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Ocean Acidification; Salinity decline

Abstract

Estuarine macroalgae are important primary producers in aquatic ecosystems, and often foundation species providing structurally complex habitat. Climate change alters many abiotic factors that affect their long-term persistence and distribution. Here, we review the existing scientific literature on the tolerance of key macroalgal species in the Baltic Sea, the world's largest brackish water body. Elevated temperature is expected to intensify coastal eutrophication, further promoting growth of opportunistic, filamentous species, especially green algae, which are often species associated with intensive filamentous algal blooms. Declining salinities will push the distributions of marine species towards south, which may alter the Baltic Sea community compositions towards a more limnic state. Together with increasing eutrophication trends this may cause losses in marine-originating foundation species such as *Fucus*, causing severe biodiversity impacts. Experimental results on ocean acidification effects on macroalgae are mixed, with only few studies conducted in the Baltic

28 Sea. We conclude that climate change can alter the structure and functioning of macroalgal
29 ecosystems especially in the northern Baltic coastal areas, and can potentially act synergistically
30 with eutrophication. We briefly discuss potential adaptation measures.

31

32 **1 Introduction: Climate change impacts in marine ecosystems**

33 In the recent decade anthropogenic climate change has been recognized as a global biodiversity
34 threat, motivating extensive research on its biological impacts (Wernberg et al., 2012). However,
35 the majority of research has focused on terrestrial ecosystems, and detailed knowledge of impacts
36 in marine ecosystems is lagging behind (Rosenzweig et al., 2008).

37 Coastal macroalgae are important foundation species providing biomass and structurally complex
38 habitats important for coastal biodiversity (Airoidi et al., 2008; Eriksson et al., 2006). Macroalgal beds
39 are highly productive environments comprising an important carbon sink (Chung et al., 2011).
40 Climate change has caused extensive poleward shifts of macroalgal distributions including range
41 contractions as species are tracking their thermal niches (Nicastro et al., 2013; Wernberg et al.,
42 2011), and more extensive shifts have been projected for the future (Jueterbock et al., 2013; Müller
43 et al., 2009). Macroalgae have been proposed to benefit from ocean acidification (OA) (Hall-Spencer
44 et al., 2008; Koch et al., 2013) but so far experimental evidence remains mixed (Hurd et al., 2009).

45 In this study we review climate change impacts on key Baltic Sea macroalgae species. As shallow
46 inland sea, the Baltic is particularly prone to warming, and observed rates of warming at the end of
47 the 20th century have been highest in all of the world's large marine ecosystems (Belkin, 2009). We
48 utilize both studies that have been conducted with climate change focus, as well as studies that
49 have been conducted on environmental tolerances of key species.

50

51 The Baltic Sea is a large, shallow brackish water epeiric sea heavily impacted by human activities.
52 Allegedly one of the biggest threats to the Baltic ecosystem during the 21st century is climate change
53 with predicted declines in salinity and elevated temperatures (Meier et al., 2012a). As the brackish
54 water environment is challenging for both marine and limnic species, the Baltic Sea ecosystem is
55 relatively species-poor, and the species distributions are controlled by a steep salinity gradient. Low
56 salinity and seasonal temperature oscillations cause many species to exist at the edges of their
57 geographic distribution (Hällfors et al., 1981), and towards the northern areas in the Baltic Sea the
58 conditions become more severe in form of shorter growing season, longer ice cover, and declining
59 salinity (Fig. 1a).

60

Fig. 1 a) Current salinity distribution of the Baltic Sea b) abundance of photic hard bottoms, the potential habitat for the macroalgae. Values are percentages of photic hard bottoms in relation to total bottom area. Data source: a) EUSeaMap (Cameron and Askew, 2011) b) Benthic biotope complexes in the Baltic Sea (HELCOM, 2010).

In the Baltic coastal zones, the habitat-forming macroalgae are the foundation species in rocky shore ecosystems, which are the prevalent shore types in the northern and western archipelago areas (Hällfors et al. 1981, Fig. 1b). The vertical zonation of algal species creates a structurally complex habitat, which is important for both juvenile fish and small invertebrates, thus harboring a large fraction of biodiversity in the Baltic coastal ecosystems (Hällfors et al., 1981; Kautsky et al., 1992). Especially the perennial, habitat-forming species have suffered from coastal eutrophication, causing declines in abundance and depth penetration during the 20th century (Kautsky and Kautsky, 1986). Eutrophication has also favoured fast-growing, filamentous species, which has culminated in the emergence of drifting, decomposing algal mats destroying soft-bottom communities (Norkko and Bonsdorff, 1996).

While in oceanic areas climate change has been projected to cause northward shifts in macroalgal distributions (Müller et al., 2009), the patterns are different in the Baltic. Declining salinities (Meier et al., 2012a) may counteract the general trends, pushing the distributions of marine-originated species towards south (Vuorinen et al., 2015). This, together with other interacting human impacts makes the Baltic macroalgae particularly interesting study organisms for climate change ecology. As the northern and western shores and archipelagos of the Baltic contain large fraction of the suitable shores for macroalgae, we focus our review on dominant species occurring in these areas.

2 The changing abiotic conditions in the Baltic Sea

The sea surface temperature (SST) of the Baltic has warmed rapidly during recent decades. Siegel *et al.* (2006) observed warming of 0.8 °C over 15 years, in good agreement of unprecedented

84 warming of 0.6 °C between 1985 and early 2000 reported by MacKenzie & Schiedek (2007), who
85 also reported increased frequency of extreme temperatures. MacKenzie & Schiedek (2007)
86 observed the warming of the Baltic and North Sea to be three times higher than the global average.
87 The BACC I report (BACC Author Team, 2008) states warming of air temperatures by 1 °C from the
88 beginning of the 1980s to 2004, while Lehmann *et al.* (2011) identified warming of 0.5 °C per decade
89 for the northern Baltic, which seems to be warming more rapidly. Finally, Belkin (2009) reported
90 observed warming of SST of 1.35 °C (1982-2006), which was higher than in any other Large Marine
91 Ecosystem in the world, and seven times higher than the observed global warming rate (Belkin,
92 2009).

93 Salinity conditions in the Baltic depend on riverine inflow of fresh water and stochastic inflow of
94 saline water through Danish straits (Leppäranta and Myrberg, 2009). No clear long-term trend in
95 salinity has been observed for the last hundred years (Fonselius and Valderrama, 2003; Winsor *et al.*,
96 2001), although large decadal oscillations exist. However, the salinity change from external
97 forcing would expectedly be slower than temperature change because of latency related to water-
98 exchange (Myrberg *et al.*, 2006). Nutrient concentrations have increased notably over the 20th
99 century as a consequence of increased anthropogenic emissions (Fonselius and Valderrama, 2003),
100 and have contributed substantially to the present-day seasonal pH oscillations (Omstedt *et al.*,
101 2009).

102 The eventual impacts of climate change in the Baltic will depend on a multitude of factors, including
103 the realized emissions, sensitivity of climate system to greenhouse gas emissions, stochastic
104 regional climate as well as interactions with other anthropogenic drivers, such as eutrophication.
105 On a broad scale, the mean annual sea surface temperatures of the Baltic have been projected to
106 increase by 2 to 4 °C by the end of century. Higher temperature increases (4 °C) have been projected

107 for the northern areas such as Bothnian Bay, and more moderate increases (2 °C) for southern areas
108 (HELCOM, 2013).

109 Warming is expected to promote an increased frequency of short-term extreme heat events near
110 the surface (MacKenzie and Schiedek, 2007; Neumann et al., 2012). Currently, sea ice lasts for 5 to
111 7 months in the northern parts of the Baltic, and during very cold winters, the entire Baltic can
112 freeze over (Leppäranta and Myrberg, 2009). Winter-time warming can cause a 60-80 % reduction
113 in the duration of sea ice by the end of the century (Meier, 2006; Neumann, 2010), promoting
114 longer growing season and increased light availability. Elevated temperatures increase respiration
115 and together with consequent increases in primary production may cause increased frequencies of
116 anoxia (Neumann et al., 2012), which promotes release of mineralized nutrients from the
117 sediments, intensifying eutrophication further (Meier et al. 2012c; Neumann et al. 2012).

118 The salinity of the Baltic has been projected to decline by 2 to 3 units by the end of the century,
119 caused by increased fresh-water runoff (Meier 2006), however, there is large uncertainty related
120 to the accuracy of salinity projections (HELCOM, 2013; Leppäranta and Myrberg, 2009; Meier, 2006;
121 Meier et al., 2006). Declining salinity decreases stratification, which slightly improves oxygen
122 conditions in suboxic areas, however, on average the future bottom oxygen conditions are expected
123 to deteriorate (Neumann 2010; Meier et al. 2012c).

124 In most parts of the Baltic, increased river inflow causes increased nutrient and organic carbon input
125 (Meier, 2006; Meier et al., 2012b), leading to increased nutrient loading, especially in winter, when
126 biological nutrient uptake is absent. Also the remobilization of nutrients stored in the sediments
127 has been predicted to increase as a consequence of elevated temperatures (Meier et al. 2012b,
128 2012c). However, in the Bothnian Bay, the increased precipitation may lead to more oligotrophic
129 conditions (HELCOM, 2013). The future nutrient loading will depend also on agricultural policy and

130 the intensity of agriculture in the drainage area, and the policies applied for nutrient emission
131 reductions (Meier et al., 2012c; Seitzinger et al., 2002). The wintertime river inflow will increase in
132 the north coupled with lower and earlier springtime peak flows, which may alter the temporal
133 salinity patterns (BACC Author Team, 2008). The intensity of springtime river flows has been
134 predicted to decrease with declining snow cover, which will also cause the peak freshwater inflow
135 to shift earlier in many areas (HELCOM, 2013).

136 Globally, the mean pH of sea water is predicted to decline by 0.3 - 0.4 units towards the end of the
137 century unless the global CO₂ emissions are controlled (Feely et al., 2009). The Baltic ecosystem is
138 especially vulnerable to acidification because of the low buffering capacity of brackish water
139 (Omstedt et al., 2010), the high freshwater input with high levels of dissolved organic carbon (DOC)
140 and low alkalinity (caused by low pH soils in the drainage area) (Omstedt et al., 2010). In the Baltic,
141 the mean pH levels have been estimated to decline by 0.25-0.34 units by the end of the century
142 (Kuznetsov and Neumann, 2013; Omstedt et al., 2010). However, on average these declines are
143 smaller than the current annual pH oscillations between summer and winter (Omstedt et al., 2010;
144 Saderne et al., 2013), and they are damped by large diurnal oscillations, which may exceed 1 unit
145 in highly productive ecosystems such as macroalgal beds (Middelboe and Hansen, 2007).

146 The acidification in the Baltic is strongly linked to nutrient emissions. If eutrophication continues,
147 also the annual oscillations will intensify in the future as carbon is taken up by primary producers
148 during the summer, and again released during the winter (Omstedt et al., 2010), resulting in more
149 frequent periods of low pH. Additional input of organic carbon through increased riverine flow may
150 further intensify these trends (Omstedt et al., 2010).

151 Acidification and elevated atmospheric CO₂ increases the concentrations of dissolved inorganic
152 carbon (DIC), and changes the relative abundances of DIC components: increased levels of dissolved

153 aquatic CO₂ and bicarbonate (HCO₃⁻), and reduced levels of carbonate (CO₃²⁻). The highest relative
154 increase will be in CO₂, which will increase by 250 % if atmospheric CO₂ rises to 1000 ppm (Koch et
155 al., 2013). This will change the carbon availability for photoautotrophs, and may potentially elevate
156 marine primary production (Hurd et al., 2009; Koch et al., 2013).

157

158 **3 Macroalgae in the Baltic Sea**

159 The Baltic macroalgal community is characterized by a salinity gradient imposing restrictions on
160 species occurrences and importance of few perennial habitat-forming species such as *Fucus* spp.
161 and *Furcellaria lumricalis*. As these characteristics of the ecosystem have been covered in earlier
162 studies (e.g. already by Waern (1952), we do not describe them in detail here but briefly summarize
163 the main features (Table 1).

164

Macroalgae of the Baltic Sea

- Total 442 macroalgae species observed (Nielsen et al., 1995)
- The majority of species have colonized Baltic from the Atlantic and have adapted to low salinity (Bäck et al., 1992; Russell, 1985)
- Biota controlled by salinity gradient, and the number of macroalgae species declines with salinity (Nielsen et al., 1995; Waern, 1952)
- Fucoids most important habitat-forming species in Baltic Proper (Kautsky et al., 1992; Malm et al., 2001)
- *Fucus vesiculosus* is the main habitat-forming species with 90 % of plant biomass in hard bottoms (Kautsky and Van der Maarel, 1990)
- In eastern and southern shores *Furcellaria lumbricalis* forms important habitats (Bučas et al., 2007)
- Filamentous algae are major seasonal primary producers with peak abundances in summer (Kautsky, 1995; Kiirikki and Lehvo, 1997)
- Eutrophication has caused extensive blooms of filamentous algae and declines in abundance and depth penetration of habitat-forming species such as fucoids (Kautsky and Kautsky, 1986; Lehvo and Bäck, 2001)

166

167 4. Methods

168 We selected the species from distributional indexing of Nielsen *et al.*, (1995) from areas with indexes
 169 from 4 to 10, consisting of Baltic Proper, Gotland Sea, Estonian coast, Gulf of Finland, Archipelago
 170 Sea, Åland Sea and Gulf of Bothnia. As we wanted to focus only on the most ecologically significant
 171 species, we selected species that were classified by Nielsen *et al.*, (1995) as “dominant” in any of
 172 these areas or “frequent” in most areas. We added to this species list two species frequent in the
 173 least saline areas (*Cladophora aegagropila* and *Cladophora fracta*), yielding a total 31 species; 8
 174 from bangiopheceae, 11 fucophyceae, and 12 chlorophyceae (Table 2). Also *Fucus radicans* was
 175 added into the species search list as this species was only relatively recently identified as species
 176 (Bergström et al., 2005) and thus not included in the indexing of Nielsen *et al.* (1995).

177 We searched ISI Web of Knowledge for scientific articles with species scientific name together
178 (operator “and”) with following keywords: “temperature”, “heat shock”, “salinity”, “osmotic stress”,
179 “nutrients”, “eutrophication” and “ocean acidification” from the topic field.

180 In addition, we performed a heuristic search with the same criteria using Google Scholar to provide
181 a quick comprehensive screening of the existing literature. If studies addressing the factors in
182 question were found with the study species, these were included even if the actual study had been
183 performed outside the Baltic.

184 We classified the responses of the species into four categories: “beneficial”, “potentially beneficial”,
185 “tolerant” and “harmful”, respectively, for four abiotic variables: warming, declining salinity,
186 eutrophication, and ocean acidification. As the literature found contained reports of laboratory
187 experiments with various treatment levels, field manipulations as well as observations of species’
188 distributions, classification of the responses required some subjective consideration.

189 We used psu 4 as a threshold for salinity decline, as salinity of 5 psu has been identified to be critical
190 threshold for persistence of many marine species (Schubert et al., 2011; Vuorinen et al., 2015), thus
191 we examined the observed responses of the species for salinities under 4 psu. Negative
192 experimental responses (declines in photosynthesis, growth or survival) or field observations which
193 showed decline in abundance, biomass or reproduction when salinity declined under 4 psu, were
194 classified as “harmful”. If no response against experimental manipulation, or no observed changes
195 in the field under 4 psu was found, the species was classified “tolerant”. Positive experimental
196 responses or increasing abundance under declining salinity were classified as “beneficial”.

197 Temperature responses were classified similarly, although here no exact temperature threshold for
198 “elevated” temperature was set. Declining growth or photosynthesis, increased mortality or
199 overgrowth by epiphytes observed in elevated temperature experiments were classified as

200 “harmful”. We also classified response as “harmful”, if the species had low thermal growth range or
201 low upper survival temperature limit, obtained through distribution observations and experiments,
202 sensu Wiencke et al. (1994), or if the observed abundance of the species in the field declined under
203 elevated temperature, for example under artificial heating. Response was classified “tolerant” if the
204 species showed no response in elevated temperature experiments, or had wide thermal growth
205 range, and high upper survival temperature, and no changes in abundance under elevated
206 temperature. “Beneficial” responses included positive experimental responses, high thermal growth
207 range, or positive changes in abundance when temperature was increased. In all temperature
208 classifications, we classified the responses considering the projected future temperatures in the
209 Northern Baltic.

210 “Harmful” responses to Ocean Acidification were cases of declining growth, photosynthesis or
211 increased photoinhibition in the laboratory, or decreased abundance under low pH condition in the
212 field. “Tolerant” responses were cases where no effects or changes in abundance were observed,
213 and “Beneficial” positive responses or increased abundance. OA was the only variable for which the
214 category “potentially beneficial” was used. In these cases, experimental responses indicated either
215 positive responses against OA treatment in only a particular season, positive photosynthesis
216 response when total inorganic carbon was increased, or indication of reliance on free CO₂ in carbon
217 acquisition, which could potentially lead to positive effects under elevated CO₂ levels (Koch et al.,
218 2013).

219 Responses to eutrophication were classified similarly as other variables. If a shift of macroalgal
220 zonation towards the surface or decreased depth penetration with increasing eutrophication was
221 observed, this was considered “harmful”, as were failures in germination or declining abundance in
222 eutrophic conditions. Species was considered “tolerant” against eutrophication, if no effects on

recruitment, growth or abundance were observed under eutrophication, and “beneficial” if the abundance of the species increased under eutrophic conditions.

225

5. Results - Impacts of climate change on Baltic macroalgae

For the selected species, a total of 3042 papers were found from the Web of Knowledge. Of these, 128 papers contained information over the variables studied here (Table 2, Table S1). Here, a summary of the responses is provided (Table 2), exact literature references for the responses are given in supplementary material (Table S1).

Table 2. Responses of key macroalgal species to expected abiotic changes. Number of papers found relating to response against each variable are given in parenthesis. Green indicates positive effects, gray neutral and red negative.

Species	No of hits WoS	No of articles referred in here	Growth form	Warming	Declining salinity	Ocean acidification	Eutrophication
RED ALGAE							
<i>Hildenbrandia rubra</i>	20	4	Perennial, encrusting	Tolerant (1)	Tolerant (3)	Beneficial (1)	
<i>Coccotylus truncatus</i> syn. <i>Phyllophora brodiaei</i> , <i>P. truncata</i>	23	4	Perennial, foliose	Beneficial (1)	Tolerant (1)	Potentially beneficial (1)	Tolerant (1)
<i>Furcellaria lumbricalis</i>	61	8	Perennial, dichotomous, corticated	Beneficial (2)	Harmful (3)	Beneficial (2)	Tolerant (2)
<i>Ceramium tenuicorne</i>	35	7	Annual, filamentous, partial cortication	Harmful (1)	Tolerant (5)		Beneficial (1) Harmful (1)
<i>Ceramium virgatum</i> syn. <i>C. rubrum</i> , <i>C. nodulosum</i>	24 59	0	Annual, filamentous, corticated				
<i>Polysiphonia fucoides</i> syn. <i>P. nigrescens</i>	22 7	4	Perennial, polysiphonous		Harmful (2)		Beneficial (1) Tolerant (1)
<i>Polysiphonia fibrillosa</i> syn. <i>P. violacea</i>	3 6	2	Annual, polysiphonous		Harmful (2)		
<i>Rhodomela confervoides</i>	73	4	Annual, corticated		Tolerant (2) Harmful (1)		Beneficial (1)
BROWN ALGAE							

<i>Pylaiella littoralis</i> often misspelled	103 93	10	Annual, filamentous uniseriate	Harmful (2)	Tolerant (4)		Beneficial (4)
<i>Pilayella littoralis</i>	342	10	Annual, filamentous uniseriate	Tolerant (2) Beneficial (1)	Tolerant (2) Harmful (1)		Beneficial (4)
<i>Ectocarpus siliculosus</i>							
<i>Elachista fucicola</i>	13	0	Annual, filamentous uniseriate				
<i>Eudesme virescens</i>	3	1		Beneficial (1)			
<i>Pseudolithoderma spp.</i>	11	0	Perennial, encrusting				
<i>Dictyosiphon foeniculaceus</i>	11	0	Cylindrical, branched thallus				
<i>Stictyosiphon tortilis</i>	2	1	Cylindrical, branched thallus				Harmful (1)
<i>Scytosiphon lomentaria</i>	130	4	Annual, tubular, often regular constrictions	Tolerant (3)	Tolerant (1)		
<i>Chorda filum</i>	33	3	Annual, strapshaped multicellular thallus	Tolerant (1) Harmful (1)	Tolerant (1)		
<i>Fucus vesiculosus</i>	1450	53	Perennial, multicellular thallus with differentiated cell structures	Beneficial (5) Harmful (8) Tolerant (1)	Tolerant (5) Harmful (3)	Tolerant (2) Potentially beneficial (2) Harmful (3)	Harmful (30)
<i>Fucus radicans</i>	11	2	Perennial, multicellular thallus with differentiated cell structures	Harmful (2)	Tolerant (1)		
GREEN ALGAE							
<i>Ulva flexuosa</i> syn. <i>Enteromorpha flexuosa</i>	9 18	6	Annual, tubular	Beneficial (3)	Tolerant (2)		Beneficial (3)
<i>Ulva intestinalis</i> syn. <i>Enteromorpha intestinalis</i>	24 90	26	Annual, tubular	Beneficial (6)	Tolerant (7) Harmful (1)	Beneficial (1)	Beneficial (11)
<i>Ulva linza</i> syn. <i>Enteromorpha ahleriana</i>	38 1	10	Annual, tubular	Beneficial (6) Tolerant (1)	Harmful (2) Tolerant (1)		Beneficial (2)
<i>Ulva prolifera</i> syn. <i>Enteromorpha prolifera</i>	99 71	11	Annual, tubular	Beneficial (2)	Tolerant (4)	Potentially beneficial (1) Harmful (1)	Beneficial (4)
<i>Ulothrix subflaccida</i>	1	3	Annual, filamentous uniseriate	Harmful (1)	Tolerant (2)		
<i>Ulothrix zonata</i>	11	0	Annual, filamentous uniseriate				

<i>Monostroma grevillei</i> syn. <i>Ulvopsis grevillei</i>	4	2	Annual, filamentous uniseriate	Harmful (2)	Harmful (1)	
<i>Urospora penicilliformis</i>	5	1	Annual, filamentous uniseriate		Tolerant (1)	
<i>Cladophora aegagropila</i>	3	1	Annual, filamentous uniseriate		Beneficial (1)	
<i>Cladophora fracta</i>	7	0	Annual, filamentous uniseriate			
<i>Cladophora glomerata</i>	112	15	Annual, filamentous uniseriate	Beneficial (6) Tolerant (2)	Beneficial (3) Tolerant (2) Harmful (1)	Beneficial (3)
<i>Cladophora rupestris</i>	22	3	Annual, filamentous uniseriate	Tolerant (1)	Harmful (2) Tolerant (1)	

5.1. Temperature and light: direct physiological effects

In oceans, temperature is one of the most important determinants for the geographic ranges of macroalgal species (Eggert, 2012), and elevated temperatures expectedly shift macroalgal distributions towards the poles (Jueterbock et al., 2013; Müller et al., 2009; Nicastro et al., 2013). However, in the Baltic Sea scale, species distributions are mainly controlled by salinity gradient (Eriksson and Bergström, 2005; Nielsen et al., 1995; Schubert et al., 2011), and thus the exact effects of temperature increases on species' distributions are hard to predict, although some studies suggest northward shift of fucoid distributions (Leidenberger and Giovanni, 2015). Elevated temperature has a direct control over many phenological processes. Increased temperature, in the form of mild winters, has been shown to accelerate receptacle growth of *F. vesiculosus*, causing earlier reproduction in the Baltic Sea (Kraufvelin et al., 2012). Ice-free winters may allow also the perennial species to grow in the filamentous algal zone near the surface, if disturbance from ice scraping is missing (Kiirikki, 1996). Temperature effects also depend on local habitat features and may be especially pronounced on e.g. sheltered sites (Gubelit, 2015).

248 Species living in areas with high seasonal temperature fluctuations (such as the Baltic) generally
249 have a higher ability to acclimate to ambient temperature changes (Eggert, 2012). If the geographic
250 distribution of the species covers a wide temperature gradient, intraspecific differences in optimal
251 temperatures may also occur between local populations. Indeed, *F. radicans* has been shown to
252 have higher sensitivity to short-term heat shocks than *F. vesiculosus* (Lago-Lestón et al., 2009),
253 possibly as an indication of more cold-adapted physiology.

254 The exact thermal tolerances of Baltic macroalgae have not been widely studied, but many large
255 macroalgal species in the North Sea have a broad temperature optima between 10 and 15 °C (Fortes
256 and Lüning, 1980). Baltic *F. vesiculosus* has been found to have lower temperature optima for
257 growth and photosynthesis than the Atlantic populations (Nygård and Dring, 2008). Moderate
258 warming has been observed to increase the growth of *F. vesiculosus* (Al-Janabi et al., 2016a; Lehvo
259 et al., 2001), however, even short exposures to temperatures higher than 27 °C are lethal for both
260 juvenile and adult thalli (Al-Janabi et al., 2016a; Graiff et al., 2015).

261 Our literature review reveals that species that would benefit most from the warming are
262 filamentous green algae, mainly *Ulva* spp. and *C. glomerata*. In addition, some positive responses
263 were found for leathery red alga *Coccotylus truncatus*, as well as filamentous brown *Ectocarpus*
264 *siliculosus* and *Eudesme virescens* (Table 2).

265 Few clearly cold-water species were identified, for which temperature increases may be harmful.
266 These were the filamentous red alga *Ceramium tenuicorne*, filamentous brown alga *Pylaiella*
267 *littoralis*, and green algae *Ulothrix subflaccida* and *Ulothrix grevillei* (Table 2), although in general,
268 responses for warming in green algae were positive. Expected responses of *F. vesiculosus* were
269 quite divergent, reflecting the difficulty of assessing the complex causal effects caused by
270 temperature increase (Table 2, Table S1).

271 5.2. Temperature and light: Ecosystem-level changes

272 Although there are many studies of climate change impacts on the ecology and physiology of
273 macroalgae, these have often been conducted with single species and under controlled conditions.
274 The eventual outcomes will depend on ecosystem-level responses. Surveys carried out near Finnish
275 and Swedish nuclear power plants have shown that temperature increases, caused by discharge of
276 cooling water, promote excess growth in filamentous algae and increase primary production of the
277 littoral ecosystem (Ilus, 2009; Snoeijs and Prentice, 1989). Under high external nutrient load, this
278 can lead to bottom anoxia, internal loading and eventual destruction of benthic faunal
279 communities. On the other hand, in less eutrophic conditions the impacts of warming were less
280 severe, and the diversity of benthic fauna increased (Ilus, 2009). Near Olkiluoto power plant (West
281 coast of Finland), a rise of mean annual temperature by 2-4 °C increased abundance of green alga
282 *C. glomerata*, and the *Cladophora* belt formed 2-3 months earlier than in natural conditions (Ilus
283 et al., 1986; Keskitalo and Heitto, 1987). Other species favoured by elevated temperatures were
284 *Enteromorpha ahleriana* (current name *Ulva linza*) and *Ectocarpus siliculosus* (Keskitalo and Ilus,
285 1987). Interestingly, artificial heating favoured *Ectocarpus siliculosus*, but occurrence of
286 macroscopically similar cold-water species, *Pylaiella littoralis*, was inhibited (Keskitalo and Heitto,
287 1987; Keskitalo and Ilus, 1987; Snoeijs and Prentice, 1989).

288 In Sweden, a monitoring survey near a nuclear power plant displayed increased growth, abundance
289 and species diversity of green macroalgae in summer, while red and brown macroalgae declined,
290 except during the winter months (Snoeijs and Prentice, 1989). Overall, the increased temperature
291 and decline of winter ice cover favored opportunistic, short-lived species, which became dominant
292 in the algal communities (Snoeijs and Prentice, 1989).

Future warming of the Baltic is coupled with changing light conditions, as the sea ice range and duration decreases (Neumann, 2010) and there is more light available for the onset of growing season in early spring, which may affect phenology of many species (Kraufvelin et al., 2012, 2007). However, the input of organic material into Baltic has been predicted to increase (Meier et al., 2012b) resulting in deteriorating underwater light conditions, which may narrow the macroalgal zones towards the surface, as observed in eutrophic conditions (Kautsky and Kautsky, 1986; Rinne et al., 2011). Increased organic matter increases sedimentation, which impedes macroalgal growth, especially the recruitment of *Fucus* spp. (Eriksson & Johansson, 2003, 2005; Isæus et al., 2004, Table 2).

5.3. Responses to low salinity

Based on our literature search, the red algae on average had lowest salinity tolerances, followed by brown algae (Table 2). Green algae contained many species which were very tolerant of low salinities or would actually be expected to benefit from low salinity (Table 2). This pattern is in accordance with physiological tolerance ranges obtained through laboratory experiments (Larsen and Sand-Jensen, 2006) and observed species distributions in field surveys (Bergström and Bergström, 1999).

Although Baltic macroalgae have adapted to brackish water, and have generally very high tolerance against low salinity (Larsen and Sand-Jensen, 2006), many species have not been able to inhabit the inner parts of the Baltic Sea (Nielsen et al., 1995; Snoeijs, 1999), and the perennial species of marine origin are absent from regions with lowest salinities (Eriksson and Bergström, 2005). One of the reasons is a failure to reproduce in low salinities. The northern and eastern ranges of *F. vesiculosus* in the Baltic have been suggested to depend on the osmotic tolerance of the gametes (Serrão et al., 1996). At the Gulf of Finland, *F. vesiculosus* is found in salinities down to 3 units (Bäck and

316 Ruuskanen, 2000), at the Swedish coast the distribution limit is at salinity of 4 (Kautsky et al., 1992).
 317 *F. radicans* tolerates lower salinity than *F. vesiculosus*, and its distribution in the Bothnian Sea lies
 318 in the salinity range of 3 to 5 (Bergström et al., 2005; Leidenberger and Giovanni, 2015). *F. radicans*
 319 reproduces asexually in low salinities (Tatarenkov et al., 2005), and the rapid speciation of *F.*
 320 *radicans* from *F. vesiculosus* has been attributed to low salinity levels (Pereyra et al., 2009). In *F.*
 321 *vesiculosus*, low salinity alters sex ratios, as populations become dominated by female plants in low
 322 salinities (Malavenda and Voskoboinikov, 2009). This kind of responses may decrease genetic
 323 diversity, and make the local populations more vulnerable to other environmental changes.
 324 Although some studies indicate salinities below 4 psu to be harmful for *F. vesiculosus* (Serrão et al.,
 325 1999, 1996), field observations have identified persistence of local populations even in salinities
 326 down to 2 psu (Ardehed et al., 2016; Munda, 1999; Ruuskanen and Bäck, 2002), with high rates of
 327 sexual reproduction (Ardehed et al., 2016). This indicates that local populations may differ in their
 328 salinity tolerance, although the size of *F. vesiculosus* plants decreases rapidly with declining salinity
 329 (Bäck, 1993; Bäck and Ruuskanen, 2000; Kalvas and Kautsky, 1998; Ruuskanen and Bäck, 1999).
 330 Inhibition of sexual reproduction occurs also in other species in low salinities. The abundance of the
 331 perennial, coarsely branched red alga *F. lumbricalis* declines with salinity (Bergström and
 332 Bergström, 1999) and no sexual reproduction was observed in lowest salinities (3.6 units) sampled
 333 (Kostamo and Mäkinen, 2006). The filamentous red alga *C. tenuicorne* has been observed to grow
 334 in salinities from 25 to 1 units, and in the lowest salinities asexual reproduction is common
 335 (Bergström et al., 2003). Some local populations in the Bothnian Bay have salinity optima as low as
 336 1.5 units, but growth is severely reduced in these conditions (Bergström and Kautsky, 2006).
 337 Many brown and green algal species in the Baltic can tolerate low salinity reasonably well. The Baltic
 338 *P. littoralis* has shown vigorous growth in laboratory in salinity levels of 1.5 units (Russell, 1994),

339 and also *E. siliculosus* tolerates low salinities (Dittami et al., 2012; Munda, 1999). The filamentous
340 green algae *C. glomerata* is originally a fresh-water species and is expected to be favoured by low
341 salinities (Munda, 1999; Thomas et al., 1990, 1988). *Cladophora rupestris* is of marine origin, and
342 in the Atlantic it grows in the intertidal zone, while in the Baltic it is found in the upper sublittoral.
343 Salinity tolerance of *C. rupestris* is lower than that of *C. glomerata* (Bergström and Bergström, 1999;
344 Thomas et al., 1990, 1988), and thus it is expected to decline with low salinity. Another abundant
345 filamentous green alga *U. intestinalis* showed the highest tolerance for low salinity of 44 macroalgal
346 species studied by Larsen and Sand-Jensen (2006) with no decline in photosynthesis at 0 salinity
347 after 4 days of incubation. As species tolerant of low salinity (Alström-Rapaport et al., 2010;
348 McAvoy and Klug, 2005; Reed and Russell, 1979), *U. intestinalis* extends its distribution throughout
349 the Baltic (Leskinen et al., 2004).

350 The decrease in number of macroalgal species along the salinity gradient causes a steep decline in
351 the overall biodiversity and biomass of rocky shore communities (Bergström and Bergström, 1999).
352 The ratio of marine to freshwater algal species declines from 4.2 to 1 in the Gulf of Bothnia in a
353 salinity gradient of 5 to 3.5 (Bergström and Bergström, 1999). In the Baltic, there is a decline in red
354 algal (Rhodophyta) and brown algal species (Phaeophyceae) and an increase in green algae
355 (Chlorophyta) along declining salinity (Nielsen et al., 1995; Ojaveer et al., 2010; Snoeijs, 1999),
356 which matches with salinity tolerances derived from experiments (Larsen and Sand-Jensen, 2006),
357 as well as with the results of our literature search (Table 2). The Chlorophyta contain more species
358 of fresh-water origin (Johansson, 2002) with optima in low salinities and even fresh water (Larsen
359 and Sand-Jensen, 2006). In the Bothnian Bay, some macroalgal communities in low salinities are
360 dominated by lacustrine green alga *Cladophora aegagropila*, which extends its distribution down
361 to 10 meters (Bergström and Bergström, 1999).

362 Substantial reductions in biodiversity of marine-associated species with declining salinities have
363 been predicted especially through the loss of fucoids (Vuorinen et al., 2015). Our results suggest
364 that *F. vesiculosus* could potentially show some adaption to low salinities as local populations may
365 have salinity tolerances lower than the generally assumed 4 psu. However, as the size of the plants
366 decreases concurrently with salinity, the ecosystem functions provided by *F. vesiculosus*, such as
367 year-round habitat persistence and complexity, biomass, and nutrient uptake, may be lost or
368 diminished. As an example, *F. radicans* (which could potentially replace *F. vesiculosus* in areas of
369 low salinity in the future), harbors less diverse communities of associated flora and fauna because
370 of smaller size of the thallus (Schagerström et al., 2014).

371 Since many species in Chlorophyta manage well or even prefer low salinity conditions, the
372 macroalgal community in the Baltic may become increasingly dominated by green algae if salinity
373 declines. This would change ecosystem functions and associated species as well, since many green
374 algae are fast-growing, opportunistic annual species, often overwintering as spores, and thus being
375 unable to provide habitat for faunal species during e.g. winters. . The macroalgal beds in the Baltic
376 are important nurseries for fishes and invertebrates (Kautsky et al., 1992), and possible changes
377 would be mediated also to higher trophic levels of pelagic and terrestrial coastal ecosystems
378 through altered energy and nutrient flows.

379 Although potentially some compensation could be gained from colonization by freshwater algal
380 species, these mostly lack large, perennial species. Also, large-scale replacement of marine species
381 by freshwater species under horohalinicum (5 to 8 units) has not been observed with macroalgae
382 (Schubert et al., 2011).

383 5.4. Ocean acidification and CO₂ fertilization

384 The macroalgal photosynthesis is mainly C₃-based (Koch et al., 2013) and utilizes RuBisCO, which is
385 the core enzyme in fixing organic carbon (Raven et al., 2008). Diffusion of CO₂ in water is several
386 orders of magnitude lower than in air (Falkowski and Raven, 2007), which means that
387 photoautotrophs may easily become carbon limited, if they only rely on passive diffusion for their
388 carbon acquisition. Most macroalgae use dissolved CO₂ as a source of inorganic carbon (Koch et al.,
389 2013). Carbon uptake by photosynthesis may cause high local fluctuations of pH and depletion of
390 free dissolved CO₂ (Hurd et al., 2009; Middelboe and Hansen, 2007). To overcome this problem,
391 most macroalgae have evolved carbon concentrating mechanisms (CCMs), which increase CO₂
392 concentration at the site of RubisCO activity (Koch et al., 2013; Raven et al., 2008). This may involve
393 active uptake and transport of CO₂ or HCO₃⁻ (Raven et al., 2008), or secretion of H⁺ to enhance
394 dissociation of HCO₃⁻ to CO₂ (Koch et al., 2013), but with an energetic cost related to the transport,
395 secretion and maintenance/production of the cellular machinery involved (Raven et al., 2014).
396 Species using bicarbonate convert HCO₃⁻ to CO₂ either using intracellular or periplasmic carbonic
397 anhydrases (CA) or CCMs (Hurd et al., 2009). Many macroalgal species use CCMs facultatively at low
398 CO₂ concentrations (Koch et al., 2013). Species lacking CCMs are often found in high-flow
399 environments, where currents replenish the CO₂ pool near the plant, or in low-light environments,
400 where overall photosynthesis rates are low, and species do not have the energy to utilize CCMs
401 (Koch et al., 2013).

402 Since usage of CCMs is energetically limited (Hurd et al., 2009; Raven et al., 2011), in most
403 macroalgal species studied so far photosynthesis appears unsaturated in current ocean DIC
404 concentrations despite possessing HCO₃⁻-based CCMs (Koch et al., 2013). This implies that
405 increasing atmospheric CO₂ concentration could have a positive impact on macroalgal
406 photosynthesis through improved carbon uptake energetics (Raven et al., 2011). However, results

407 from CO₂ enrichment experiments in macroalgae have shown a wide range of responses, possibly
408 relating to different experimental techniques (Hurd et al., 2009).

409 We found only few studies investigating OA effects on Baltic macroalgae. These (Table 2) would
410 indicate, that red algae and potentially green algae, would benefit from OA. As red algae generally
411 grow deeper, they are more reliant on passive CO₂ diffusion (Snoeijs et al., 2002), and thus would
412 benefit more from the increased CO₂ availability, in contrary to species utilizing efficient CCMs,
413 which frequently grow in high irradiances where CO₂ pool may become depleted by photosynthesis
414 (Koch et al., 2013; Middelboe and Hansen, 2007). Red alga *Hildenbrandia rubra*, abundant
415 throughout the Baltic (Nielsen et al., 1995) was one of the few species that dominated the species-
416 impoverished algal community under high CO₂ (pH 6.7) near volcanic vents in the Mediterranean
417 (Porzio et al., 2011), although as *Hildenbrandia* has been suggested to be a subordinate competitor
418 (Kaehler and Williams, 1996), this result may also stem from competitive release rather than direct
419 pH response. A decline from pH 8.1 to 7.8 changed the structure of macroalgal community, which
420 became dominated by few erect leathery species, when turf type algae declined (Porzio et al., 2011).

421 Ocean acidification experiments conducted on Baltic macroalgae have provided mixed results. In a
422 short-term experiment (duration 3 days), Pajusalu et al. (2013) found photosynthesis of *U.*
423 *intestinalis* (green) and *F. lumbricalis* (red) to be stimulated by CO₂ addition, while *F. vesiculosus*
424 (brown) showed no response. Of three species studied, *U. intestinalis* showed the highest
425 stimulation by CO₂. In a second 3-days study, Pajusalu et al. (2016) found the fertilization effect on
426 *F. lumbricalis* to depend on interactions with other environmental factors such as temperature and
427 light. Another green alga, *Ulva prolifera*, showed increased vegetative growth when subjected to
428 low salinity and low pH, but at the same time reproductive cell growth declined (Lin et al., 2011). In
429 another study, OA increased photosynthesis (measured as electron transport rate) in *U. prolifera*,

430 but at the same time caused increased non-photochemical quenching, indicating lower tolerances
431 to high irradiance as energy-dissipating CCM was downregulated in high CO₂ treatment (Liu et al.,
432 2012). If species within green algae genus respond differently to OA, this may change outcome of
433 competitive interactions in the upper littoral zone. For example, more shade-adapted, opportunistic
434 *Ulva procera*, which is frequently observed in the *Cladophora* belt during summer (Choo et al.,
435 2005), secretes H₂O₂, which reduces photosynthesis of competing macroalgae such as *C. glomerata*
436 (Choo et al., 2005), and secretion of such halocarbons depend on temperature and carbon
437 availability (Abrahamsson et al., 2003; Choo et al., 2004).

438 The brown alga *F. vesiculosus* was the most intensively studied species in our screening with 7
439 studies found (Table 2, Table S1). These investigations provided contradicting results, some studies
440 indicating no (Pajusalu et al., 2013) or very weak (Werner et al., 2016) response to acidification.
441 Three studies (Al-Janabi et al., 2016b; Gutow et al., 2014; Werner et al., 2016) found negative
442 responses; however, in the last study CO₂ treatment was coupled with elevated temperature, which
443 the authors interpreted to be driving the decline in *Fucus* biomass (Werner et al., 2016). In a 4-week
444 experiment in Helgoland, North Sea, Gutow *et al.* (2014) found that in atmospheric CO₂ of 700 µatm
445 compared to present atmospheric level, *F. vesiculosus* growth was reduced by 10-15 % and the C:N
446 ratio was lower. Two studies (Al-Janabi et al., 2016a; Nygård and Dring, 2008) found potentially
447 beneficial effects. In Kiel Fjord, Southern Baltic Sea, OA was found to increase survival of *F.*
448 *vesiculosus* germlings in spring and growth during summer, but no interaction with elevated
449 temperatures was observed (Al-Janabi et al., 2016a). In a laboratory setting, increasing DIC content
450 (but with constant pH) in seawater was found to increase growth and photosynthesis in mature *F.*
451 *vesiculosus* thalli, and effects of DIC were additive with nutrient increase (Nygård and Dring, 2008).

452 The extrapolation of results from laboratory experiments to nature has numerous challenges, and
453 the contradicting results described above may arise from interplay between other environmental
454 variables such as nutrients and light (Celis-Plá et al., 2015; Verspagen et al., 2014). If photosynthesis
455 is limited by nutrient availability, carbon increase in the form of OA would have only minor effect
456 (Verspagen et al., 2014), but if ample nutrients and carbon are provided, photosynthesis should
457 increase, given no light limitation ensues (Verspagen et al., 2014). As light energy is used to convert
458 inorganic carbon to photosynthates, algae may respond to increases in carbon availability by
459 altering photobiological mechanisms. For example, the increased photochemical quenching in *U.*
460 *prolifera* observed by Liu et al. (2012), coupled with lower light requirements may indicate that the
461 plant downregulates light utilization as a response to increased carbon availability. Although
462 macroalgae have been proposed to benefit from OA through improved energetics through CCM
463 downregulation (Koch et al., 2013), this may under high irradiances lead to increased
464 photoinhibition, as CCMs acts as a sink for excessive energy (Liu et al., 2012; Wu et al., 2010). Thus,
465 the OA impacts on Baltic macroalgae expectedly will depend on interactions with nutrient and light
466 availability. In general, OA has been observed to have positive effects on photoautotroph growth
467 and photosynthesis under low irradiance, but negative under high irradiance (Gao et al., 2012). If
468 eutrophication will increase in the future Baltic, also underwater light conditions will deteriorate, as
469 increased turbidity is one of the main consequences of eutrophication. Thus to some extent, OA
470 may benefit some species inhabiting the low irradiance environments in the coastal zone, and
471 potentially could counter some of the adverse effects of eutrophication, if macroalgae are able to
472 photosynthesize more efficiently under low irradiance conditions.

473 The coastal ecosystems of the Baltic Sea have naturally high diurnal and seasonal pH fluctuations
474 caused by photosynthesis (Middelboe and Hansen, 2007) and upwelling of CO₂-rich water (Saderne
475 et al. 2013). An upwelling event recorded September 2011 caused pH to decline from 7.7 (day) to

7.26 (night) in a macrophyte meadow at Eckenförde Bay, Germany (Saderne et al., 2013). The expected future drop in global ocean pH of 0.4 units by the end of the century (Feely et al., 2009) is in the same order of magnitude as the amplitudes in diurnal pH fluctuations (0.34 units, August and 0.3 - 0.4 units, May) observed by Saderne et al. (2013) and Middelboe & Hansen (2007) in the Baltic macrophyte ecosystems. Photosynthesis of several macroalgae, including *Ulva* spp. and *F. vesiculosus*, was measured by Middelboe and Hansen (2007) in pH 8 and 9.3 with several DIC concentrations. All species were able to utilize DIC pool more efficiently in lower pH, showing significantly higher rates of photosynthesis.

Annual pH fluctuations measured in Baltic macroalgal habitats in Denmark may exceed 1 units (Middelboe and Hansen, 2007). High pH (~9) occur frequently in spring, summer and autumn, when photosynthetic activity removes carbon from seawater, and is contrasted by lower pH values (~8) in winters (Middelboe and Hansen, 2007). The stochastic upwelling of CO₂-rich water may shortly disrupt this pattern (Saderne et al., 2013), and with future climate change, the intensity of such pulses might increase as the deep waters absorb more atmospheric carbon (Omstedt et al., 2012). As seagrass and macroalgal habitats frequently maintain high pH, they may act as sanctuary habitats against ocean acidification, and increase their importance for especially calcifying species and their juvenile stages. The seasonal fluctuations of pH, light and nutrients mediate the effects of ocean acidification on macroalgae and other organisms and should also be taken into consideration when results of ocean acidification laboratory experiments are extrapolated to natural ecosystems.

5.5 Intensifying eutrophication

As the effects of eutrophication on Baltic macroalgae and coastal ecosystems in general have been covered in different studies in recent decades (Andersen et al., 2017; Kautsky, 1991; Kautsky and Kautsky, 1986; Middelboe and Sand-Jensen, 2000) , we do not address all these effects in detail

499 here, but only briefly reflect on the results of our literature search. Based on our results, the green
500 algae as a group will clearly benefit from intensifying eutrophication (Table 2, Table S1), together
501 with many red algal species, which, in contrary to our expectations, were quite tolerant against
502 eutrophication and also against subsequent increases in sedimentation. Two brown algae
503 associated with filamentous algae blooms, *P. littoralis* and *E. siliculosus*, showed positive responses.
504 Most of the studies (N = 30) we found quantified either direct or indirect negative effects of
505 eutrophication on the foundation species *F. vesiculosus* (Table 2).

506 5.6 Multiple drivers and biotic interactions

507 Many studies assessing climate change impacts on marine organisms are short-term and manipulate
508 only one single species and factor of interest (Forsman et al., 2016; Wernberg et al., 2012), often
509 with limited duration (Forsman et al., 2016). In reality, various abiotic components of climate
510 change, such as salinity, temperature, and pH interact influencing the complex biotic community,
511 often under simultaneous non-climatic stressors. Changes in abiotic conditions may alter species
512 interactions leading to rapid changes in abundance. When several abiotic factors change
513 simultaneously, the resulting effects are difficult to predict. We exemplify this with the example of
514 the brown filamentous alga *P. littoralis* (Fig. 2), which frequently forms drifting algal mats. *P.*
515 *littoralis* seems tolerant to salinity declines (Bergström and Bergström, 1999; Munda, 1999; Russell,
516 1994), but being a cold-water species might suffer from temperature increases, and in artificially
517 heated areas has been replaced by the sibling species *E. siliculosus* (Keskitalo and Heitto, 1987;
518 Keskitalo and Ilus, 1987). Such declines of *P. littoralis* with increasing temperatures would remove
519 the competitive exclusion pressure on *Ulva* spp. (Lotze et al., 1999), potentially leading to more
520 frequent blooms of *Ulva* spp. in late spring. But *P. littoralis* could also benefit from warming, if ice
521 cover declines result in more light for photosynthesis during early spring when surface water is still

522 cold. This could shift the peak abundance of *P. littoralis* earlier in spring, which would have
523 important implications for other species, including reproduction and settlement of fucoids and
524 other algae (Berger et al., 2003; Kraufvelin et al., 2007).

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526 Figure 2. Interacting climate-change related effects on *Pylaiella littoralis*. Blue boxes indicate climate change related
527 external processes. Gray solid lines indicate positive, black solid lines negative and light gray dashed lines unknown
528 effects.

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530 We did not find any studies discussing OA effects on *P. littoralis* nor any information regarding its
531 carbon acquisition physiology, so the OA effects remain unknown. *P. littoralis* is strongly favoured
532 by eutrophication (Table 2), and hence increased nutrient input predicted for the future (Meier et
533 al., 2012b) may intensify *P. littoralis* blooms when water temperature remains optimal for the
534 species. Although OA responses could not be identified, it is possible that OA would favor *P. littoralis*
535 in similar way as other species under moderate irradiance (see above). As underwater light
536 environment may further deteriorate by intensifying eutrophication, this kind of conditions may be
537 more abundant in the future.

538 The eventual responses to eutrophication are influenced by grazing (Lotze and Worm, 2000), while
539 grazers themselves are affected by abiotic changes (Hørlyck, 1973; Łapucki and Normant, 2008; Roth
540 et al., 2010). Grazing on *P. littoralis* also intensifies grazing on fucoids as the juveniles thriving on
541 filamentous algae move to feeding on fucoids when reaching adulthood (Orav-Kotta and Kotta,
542 2004). Besides grazing, *P. littoralis* is also affected by shading epiphytes, especially by diatoms which
543 have varying tolerances to salinity (Snoeijs, 1995). *P. littoralis* has nonetheless been shown to have
544 good potential for adaptation to new habitats and changing environmental conditions through
545 emergence of local ecotypes (Bolton, 1979; Russell, 1994), but the evolutionary time required for
546 such changes remains unknown.

547 Similar interacting, synergistic and/or competing effects have been more extensively studied for
548 *Fucus vesiculosus*. For example, increased temperature has been observed to have synergistic

549 effects with low salinity and elevated nutrient concentrations, and may either intensify or decrease
550 grazing pressure (reviewed in Wahl *et al.*, 2011). Experiments with longer exposure times and
551 multiple drivers should be conducted for other key species also, as the existing literature at present
552 seems to be strongly biased on studies on fucoids, more specifically *F. vesiculosus* (Table 2).

553 5.7 Adaptation

554 When a species is exposed to environmental change, a potential evolutionary change will take
555 several generations. In the context of climate change this may happen rapidly, if there is a strong
556 selection pressure for genotypes carrying suitable alleles (Jump and Penuelas, 2005; Parmesan,
557 2006). Capability of adaptation then depends highly on variation in genes responsible for climate-
558 related traits in any given population (Jump and Penuelas, 2005). Generally, very few examples of
559 genetic adaptation attributed to climate change exists across taxa (Merilä and Hendry, 2014), many
560 adaptive responses in marine organisms being plastic rather than genetic (Collins *et al.*, 2014;
561 Reusch, 2014). Some genetic adaptations to heat (Padfield *et al.*, 2016) and ocean acidification
562 (Lohbeck *et al.*, 2012; Scheinin *et al.*, 2015) have been identified for phytoplankton, but macroalgae
563 with long life-span and generation times are challenging organisms for such studies. However, being
564 sessile organisms macroalgae live in constantly fluctuating environmental conditions and thus
565 possess high intrinsic plasticity (Charrier *et al.*, 2012; Ensminger *et al.*, 2005), which may allow some
566 tolerance against adverse environmental conditions.

567 On one hand bottle necks and founder effects have resulted in overall low genetic variability in Baltic
568 populations (Johannesson *et al.*, 2011), and harsh environmental conditions have resulted in many
569 macroalgae reproducing asexually (Kostamo and Mäkinen, 2006; Tatarenkov *et al.*, 2005). These factors point
570 to low capacity for evolutionary adaption. Yet the Baltic has evolved ecotypes well adapted to local conditions
571 over millennia (Russell, 1985), with subsequent emergence of Baltic ecotypes tolerant of low salinity

572 (Gylle et al., 2009; Johansson et al., 2003; Kostamo et al., 2011; Rueness and Kornfeldt, 1992;
573 Russell, 1994, 1988) and temperature (Nygård and Dring, 2008; Thomas et al., 1988), and also the
574 emergence of an endemic fucoid, *F. radicans*, which has been interpreted as an adaptation to low
575 salinity (Pereyra et al., 2009). Given the speed of observed (Belkin, 2009) and projected (Meier et
576 al., 2012b; Omstedt et al., 2012) environmental change, the potential for similar adaptations in the
577 context of climate change is uncertain. Although some studies on genetic variability in Baltic
578 macroalgae have been conducted (e.g. Leskinen et al. 2004, Tatarenkov et al. 2007), there is very
579 limited knowledge on size of genetic variability related to quantitative traits selected upon in times
580 of rapid environmental change, which makes assessing adaptive capacity difficult.

581 **6 Conclusions**

582 Summarizing the effects of the different drivers, the combined effects of climate change for
583 macroalgal communities in the Baltic appear similar and additive to those of anthropogenic nutrient
584 increase: elevated primary production and increased abundance of filamentous algae. Climate
585 change will elevate primary production in the littoral ecosystem directly, and through increased
586 nutrient emissions provided by increased river inflow. We illustrate the overall expected responses
587 of macroalgae on abiotic changes in a conceptual model (Fig. 3).

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Figure 3. Conceptual model of expected responses in the macroalgae community. Blue boxes (italics) indicate external climate-change related processes, white boxes indicate responses on the ecosystem level, pink boxes expected responses of the macroalgae community, and gray boxes consequences for other species and the littoral ecosystem. Increases in a process are indicated by + sign and solid box, decreases with - sign and dashed box, respectively.

Effects of OA on macroalgae remain uncertain, but may potentially increase primary production, especially in red algae. If OA stimulates photosynthesis and growth of phytoplankton (Brading et al., 2011; Sandrini et al., 2016; Scheinin et al., 2015), underwater light conditions could potentially

deteriorate even further from what is expected based on eutrophication scenarios, causing decreased depth penetration of macrophytes. On the other hand, if effects of OA on macroalgal photosynthesis in low light are positive (see above), this may provide some compensation against eutrophication-caused light limitation.

Put together, declining salinity, elevated temperature and increases in nutrient concentrations all strongly favor green, filamentous algae (Table 2). Red algae appear tolerant against eutrophication, but will be negatively affected by low salinity, as they contain more marine species with lower salinity tolerances. Among brown algae, filamentous species such as *E. siliculosus* that benefit from eutrophication, are tolerant against low salinity, and are tolerant or favored by warming, are clearly “future winners”, whereas fucoids will likely decline. The reason for this is their low tolerance of eutrophication and mostly harmful direct and indirect effects of warming (Table 2). Although we found some evidence of local population resilience against low salinity, the declining size of individuals, with the loss of genetic diversity in these conditions suggests that for the fucoids the likely outcome is negative. As they are linked with large number of associated species, their possible decline would have serious biodiversity impacts in coastal ecosystems. Although green algae such as *C. glomerata* may maintain dense faunal populations during summer (Kraufvelin and Salovius, 2004), they lack the year-round persistence of fucoids. Thus through potential loss of foundation species such as *F. vesiculosus*, the structural complexity and annual habitat availability would be severely reduced. If *F. vesiculosus* is lost from the ecosystem, also grazing pressure may intensify on remaining species (Kotta et al., 2000). If green algae proliferate extensively, consequences to benthic fauna are severe as decomposing algae deplete oxygen, leading to severe decreases in faunal abundance, as has been observed in eutrophied conditions (Berezina et al., 2016).

619 With changes in temperature and salinity conditions, not only the existing interspecific interactions
620 will change, but also the resilience against invasive species, including macroalgae, may diminish in
621 Baltic ecosystems. Invasive species have been identified as one of the major threats to the Baltic
622 ecosystem (Elmgren, 2001). The warmer and less saline conditions in the future may make the Baltic
623 ecosystem more hospitable to a number of potential invaders (Holopainen et al., 2016) especially
624 from estuarine conditions, which could easily transgress the salinity and temperature barriers by
625 traveling via e.g. commercial shipping ballast waters.

626 Although the temperature and salinity tolerances have been investigated for the most abundant
627 macroalgal species in the context of evolutionary adaptation, the interactions between different
628 drivers have only been studied in fucoids (Wahl et al., 2011) despite the importance of the issue
629 (Koch et al., 2013). In the Baltic Sea the stressors connected to climate change are interacting with
630 eutrophication, hence it is important to investigate the combined effects of salinity, temperature,
631 CO₂ and nutrient concentrations at least on the habitat forming species. In different stages of
632 macroalgal life cycle the environmental conditions may vary widely and this natural variability
633 should be incorporated in the experimental design when planning research campaigns (Wahl et al.,
634 2016). Although in experiments, the projected changes in climatic variables are often simulated
635 through changes in the mean (Boersma et al., 2016), it is frequently extremes that are driving
636 changes in biological systems (Parmesan, 2006). Currently the Baltic macroalgae have to tolerate
637 highly variable biotopes, especially in relation to annual fluctuations in pH and temperature, but
638 the future shifts will likely be accompanied with an increased frequency of climatic events classified
639 as “extreme” (Neumann et al., 2012; Solomon, 2007) exceeding the conditions they are adapted to.
640 Multiple stressors may often cause synergistic effects (Wahl et al., 2011) increasing the likelihood
641 of surpassing a critical tolerance threshold in the future, which should also be considered in
642 planning future research.

Very few CO₂ fertilization experiments have been performed on Baltic macroalgae, with mixed results making it hard to extrapolate to the future. Longer experiments (but see Al-Janabi et al., 2016a, 2016b) with well-designed methods for producing the predicted future ocean chemistry (Hurd et al., 2009) should be applied on a wider spectrum of species. In these settings, also other environmental factors such as irradiance, nutrient levels and temperature should be included, as these all may influence the responses of primary producers against OA.

The coastal states of the Baltic have limited capacities in stopping or mitigating climate change, and it is therefore important to identify adaptation strategies which maximize the resilience of coastal ecosystems. Since the impacts of climate change intensify those of coastal eutrophication, controlling nutrient emissions is a feasible adaptation strategy in the future, especially since the cost-effectiveness of nutrient emission reductions has been widely studied. As macroalgal beds are environments that can act as buffers against OA as they elevate water pH through photosynthesis (Middelboe and Hansen, 2007), protecting them will also yield benefits for associated species, such as calcifiers, which may be more vulnerable against acidification.

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