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

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

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

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

In this study we review climate change impacts on key Baltic Sea macroalgae species. As shallow inland sea, the Baltic is particularly prone to warming, and observed rates of warming at the end of the 20th century have been highest in all of the world’s large marine ecosystems (Belkin, 2009). We utilize both studies that have been conducted with climate change focus, as well as studies that have been conducted on environmental tolerances of key species.
The Baltic Sea is a large, shallow brackish water epeiric sea heavily impacted by human activities. Allegedly one of the biggest threats to the Baltic ecosystem during the 21st century is climate change with predicted declines in salinity and elevated temperatures (Meier et al., 2012a). As the brackish water environment is challenging for both marine and limnic species, the Baltic Sea ecosystem is relatively species-poor, and the species distributions are controlled by a steep salinity gradient. Low salinity and seasonal temperature oscillations cause many species to exist at the edges of their geographic distribution (Hällfors et al., 1981), and towards the northern areas in the Baltic Sea the conditions become more severe in form of shorter growing season, longer ice cover, and declining salinity (Fig. 1a).
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
warming of 0.6 °C between 1985 and early 2000 reported by MacKenzie & Schiedek (2007), who also reported increased frequency of extreme temperatures. MacKenzie & Schiedek (2007) observed the warming of the Baltic and North Sea to be three times higher than the global average. The BACC I report (BACC Author Team, 2008) states warming of air temperatures by 1 °C from the beginning of the 1980s to 2004, while Lehmann et al. (2011) identified warming of 0.5 °C per decade for the northern Baltic, which seems to be warming more rapidly. Finally, Belkin (2009) reported observed warming of SST of 1.35 °C (1982-2006), which was higher than in any other Large Marine Ecosystem in the world, and seven times higher than the observed global warming rate (Belkin, 2009).

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

The eventual impacts of climate change in the Baltic will depend on a multitude of factors, including the realized emissions, sensitivity of climate system to greenhouse gas emissions, stochastic regional climate as well as interactions with other anthropogenic drivers, such as eutrophication. On a broad scale, the mean annual sea surface temperatures of the Baltic have been projected to increase by 2 to 4 °C by the end of century. Higher temperature increases (4 °C) have been projected
for the northern areas such as Bothnian Bay, and more moderate increases (2 °C) for southern areas (HELCOM, 2013).

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

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

In most parts of the Baltic, increased river inflow causes increased nutrient and organic carbon input (Meier, 2006; Meier et al., 2012b), leading to increased nutrient loading, especially in winter, when biological nutrient uptake is absent. Also the remobilization of nutrients stored in the sediments has been predicted to increase as a consequence of elevated temperatures (Meier et al. 2012b, 2012c). However, in the Bothnian Bay, the increased precipitation may lead to more oligotrophic conditions (HELCOM, 2013). The future nutrient loading will depend also on agricultural policy and
the intensity of agriculture in the drainage area, and the policies applied for nutrient emission reductions (Meier et al., 2012c; Seitzinger et al., 2002). The wintertime river inflow will increase in the north coupled with lower and earlier springtime peak flows, which may alter the temporal salinity patterns (BACC Author Team, 2008). The intensity of springtime river flows has been predicted to decrease with declining snow cover, which will also cause the peak freshwater inflow to shift earlier in many areas (HELCOM, 2013).

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

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

Acidification and elevated atmospheric CO₂ increases the concentrations of dissolved inorganic carbon (DIC), and changes the relative abundances of DIC components: increased levels of dissolved
aquatic CO₂ and bicarbonate (HCO₃⁻), and reduced levels of carbonate (CO₃²⁻). The highest relative increase will be in CO₂, which will increase by 250 % if atmospheric CO₂ rises to 1000 ppm (Koch et al., 2013). This will change the carbon availability for photoautotrophs, and may potentially elevate marine primary production (Hurd et al., 2009; Koch et al., 2013).

### 3 Macroalgae in the Baltic Sea

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

<table>
<thead>
<tr>
<th>Macroalgae of the Baltic Sea</th>
</tr>
</thead>
<tbody>
<tr>
<td>• Total 442 macroalgae species observed (Nielsen et al., 1995)</td>
</tr>
<tr>
<td>• The majority of species have colonized Baltic from the Atlantic and have adapted to low salinity (Bäck et al., 1992; Russell, 1985)</td>
</tr>
<tr>
<td>• Biota controlled by salinity gradient, and the number of macroalgae species declines with salinity (Nielsen et al., 1995; Waern, 1952)</td>
</tr>
<tr>
<td>• Fucoids most important habitat-forming species in Baltic Proper (Kautsky et al., 1992; Malm et al., 2001)</td>
</tr>
<tr>
<td>• <em>Fucus vesiculosus</em> is the main habitat-forming species with 90% of plant biomass in hard bottoms (Kautsky and Van der Maarel, 1990)</td>
</tr>
<tr>
<td>• In eastern and southern shores <em>Furcellaria lumbricalis</em> forms important habitats (Bučas et al., 2007)</td>
</tr>
<tr>
<td>• Filamentous algae are major seasonal primary producers with peak abundances in summer (Kautsky, 1995; Kiirikki and Lehvo, 1997)</td>
</tr>
<tr>
<td>• 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)</td>
</tr>
</tbody>
</table>

4. Methods

We selected the species from distributional indexing of Nielsen et al., (1995) from areas with indexes from 4 to 10, consisting of Baltic Proper, Gotland Sea, Estonian coast, Gulf of Finland, Archipelago Sea, Åland Sea and Gulf of Bothnia. As we wanted to focus only on the most ecologically significant species, we selected species that were classified by Nielsen et al., (1995) as “dominant” in any of these areas or “frequent” in most areas. We added to this species list two species frequent in the least saline areas (*Cladophora aegagropila* and *Cladophora fracta*), yielding a total 31 species; 8 from bangiopheceae, 11 fucophyceae, and 12 chlorophyceae (Table 2). Also *Fucus radicans* was added into the species search list as this species was only relatively recently identified as species (Bergström et al., 2005) and thus not included in the indexing of Nielsen et al. (1995).
We searched ISI Web of Knowledge for scientific articles with species scientific name together (operator “and”) with following keywords: “temperature”, “heat shock”, “salinity”, “osmotic stress”, “nutrients”, “eutrophication” and “ocean acidification” from the topic field.

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

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

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

Temperature responses were classified similarly, although here no exact temperature threshold for “elevated” temperature was set. Declining growth or photosynthesis, increased mortality or 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 CO₂ in carbon acquisition, which could potentially lead to positive effects under elevated CO₂ 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
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.

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

| **BROWN ALGAE** | | | | | | | |

recruitment, growth or abundance were observed under eutrophication, and “beneficial” if the abundance of the species increased under eutrophic conditions.
<table>
<thead>
<tr>
<th>Species</th>
<th>Count</th>
<th>Diversity</th>
<th>Habitats</th>
<th>Dominance</th>
<th>Conductivity</th>
<th>Other Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pylaiella littoralis</strong></td>
<td>103</td>
<td>10</td>
<td>Annual, filamentous uniseriate</td>
<td>Harmful (2)</td>
<td>Tolerant (4)</td>
<td>Beneficial (4)</td>
</tr>
<tr>
<td><em>Pilayella littoralis</em></td>
<td>93</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Ectocarpus siliculosus</strong></td>
<td>342</td>
<td>10</td>
<td>Annual, filamentous uniseriate</td>
<td>Tolerant (2)</td>
<td>Tolerant (2)</td>
<td>Beneficial (4)</td>
</tr>
<tr>
<td>Elachista fucicola</td>
<td>13</td>
<td>0</td>
<td>Annual, filamentous uniseriate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Eudesme virescens</strong></td>
<td>3</td>
<td>1</td>
<td>Perennial</td>
<td>Tolerant (2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pseudolithoderma spp.</strong></td>
<td>11</td>
<td>0</td>
<td>Perennial, encrusting</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Dictyosiphon foeniculaceus</strong></td>
<td>11</td>
<td>0</td>
<td>Cylindrical, branched thallus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Stictyosiphon tortilis</strong></td>
<td>2</td>
<td>1</td>
<td>Cylindrical, branched thallus</td>
<td></td>
<td></td>
<td>Harmful (1)</td>
</tr>
<tr>
<td><strong>Scytosiphon lomentaria</strong></td>
<td>130</td>
<td>4</td>
<td>Annual, tubular, often regular constrictions</td>
<td>Tolerant (3)</td>
<td>Tolerant (1)</td>
<td></td>
</tr>
<tr>
<td><strong>Chorda filum</strong></td>
<td>33</td>
<td>3</td>
<td>Annual, strapshaped multicellular thallus</td>
<td>Tolerant (1)</td>
<td>Harmful (1)</td>
<td>Tolerant (1)</td>
</tr>
<tr>
<td><strong>Fucus vesiculosus</strong></td>
<td>1450</td>
<td>53</td>
<td>Perennial, multicellular thallus with differentiated cell structures</td>
<td>Beneficial (5)</td>
<td>Tolerant (5)</td>
<td>Tolerant (2)</td>
</tr>
<tr>
<td><strong>Fucus radicans</strong></td>
<td>11</td>
<td>2</td>
<td>Perennial, multicellular thallus with differentiated cell structures</td>
<td>Harmful (2)</td>
<td>Tolerant (1)</td>
<td></td>
</tr>
</tbody>
</table>

**GREEN ALGAE**

<table>
<thead>
<tr>
<th>Species</th>
<th>Count</th>
<th>Diversity</th>
<th>Habitats</th>
<th>Dominance</th>
<th>Conductivity</th>
<th>Other Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ulva flexuosa</em> syn. <em>Enteromorpha flexuosa</em></td>
<td>9</td>
<td>6</td>
<td>Annual, tubular</td>
<td>Beneficial (3)</td>
<td>Tolerant (2)</td>
<td>Beneficial (3)</td>
</tr>
<tr>
<td><em>Ulva intestinalis</em> syn. <em>Enteromorpha intestinalis</em></td>
<td>24</td>
<td>26</td>
<td>Annual, tubular</td>
<td>Beneficial (6)</td>
<td>Tolerant (7)</td>
<td>Beneficial (11)</td>
</tr>
<tr>
<td><em>Ulva linza</em> syn. <em>Enteromorpha ahleriana</em></td>
<td>38</td>
<td>10</td>
<td>Annual, tubular</td>
<td>Beneficial (6)</td>
<td>Harmful (1)</td>
<td>Tolerant (1)</td>
</tr>
<tr>
<td><em>Ulva prolifera</em> syn. <em>Enteromorpha prolifera</em></td>
<td>99</td>
<td>11</td>
<td>Annual, tubular</td>
<td>Beneficial (2)</td>
<td>Tolerant (4)</td>
<td>Potentially beneficial (1)</td>
</tr>
<tr>
<td>Ulothrix subflaccida</td>
<td>1</td>
<td>3</td>
<td>Annual, filamentous uniseriate</td>
<td>Harmful (1)</td>
<td>Tolerant (2)</td>
<td></td>
</tr>
<tr>
<td>Ulothrix zonata</td>
<td>11</td>
<td>0</td>
<td>Annual, filamentous uniseriate</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Monostroma grevillei
syn. Ulvopsis grevillei

- Annual, filamentous uniseriate
- Harmful (2)
- Harmful (1)

Urospora penicilliformis

- Annual, filamentous uniseriate
- Tolerant (1)

Cladophora aegagropila

- Annual, filamentous uniseriate
- Beneficial (1)

Cladophora fracta

- Annual, filamentous uniseriate

Cladophora glomerata

- Annual, filamentous uniseriate
- Beneficial (6)
- Beneficial (3)
- Tolerant (2)
- Tolerant (2)
- Harmful (1)
- Beneficial (3)

Cladophora rupestris

- 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).
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 *Coccolithus 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; Snoeij 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; Snoeijj 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 (Snoeij 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 (Snoeij 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...
Ruuskanen, 2000), at the Swedish coast the distribution limit is at salinity of 4 (Kautsky et al., 1992). *F. radicans* tolerates lower salinity than *F. vesiculosus*, and its distribution in the Bothnian Sea lies in the salinity range of 3 to 5 (Bergström et al., 2005; Leidenberger and Giovanni, 2015). *F. radicans* reproduces asexually in low salinities (Tatarenkov et al., 2005), and the rapid speciation of *F. radicans* from *F. vesiculosus* has been attributed to low salinity levels (Pereyra et al., 2009). In *F. vesiculosus*, low salinity alters sex ratios, as populations become dominated by female plants in low salinities (Malavenda and Voskoboinikov, 2009). This kind of responses may decrease genetic diversity, and make the local populations more vulnerable to other environmental changes.

Although some studies indicate salinities below 4 psu to be harmful for *F. vesiculosus* (Serrão et al., 1999, 1996), field observations have identified persistence of local populations even in salinities down to 2 psu (Ardehed et al., 2016; Munda, 1999; Ruuskanen and Bäck, 2002), with high rates of sexual reproduction (Ardehed et al., 2016). This indicates that local populations may differ in their salinity tolerance, although the size of *F. vesiculosus* plants decreases rapidly with declining salinity (Bäck, 1993; Bäck and Ruuskanen, 2000; Kalvas and Kautsky, 1998; Ruuskanen and Bäck, 1999).

Inhibition of sexual reproduction occurs also in other species in low salinities. The abundance of the perennial, coarsely branched red alga *F. lumbricalis* declines with salinity (Bergström and Bergström, 1999) and no sexual reproduction was observed in lowest salinities (3.6 units) sampled (Kostamo and Mäkinen, 2006). The filamentous red alga *C. tenuicorne* has been observed to grow in salinities from 25 to 1 units, and in the lowest salinities asexual reproduction is common (Bergström et al., 2003). Some local populations in the Bothnian Bay have salinity optima as low as 1.5 units, but growth is severely reduced in these conditions (Bergström and Kautsky, 2006).

Many brown and green algal species in the Baltic can tolerate low salinity reasonably well. The Baltic *P. littoralis* has shown vigorous growth in laboratory in salinity levels of 1.5 units (Russell, 1994),
and also *E. siliculosus* tolerates low salinities (Dittami et al., 2012; Munda, 1999). The filamentous green algae *C. glomerata* is originally a fresh-water species and is expected to be favoured by low salinities (Munda, 1999; Thomas et al., 1990, 1988). *Cladophora rupestris* is of marine origin, and in the Atlantic it grows in the intertidal zone, while in the Baltic it is found in the upper sublittoral. Salinity tolerance of *C. rupestris* is lower than that of *C. glomerata* (Bergström and Bergström, 1999; Thomas et al., 1990, 1988), and thus it is expected to decline with low salinity. Another abundant filamentous green alga *U. intestinalis* showed the highest tolerance for low salinity of 44 macroalgal species studied by Larsen and Sand-Jensen (2006) with no decline in photosynthesis at 0 salinity after 4 days of incubation. As species tolerant of low salinity (Alström-Rapaport et al., 2010; McAvoy and Klug, 2005; Reed and Russell, 1979), *U. intestinalis* extends its distribution throughout the Baltic (Leskinen et al., 2004).

The decrease in number of macroalgal species along the salinity gradient causes a steep decline in the overall biodiversity and biomass of rocky shore communities (Bergström and Bergström, 1999). The ratio of marine to freshwater algal species declines from 4.2 to 1 in the Gulf of Bothnia in a salinity gradient of 5 to 3.5 (Bergström and Bergström, 1999). In the Baltic, there is a decline in red algal (Rhodophyta) and brown algal species (Phaeophyceae) and an increase in green algae (Chlorophyta) along declining salinity (Nielsen et al., 1995; Ojaveer et al., 2010; Snoeijfs, 1999), which matches with salinity tolerances derived from experiments (Larsen and Sand-Jensen, 2006), as well as with the results of our literature search (Table 2). The Chlorophyta contain more species of fresh-water origin (Johansson, 2002) with optima in low salinities and even fresh water (Larsen and Sand-Jensen, 2006). In the Bothnian Bay, some macroalgal communities in low salinities are dominated by lacustrine green alga *Cladophora aegagropila*, which extends its distribution down to 10 meters (Bergström and Bergström, 1999).
Substantial reductions in biodiversity of marine-associated species with declining salinities have been predicted especially through the loss of fucoids (Vuorinen et al., 2015). Our results suggest that *F. vesiculosus* could potentially show some adaptation to low salinities as local populations may have salinity tolerances lower than the generally assumed 4 psu. However, as the size of the plants decreases concurrently with salinity, the ecosystem functions provided by *F. vesiculosus*, such as year-round habitat persistence and complexity, biomass, and nutrient uptake, may be lost or diminished. As an example, *F. radicans* (which could potentially replace *F. vesiculosus* in areas of low salinity in the future), harbors less diverse communities of associated flora and fauna because of smaller size of the thallus (Schagerström et al., 2014).

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

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

### 5.4. Ocean acidification and CO₂ 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
from CO₂ enrichment experiments in macroalgae have shown a wide range of responses, possibly relating to different experimental techniques (Hurd et al., 2009).

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

Ocean acidification experiments conducted on Baltic macroalgae have provided mixed results. In a short-term experiment (duration 3 days), Pajusalu et al. (2013) found photosynthesis of *U. intestinalis* (green) and *F. lumbricalis* (red) to be stimulated by CO₂ addition, while *F. vesiculosus* (brown) showed no response. Of three species studied, *U. intestinalis* showed the highest stimulation by CO₂. In a second 3-days study, Pajusalu et al. (2016) found the fertilization effect on *F. lumbricalis* to depend on interactions with other environmental factors such as temperature and light. Another green alga, *Ulva prolifera*, showed increased vegetative growth when subjected to low salinity and low pH, but at the same time reproductive cell growth declined (Lin et al., 2011). In 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$_2$O$_2$, 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).
The extrapolation of results from laboratory experiments to nature has numerous challenges, and the contradicting results described above may arise from interplay between other environmental variables such as nutrients and light (Celis-Plá et al., 2015; Verspagen et al., 2014). If photosynthesis is limited by nutrient availability, carbon increase in the form of OA would have only minor effect (Verspagen et al., 2014), but if ample nutrients and carbon are provided, photosynthesis should increase, given no light limitation ensues (Verspagen et al., 2014). As light energy is used to convert inorganic carbon to photosynthates, algae may respond to increases in carbon availability by altering photobiological mechanisms. For example, the increased photochemical quenching in *U. prolifera* observed by Liu *et al.* (2012), coupled with lower light requirements may indicate that the plant downregulates light utilization as a response to increased carbon availability. Although macroalgae have been proposed to benefit from OA through improved energetics through CCM downregulation (Koch *et al.*, 2013), this may under high irradiances lead to increased photoinhibition, as CCMs acts as a sink for excessive energy (Liu *et al.*, 2012; Wu *et al.*, 2010). Thus, the OA impacts on Baltic macroalgae expectedly will depend on interactions with nutrient and light availability. In general, OA has been observed to have positive effects on photoautotroph growth and photosynthesis under low irradiance, but negative under high irradiance (Gao *et al.*, 2012). If eutrophication will increase in the future Baltic, also underwater light conditions will deteriorate, as increased turbidity is one of the main consequences of eutrophication. Thus to some extent, OA may benefit some species inhabiting the low irradiance environments in the coastal zone, and potentially could counter some of the adverse effects of eutrophication, if macroalgae are able to photosynthesize more efficiently under low irradiance conditions.

The coastal ecosystems of the Baltic Sea have naturally high diurnal and seasonal pH fluctuations caused by photosynthesis (Middelboe and Hansen, 2007) and upwelling of CO$_2$-rich water (Saderne *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.
here, but only briefly reflect on the results of our literature search. Based on our results, the green algae as a group will clearly benefit from intensifying eutrophication (Table 2, Table S1), together with many red algal species, which, in contrary to our expectations, were quite tolerant against eutrophication and also against subsequent increases in sedimentation. Two brown algae associated with filamentous algae blooms, *P. littoralis* and *E. siliculosus*, showed positive responses. Most of the studies (N = 30) we found quantified either direct or indirect negative effects of eutrophication on the foundation species *F. vesiculosus* (Table 2).

5.6 Multiple drivers and biotic interactions

Many studies assessing climate change impacts on marine organisms are short-term and manipulate only one single species and factor of interest (Forsman et al., 2016; Wernberg et al., 2012), often with limited duration (Forsman et al., 2016). In reality, various abiotic components of climate change, such as salinity, temperature, and pH interact influencing the complex biotic community, often under simultaneous non-climatic stressors. Changes in abiotic conditions may alter species interactions leading to rapid changes in abundance. When several abiotic factors change simultaneously, the resulting effects are difficult to predict. We exemplify this with the example of the brown filamentous alga *P. littoralis* (Fig. 2), which frequently forms drifting algal mats. *P. littoralis* seems tolerant to salinity declines (Bergström and Bergström, 1999; Munda, 1999; Russell, 1994), but being a cold-water species might suffer from temperature increases, and in artificially heated areas has been replaced by the sibling species *E. siliculosus* (Keskitalo and Heitto, 1987; Keskitalo and Ilus, 1987). Such declines of *P. littoralis* with increasing temperatures would remove the competitive exclusion pressure on *Ulva* spp. (Lotze et al., 1999), potentially leading to more frequent blooms of *Ulva* spp. in late spring. But *P. littoralis* could also benefit from warming, if ice 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).
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
effects with low salinity and elevated nutrient concentrations, and may either intensify or decrease grazing pressure (reviewed in Wahl et al., 2011). Experiments with longer exposure times and multiple drivers should be conducted for other key species also, as the existing literature at present seems to be strongly biased on studies on fucoids, more specifically *F. vesiculosus* (Table 2).

### 5.7 Adaptation

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

On one hand bottle necks and founder effects have resulted in overall low genetic variability in Baltic populations (Johannesson et al., 2011), and harsh environmental conditions have resulted in many macroalgae reproducing asexually (Kostamo and Mäkinen, 2006; Tatarenkov et al., 2005). These factors point to low capacity for evolutionary adaption. Yet the Baltic has evolved ecotypes well adapted to local conditions over millennia (Russell, 1985), with subsequent emergence of Baltic ecotypes tolerant of low salinity.
(Gylle et al., 2009; Johansson et al., 2003; Kostamo et al., 2011; Rueness and Kornfeldt, 1992; Russell, 1994, 1988) and temperature (Nygård and Dring, 2008; Thomas et al., 1988), and also the emergence of an endemic fucoid, *F. radicans*, which has been interpreted as an adaptation to low salinity (Pereyra et al., 2009). Given the speed of observed (Belkin, 2009) and projected (Meier et al., 2012b; Omstedt et al., 2012) environmental change, the potential for similar adaptations in the context of climate change is uncertain. Although some studies on genetic variability in Baltic macroalgae have been conducted (e.g. Leskinen et al. 2004, Tatarenkov et al. 2007), there is very limited knowledge on size of genetic variability related to quantitative traits selected upon in times of rapid environmental change, which makes assessing adaptive capacity difficult.

**6 Conclusions**

Summarizing the effects of the different drivers, the combined effects of climate change for macroalgal communities in the Baltic appear similar and additive to those of anthropogenic nutrient increase: elevated primary production and increased abundance of filamentous algae. Climate change will elevate primary production in the littoral ecosystem directly, and through increased nutrient emissions provided by increased river inflow. We illustrate the overall expected responses of macroalgae on abiotic changes in a conceptual model (Fig. 3).
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
declined 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).
With changes in temperature and salinity conditions, not only the existing interspecific interactions will change, but also the resilience against invasive species, including macroalgae, may diminish in Baltic ecosystems. Invasive species have been identified as one of the major threats to the Baltic ecosystem (Elmgren, 2001). The warmer and less saline conditions in the future may make the Baltic ecosystem more hospitable to a number of potential invaders (Holopainen et al., 2016) especially from estuarine conditions, which could easily transgress the salinity and temperature barriers by traveling via e.g. commercial shipping ballast waters.

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