</p>

	increased (Horn et al. 2016)			(Horn et al. 2016)	AT (Lindh et al. 2013); EXP: Biovolume of ciliates decline with AS (Wulff et al. 2018)		mixotrophic ciliate <i>Myrionecta (Mesodinium)</i> 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 <i>Eurytemora affinis</i> can adapt to T (Karlsson & Winder 2020)	EXP: Respiration of copepod <i>Acartia longiremis</i> 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 (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)
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 <i>Fucus</i> 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 <i>Furcellaria</i> distribution will be restricted (Torn et al. 2020); EXP: Populations of <i>F. vesiculosus</i> show different responses to S (Kinby 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 <i>Ulva intestinalis</i> 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 filamentous algae; in winter, T enhances grazing by invertebrates, resulting in decline of bladderwrack (Werner et al. 2016)
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 <i>Zostera marina</i> (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	LTS: Salinity	LTS: Long-term	EXP: Develop-		MOD: Climate-	MOD: Abundance

	<p>response to T in isopod <i>Idothea balthica</i> (Ito et al. 2019); EXP: Heat waves induce a shift in community structure (Pansch et al. 2018); LTS: T increase induces a higher biomass of gammarids and snails (Salo et al. 2020)</p>	<p>decline affected zoobenthos variations in Åland Islands (Snickars et al. 2015)</p>	<p>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 <i>Marenzelleria</i> sp. explained by TSO (Rousi et al. 2013); EXP: Survival of isopod <i>Idothea Baltica</i> decreases (Rugiu et al. 2018c); MOD: Biomass of <i>Saduria entomon</i> increases due to S (Gogina et al. 2020)</p>	<p>ment 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 <i>Saduria entomon</i> (Jakubowska et al. 2013); EXP: No effect of A on isopod <i>Idothea balthica</i> in Kattegat but strong effects in the other parts of the Baltic Sea (Wood et al. 2014)</p>		<p>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)</p>	<p>of isopod <i>Idothea balthica</i> will decline due to salinity-induced decline in bladderwrack (Kotta et al. 2019)</p>
<p>Non-indigenous invertebrates</p>	<p>FIE: T induced higher biomass of gastropod <i>Potamopyrgus</i> (Salo et al. 2020)</p>		<p>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</p>				

			high T and low S (Jänes et al. 2017)				
Fish	<p>LTS: Sprat has benefited from T (Voss et al. 2011; MacKenzie et al. 2012; Eero et al. 2016);</p> <p>LTS: Warm water Atlantic species (e.g. anchovy, sole and turbot) occur in the western Baltic (Alheit 2012; Sparrevojn et al. 2013);</p> <p>MOD: Sprat productivity will increase with T (Voss et al. 2011; MacKenzie et al. 2012; Pansch et al. 2012);</p> <p>MOD: Herring stocks will increase due to T (Bartolino et al., 2014);</p> <p>LTS: Pike-perch more abundant in the northernmost Baltic Sea due to T (Peckan-Hekim et al. 2011)</p>	<p>LT: S and associated decline of marine copepods induced a halving of herring weight-at-age (Dippner et al. 2019);</p> <p>LTS/MOD: Different effects of T and S on sprat and cod cause a spatial mismatch between these species (Eero et al. 2012);</p> <p>LTS: Decline in S intensified resource competition between herring and vendace in the Bothnian Bay (Pekcan-Hekim et al. 2012)</p>	<p>MOD: Cod reproductive volume will diminish towards the end of the century due to TSO (Niiranen et al. 2013; Wählström et al. 2020);</p> <p>FIELD, EXP & MOD: Digestion, food consumption, growth and maximum length of cod declines in low O conditions (Limburg et al. 2019; Brander et al. 2020; Orio et al. 2021)</p>	<p>EXP: No effect of A on cod larvae (Frommel et al. 2013);</p> <p>EXP: Mortality of cod larvae doubles when treated with RCP8.5 scenarios (Stiasny et al. 2016)</p>	<p>EXP: No effect on cod larvae with AT (Frommel et al. 2013)</p>	<p>LTS/MOD: cod declined due to the climate- and human-induced decrease of 'reproductive volume' (Gårdmark et al., 2013; Niiranen et al., 2013; Wählström et al., 2020).</p>	<p>MOD: Climate-induced decoupling of benthic feeding fish from their food source (Törnroos et al. 2019);</p> <p>MOD: Herring stocks decrease in short term (Niiranen et al. 2013);</p> <p>FIE: Perch shift from feeding on small fish to gammarids, which releases grazing from filamentous algae (Svensson et al. 2017);</p> <p>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)</p>

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