Climate change can cause complex responses in Baltic Sea macroalgae: A systematic review

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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 (Airoldi et al., 2008; Eriksson et al., 2006). Macrolgal 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).
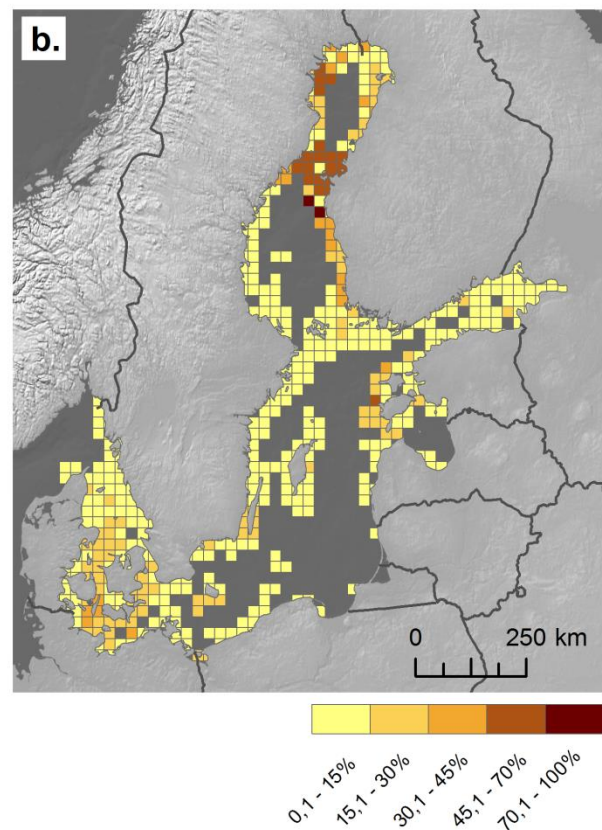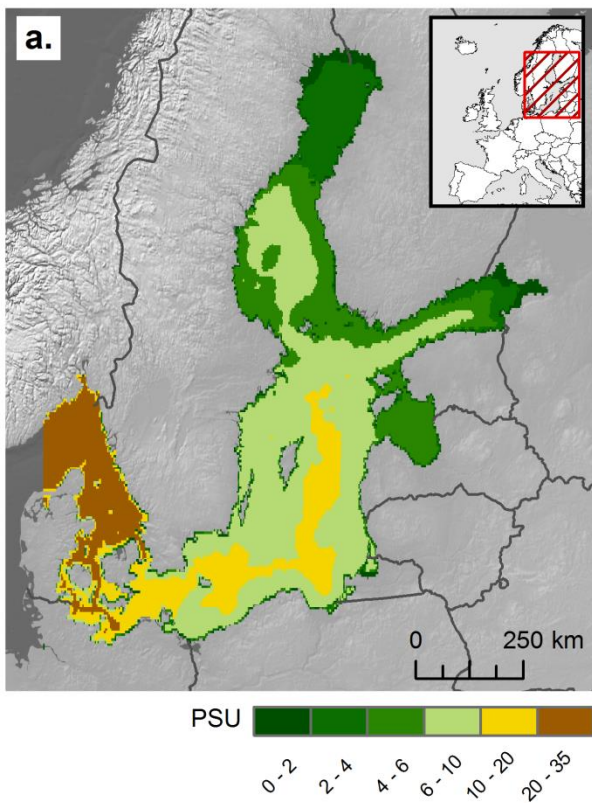
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61 Fig. 1 a) Current salinity distribution of the Baltic Sea b) abundance of photic hard bottoms, the potential habitat for the

62 macroalgae. Values are percentages of photic hard bottoms in relation to total bottom area. Data source: a) EUSeaMap

63 (Cameron and Askew, 2011) b) Benthic biotope complexes in the Baltic Sea (HELCOM, 2010).

64 In the Baltic coastal zones, the habitat-forming macroalgae are the foundation species in rocky shore

65 ecosystems, which are the prevalent shore types in the northern and western archipelago areas

66 (Hällfors et al. 1981, Fig. 1b). The vertical zonation of algal species creates a structurally complex

67 habitat, which is important for both juvenile fish and small invertebrates, thus harboring a large

68 fraction of biodiversity in the Baltic coastal ecosystems (Hällfors et al., 1981; Kautsky et al., 1992).

69 Especially the perennial, habitat-forming species have suffered from coastal eutrophication, causing

70 declines in abundance and depth penetration during the 20th century (Kautsky and Kautsky, 1986).

71 Eutrophication has also favoured fast-growing, filamentous species, which has culminated in the

72 emergence of drifting, decomposing algal mats destroying soft-bottom communities (Norkko and

73 Bonsdorff, 1996).

74 While in oceanic areas climate change has been projected to cause northward shifts in macroalgal

75 distributions (Müller et al., 2009), the patterns are different in the Baltic. Declining salinities (Meier

76 et al., 2012a) may counteract the general trends, pushing the distributions of marine-originated

77 species towards south (Vuorinen et al., 2015). This, together with other interacting human impacts

78 makes the Baltic macroalgae particularly interesting study organisms for climate change ecology. As

79 the northern and western shores and archipelagos of the Baltic contain large fraction of the suitable

80 shores for macroalgae, we focus our review on dominant species occurring in these areas.

81 **2 The changing abiotic conditions in the Baltic Sea**

82 The sea surface temperature (SST) of the Baltic has warmed rapidly during recent decades. Siegel

83 *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

96   al., 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 CO_2 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 CO_2 increases the concentrations of dissolved inorganic

152   carbon (DIC), and changes the relative abundances of DIC components: increased levels of dissolved

153 aquatic CO_2 and bicarbonate (HCO_3^-), and reduced levels of carbonate (CO_3^{2-}). The highest relative

154 increase will be in CO_2, which will increase by 250 % if atmospheric CO_2 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

165   Table 1. Main characteristics of macroalgal community of the Baltic

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 an depth penetration of habitat-forming species such as fucoids (Kautsky and Kautsky, 1986; Lehvo and Bäck, 2001)

166

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).

9

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

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

"Harmful" responses to Ocean Acidification were cases of declining growth, photosynthesis or increased photoinhibition in the laboratory, or decreased abundance under low pH condition in the field. "Tolerant" responses were cases where no effects or changes in abundance were observed, and "Beneficial" positive responses or increased abundance. OA was the only variable for which the category "potentially beneficial" was used. In these cases, experimental responses indicated either positive responses against OA treatment in only a particular season, positive photosynthesis response when total inorganic carbon was increased, or indication of reliance on free CO_2 in carbon acquisition, which could potentially lead to positive effects under elevated CO_2 levels (Koch et al., 2013).

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

223 recruitment, growth or abundance were observed under eutrophication, and "beneficial" if the

224 abundance of the species increased under eutrophic conditions.

225

226 **5. Results - Impacts of climate change on Baltic macroalgae**

227 For the selected species, a total of 3042 papers were found from the Web of Knowledge. Of these,

228 128 papers contained information over the variables studied here (Table 2, Table S1). Here, a

229 summary of the responses is provided (Table 2), exact literature references for the responses are

230 given in supplementary material (Table S1).

231 Table 2. Responses of key macroalgal species to expected abiotic changes. Number of papers found relating to response

232 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							
Hildenbrandia rubra	20	4	Perennial, encrusting	Tolerant (1)	Tolerant (3)	Beneficial (1)	
Coccotylus truncatus syn. *Phyllophora brodiaei*, *P. truncata*	23	4	Perennial, foliose	Beneficial (1)	Tolerant (1)	Potentially beneficial (1)	Tolerant (1)
Furcellaria lumbricalis	61	8	Perennial, dichotomous, corticated	Beneficial (2)	Harmful (3)	Beneficial (2)	Tolerant (2)
Ceramium tenuicorne	35	7	Annual, filamentous, partial cortication	Harmful (1)	Tolerant (5)		Beneficial (1) Harmful (1)
Ceramium virgatum syn. *C. rubrum*, *C. nodulosum*	24 59	0	Annual, filamentous, corticated				
Polysiphonia fucoides syn. *P. nigrescens*	22 7	4	Perennial, polysiphonous		Harmful (2)		Beneficial (1) Tolerant (1)
Polysiphonia fibrillosa syn. *P. violacea*	3 6	2	Annual, polysiphonous		Harmful (2)		
Rhodomela confervoides	73	4	Annual, corticated		Tolerant (2) Harmful (1)		Beneficial (1)
BROWN ALGAE							

Species			Description				
Pylaiella littoralis often misspelled *Pilayella littoralis*	103 93	10	Annual, filamentous uniseriate	Harmful (2)	Tolerant (4)		Beneficial (4)
Ectocarpus siliculosus	342	10	Annual, filamentous uniseriate	Tolerant (2) Beneficial (1)	Tolerant (2) Harmful (1)		Beneficial (4)
Elachista fucicola	13	0	Annual, filamentous uniseriate				
Eudesme virescens	3	1		Beneficial (1)			
Pseudolithoderma spp.	11	0	Perennial, encrusting				
Dictyosiphon foeniculaceus	11	0	Cylindrical, branched thallus				
Stictyosiphon tortilis	2	1	Cylindrical, branched thallus				Harmful (1)
Scytosiphon lomentaria	130	4	Annual, tubular, often regular constrictions	Tolerant (3)	Tolerant (1)		
Chorda filum	33	3	Annual, strapshaped multicellular thallus	Tolerant (1) Harmful (1)	Tolerant (1)		
Fucus vesiculosus	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)
Fucus radicans	11	2	Perennial, multicellular thallus with differentiated cell structures	Harmful (2)	Tolerant (1)		

GREEN ALGAE

Species			Description				
Ulva flexuosa syn. *Enteromorpha flexuosa*	9 18	6	Annual, tubular	Beneficial (3)	Tolerant (2)		Beneficial (3)
Ulva intestinalis syn. *Enteromorpha intestinalis*	24 90	26	Annual, tubular	Beneficial (6)	Tolerant (7) Harmful (1)	Beneficial (1)	Beneficial (11)
Ulva linza syn. *Enteromorpha ahleriana*	38 1	10	Annual, tubular	Beneficial (6) Tolerant (1)	Harmful (2) Tolerant (1)		Beneficial (2)
Ulva prolifera syn. *Enteromorpha prolifera*	99 71	11	Annual, tubular	Beneficial (2)	Tolerant (4)	Potentially beneficial (1) Harmful (1)	Beneficial (4)
Ulothrix subflaccida	1	3	Annual, filamentous uniseriate	Harmful (1)	Tolerant (2)		
Ulothrix zonata	11	0	Annual, filamentous uniseriate				

13

Species			Type				
Monostroma grevillei syn. *Ulvopsis grevillei*	40	2	Annual, filamentous uniseriate	Harmful (2)	Harmful (1)		
Urospora penicilliformis	5	1	Annual, filamentous uniseriate		Tolerant (1)		
Cladophora aegagropila	3	1	Annual, filamentous uniseriate		Beneficial (1)		
Cladophora fracta	7	0	Annual, filamentous uniseriate				
Cladophora glomerata	112	15	Annual, filamentous uniseriate	Beneficial (6) Tolerant (2)	Beneficial (3) Tolerant (2) Harmful (1)		Beneficial (3)
Cladophora rupestris	22	3	Annual, filamentous uniseriate	Tolerant (1)	Harmful (2) Tolerant (1)		

233

5.1. Temperature and light: direct physiological effects

235 In oceans, temperature is one of the most important determinants for the geographic ranges of

236 macroalgal species (Eggert, 2012), and elevated temperatures expectedly shift macroalgal

237 distributions towards the poles (Jueterbock et al., 2013; Müller et al., 2009; Nicastro et al., 2013).

238 However, in the Baltic Sea scale, species distributions are mainly controlled by salinity gradient

239 (Eriksson and Bergström, 2005; Nielsen et al., 1995; Schubert et al., 2011), and thus the exact effects

240 of temperature increases on species' distributions are hard to predict, although some studies

241 suggest northward shift of fucoid distributions (Leidenberger and Giovanni, 2015). Elevated

242 temperature has a direct control over many phenological processes. Increased temperature, in the

243 form of mild winters, has been shown to accelerate receptacle growth of *F. vesiculosus,* causing

244 earlier reproduction in the Baltic Sea (Kraufvelin et al., 2012). Ice-free winters may allow also the

245 perennial species to grow in the filamentous algal zone near the surface, if disturbance from ice

246 scraping is missing (Kiirikki, 1996). Temperature effects also depend on local habitat features and

247 may be especially pronounced on e.g. sheltered sites (Gubelit, 2015).

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

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

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

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

5.2. Temperature and light: Ecosystem-level changes

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

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

293   Future warming of the Baltic is coupled with changing light conditions, as the sea ice range and

294   duration decreases (Neumann, 2010) and there is more light available for the onset of growing

295   season in early spring, which may affect phenology of many species (Kraufvelin et al., 2012, 2007).

296   However, the input of organic material into Baltic has been predicted to increase (Meier et al.,

297   2012b) resulting in deteriorating underwater light conditions, which may narrow the macroalgal

298   zones towards the surface, as observed in eutrophic conditions (Kautsky and Kautsky, 1986; Rinne

299   et al., 2011). Increased organic matter increases sedimentation, which impedes macroalgal

300   growth, especially the recruitment of *Fucus* spp. (Eriksson & Johansson, 2003, 2005; Isæus *et al.*,

301   2004, Table 2).

302   *5.3. Responses to low salinity*

303   Based on our literature search, the red algae on average had lowest salinity tolerances, followed by

304   brown algae (Table 2). Green algae contained many species which were very tolerant of low

305   salinities or would actually be expected to benefit from low salinity (Table 2). This pattern is in

306   accordance with physiological tolerance ranges obtained through laboratory experiments (Larsen

307   and Sand-Jensen, 2006) and observed species distributions in field surveys (Bergström and

308   Bergström, 1999).

309   Although Baltic macroalgae have adapted to brackish water, and have generally very high tolerance

310   against low salinity (Larsen and Sand-Jensen, 2006), many species have not been able to inhabit the

311   inner parts of the Baltic Sea (Nielsen et al., 1995; Snoeijs, 1999), and the perennial species of marine

312   origin are absent from regions with lowest salinities (Eriksson and Bergström, 2005). One of the

313   reasons is a failure to reproduce in low salinities. The northern and eastern ranges of *F. vesiculosus*

314   in the Baltic have been suggested to depend on the osmotic tolerance of the gametes (Serrão et al.,

315   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. vecisulosus* 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 CO$_2$ fertilization*

The macroalgal photosynthesis is mainly C_3-based (Koch et al., 2013) and utilizes RuBisCO, which is the core enzyme in fixing organic carbon (Raven et al., 2008). Diffusion of CO_2 in water is several orders of magnitude lower than in air (Falkowski and Raven, 2007), which means that photoautotrophs may easily become carbon limited, if they only rely on passive diffusion for their carbon acquisition. Most macroalgae use dissolved CO_2 as a source of inorganic carbon (Koch et al., 2013). Carbon uptake by photosynthesis may cause high local fluctuations of pH and depletion of free dissolved CO_2 (Hurd et al., 2009; Middelboe and Hansen, 2007). To overcome this problem, most macroalgae have evolved carbon concentrating mechanisms (CCMs), which increase CO_2 concentration at the site of RubisCO activity (Koch et al., 2013; Raven et al., 2008). This may involve active uptake and transport of CO_2 or HCO_3^- (Raven et al., 2008), or secretion of H^+ to enhance dissociation of HCO_3^- to CO_2 (Koch et al., 2013), but with an energetic cost related to the transport, secretion and maintenance/production of the cellular machinery involved (Raven et al., 2014). Species using bicarbonate convert HCO_3^- to CO_2 either using intracellular or periplasmic carbonic anhydrases (CA) or CCMs (Hurd et al., 2009). Many macroalgal species use CCMs facultatively at low CO_2 concentrations (Koch et al., 2013). Species lacking CCMs are often found in high-flow environments, where currents replenish the CO_2 pool near the plant, or in low-light environments, where overall photosynthesis rates are low, and species do not have the energy to utilize CCMs (Koch et al., 2013).

Since usage of CCMs is energetically limited (Hurd et al., 2009; Raven et al., 2011), in most macroalgal species studied so far photosynthesis appears unsaturated in current ocean DIC concentrations despite possessing HCO_3^- -based CCMs (Koch et al., 2013). This implies that increasing atmospheric CO_2 concentration could have a positive impact on macroalgal photosynthesis through improved carbon uptake energetics (Raven et al., 2011). However, results

407 from CO_2 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 CO_2 diffusion (Snoeijs et al., 2002), and thus would

412 benefit more from the increased CO_2 availability, in contrary to species utilizing efficient CCMs,

413 which frequently grow in high irradiances where CO_2 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 CO_2 (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 CO_2 addition, while *F. vesiculosus*

424 (brown) showed no response. Of three species studied, *U. intestinalis* showed the highest

425 stimulation by CO_2. 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*,

but at the same time caused increased non-photochemical quenching, indicating lower tolerances to high irradiance as energy-dissipating CCM was downregulated in high CO_2 treatment (Liu et al., 2012). If species within green algae genus respond differently to OA, this may change outcome of competitive interactions in the upper littoral zone. For example, more shade-adapted, opportunistic *Ulva procera*, which is frequently observed in the *Cladophora* belt during summer (Choo et al., 2005), secretes H_2O_2, which reduces photosynthesis of competing macroalgae such as *C. glomerata* (Choo et al., 2005), and secretion of such halocarbons depend on temperature and carbon availability (Abrahamsson et al., 2003; Choo et al., 2004).

The brown alga *F. vesiculosus* was the most intensively studied species in our screening with 7 studies found (Table 2, Table S1). These investigations provided contradicting results, some studies indicating no (Pajusalu et al., 2013) or very weak (Werner et al., 2016) response to acidification. Three studies (Al-Janabi et al., 2016b; Gutow et al., 2014; Werner et al., 2016) found negative responses; however, in the last study CO_2 treatment was coupled with elevated temperature, which the authors interpreted to be driving the decline in *Fucus* biomass (Werner et al., 2016). In a 4-week experiment in Helgoland, North Sea, Gutow *et al.* (2014) found that in atmospheric CO_2 of 700 µatm compared to present atmospheric level, *F. vesiculosus* growth was reduced by 10-15 % and the C:N ratio was lower. Two studies (Al-Janabi et al., 2016a; Nygård and Dring, 2008) found potentially beneficial effects. In Kiel Fjord, Southern Baltic Sea, OA was found to increase survival of *F. vesiculosus* germlings in spring and growth during summer, but no interaction with elevated temperatures was observed (Al-Janabi et al., 2016a). In a laboratory setting, increasing DIC content (but with constant pH) in seawater was found to increase growth and photosynthesis in mature *F. 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 CO_2-rich water (Saderne

475   et al. 2013). An upwelling event recorded September 2011 caused pH to decline from 7.7 (day) to

476   7.26 (night) in a macrophyte meadow at Eckenförde Bay, Germany (Saderne et al., 2013). The

477   expected future drop in global ocean pH of 0.4 units by the end of the century (Feely et al., 2009) is

478   in the same order of magnitude as the amplitudes in diurnal pH fluctuations (0.34 units, August and

479   0.3 - 0.4 units, May) observed by Saderne et al. (2013) and Middelboe & Hansen (2007) in the Baltic

480   macrophyte ecosystems. Photosynthesis of several macroalgae, including *Ulva* spp. and *F.*

481   *vesiculosus*, was measured by Middelboe and Hansen (2007) in pH 8 and 9.3 with several DIC

482   concentrations. All species were able to utilize DIC pool more efficiently in lower pH, showing

483   significantly higher rates of photosynthesis.

484   Annual pH fluctuations measured in Baltic macroalgal habitats in Denmark may exceed 1 units

485   (Middelboe and Hansen, 2007). High pH (~9) occur frequently in spring, summer and autumn, when

486   photosynthetic activity removes carbon from seawater, and is contrasted by lower pH values (~8) in

487   winters (Middelboe and Hansen, 2007). The stochastic upwelling of CO_2-rich water may shortly

488   disrupt this pattern (Saderne et al., 2013), and with future climate change, the intensity of such

489   pulses might increase as the deep waters absorb more atmospheric carbon (Omstedt et al., 2012).

490   As seagrass and macroalgal habitats frequently maintain high pH, they may act as sanctuary habitats

491   against ocean acidification, and increase their importance for especially calcifying species and their

492   juvenile stages. The seasonal fluctuations of pH, light and nutrients mediate the effects of ocean

493   acidification on macroalgae and other organisms and should also be taken into consideration when

494   results of ocean acidification laboratory experiments are extrapolated to natural ecosystems.

495   *5.5 Intensifying eutrophication*

496   As the effects of eutrophication on Baltic macroalgae and coastal ecosystems in general have been

497   covered in different studies in recent decades (Andersen et al., 2017; Kautsky, 1991; Kautsky and

498   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. littorali*s 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

cold. This could shift the peak abundance of *P. littoralis* earlier in spring, which would have important implications for other species, including reproduction and settlement of fucoids and other algae (Berger et al., 2003; Kraufvelin et al., 2007).
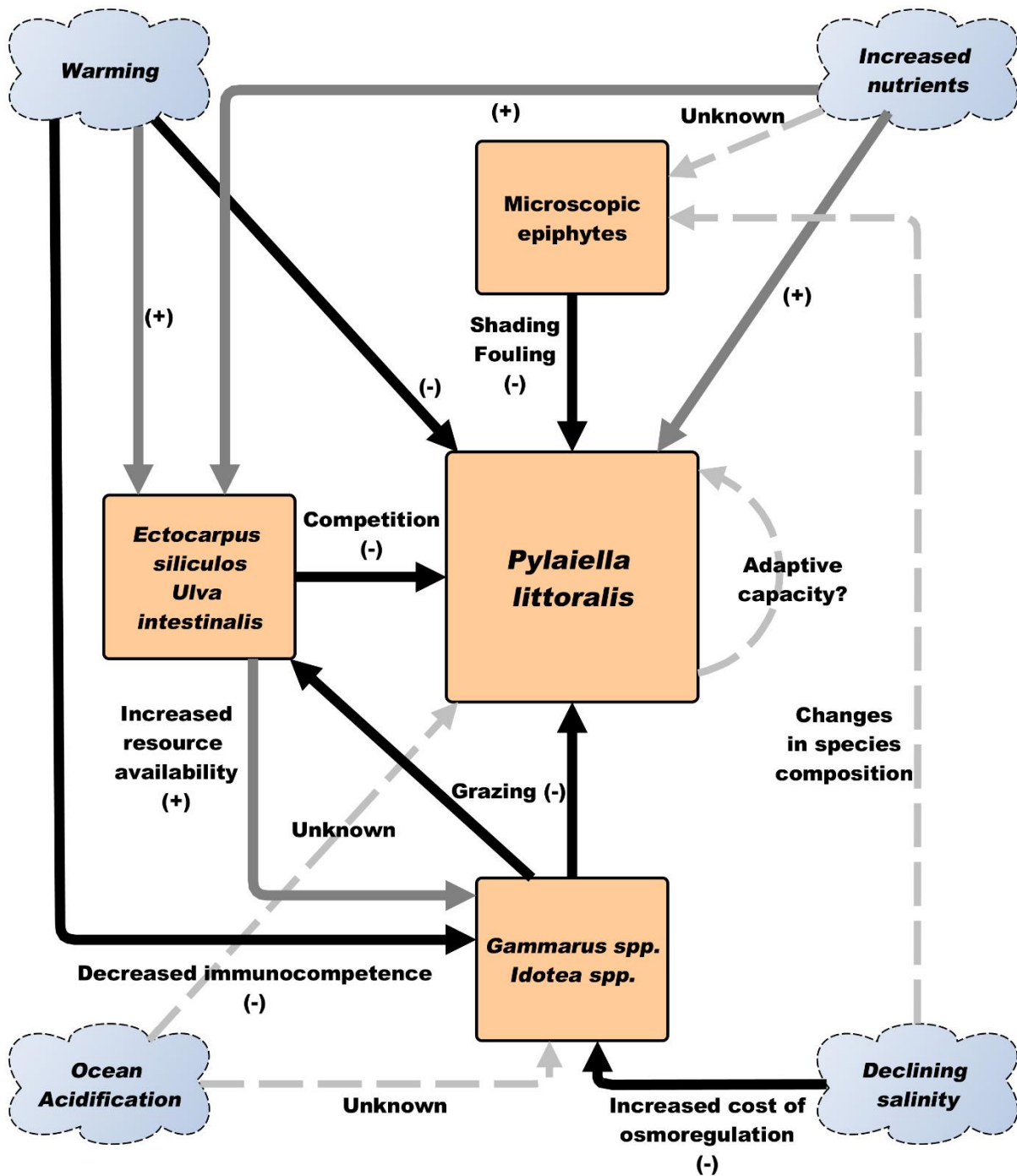
Figure 2. Interacting climate-change related effects on *Pylaiella littoralis*. Blue boxes indicate climate change related external processes. Gray solid lines indicate positive, black solid lines negative and light gray dashed lines unknown effects.

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

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

Similar interacting, synergistic and/or competing effects have been more extensively studied for *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).
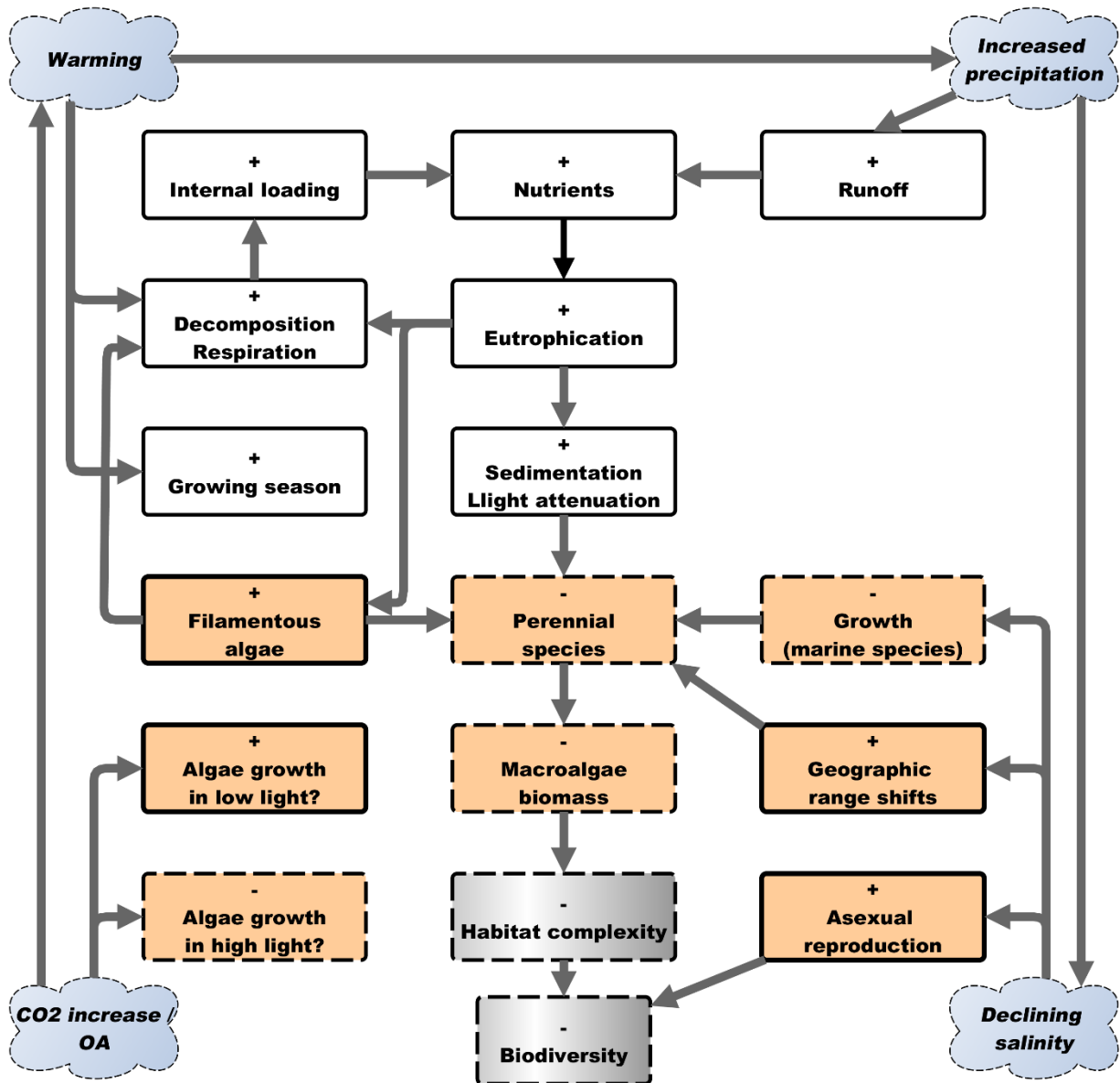
589 Figure 3. Conceptual model of expected responses in the macroalgae community. Blue boxes (italics) indicate external

590 climate-change related processes, white boxes indicate responses on the ecosystem level, pink boxes expected

591 responses of the macroalgae community, and gray boxes consequences for other species and the littoral ecosystem.

592 Increases in a process are indicated by + sign and solid box, decreases with - sign and dashed box, respectively.

593

594 Effects of OA on macroalgae remain uncertain, but may potentially increase primary production,

595 especially in red algae. If OA stimulates photosynthesis and growth of phytoplankton (Brading et al.,

596 2011; Sandrini et al., 2016; Scheinin et al., 2015), underwater light conditions could potentially

597   deteriorate even further from what is expected based on eutrophication scenarios, causing

598   decreased depth penetration of macrophytes. On the other hand, if effects of OA on macroalgal

599   photosynthesis in low light are positive (see above), this may provide some compensation against

600   eutrophication-caused light limitation.

601   Put together, declining salinity, elevated temperature and increases in nutrient concentrations all

602   strongly favor green, filamentous algae (Table 2). Red algae appear tolerant against eutrophication,

603   but will be negatively affected by low salinity, as they contain more marine species with lower

604   salinity tolerances. Among brown algae, filamentous species such as *E. siliculosus* that benefit from

605   eutrophication, are tolerant against low salinity, and are tolerant or favored by warming, are clearly

606   "future winners", whereas fucoids will likely decline. The reason for this is their low tolerance of

607   eutrophication and mostly harmful direct and indirect effects of warming (Table 2). Although we

608   found some evidence of local population resilience against low salinity, the declining size of

609   individuals, with the loss of genetic diversity in these conditions suggests that for the fucoids the

610   likely outcome isnegative. As they are linked with large number of associated species, their possible

611   decline would have serious biodiversity impacts in coastal ecosystems. Although green algae such

612   as *C. glomerata* may maintain dense faunal populations during summer (Kraufvelin and Salovius,

613   2004), they lack the year-round persistence of fucoids. Thus through potential loss of foundation

614   species such as *F. vesiculosus*, the structural complexity and annual habitat availability would be

615   severy reduced. If *F. vesiculosus* is lost from the ecosystem, also grazing pressure may intensify on

616   remaining species (Kotta et al., 2000). If green algae proliferate extensively, consequences to

617   benthic fauna are severe as decomposing algae deplete oxygen, leading to severe decreases in

618   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   CO_2 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.

643 Very few CO_2 fertilization experiments have been performed on Baltic macroalgae, with mixed

644 results making it hard to extrapolate to the future. Longer experiments (but see Al-Janabi et al.,

645 2016a, 2016b) with well-designed methods for producing the predicted future ocean chemistry

646 (Hurd et al., 2009) should be applied on a wider spectrum of species. In these settings, also other

647 environmental factors such as irradiance, nutrient levels and temperature should be included, as

648 these all may influence the responses of primary producers against OA.

649 The coastal states of the Baltic have limited capacities in stopping or mitigating climate change, and

650 it is therefore important to identify adaptation strategies which maximize the resilience of coastal

651 ecosystems. Since the impacts of climate change intensify those of coastal eutrophication,

652 controlling nutrient emissions is a feasible adaptation strategy in the future, especially since the

653 cost-effectiveness of nutrient emission reductions has been widely studied. As macroalgal beds are

654 environments that can act as buffers against OA as they elevate water pH through photosynthesis

655 (Middelboe and Hansen, 2007), protecting them will also yield benefits for associated species, such

656 as calcifiers, which may be more vulnerable against acidification.

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