

Growth and competition in a warmer ocean: A field experiment with a non-native and two native habitat-building seaweeds

Caroline S. Armitage^{1*}, Vivian Husa², Elzbieta A. Petelencz-Kurdziel¹, Kjersti Sjøtun¹

¹Department of Biology, University of Bergen, P.O. Box 7803, 5020 Bergen, Norway

²Institute of Marine Research, P.O. Box 1870, Nordnes, 5817 Bergen, Norway

*caroline.s.armitage@gmail.com

Citation information:

Armitage CS, Husa V, Petelencz-Kurdziel EA, Sjøtun K (2017) Growth and competition in a warmer ocean: A field experiment with a non-native and two native habitat-building seaweeds. *Marine Ecology Progress Series* 573: 85-99, doi: <https://doi.org/10.3354/meps12161>

ABSTRACT

Kelps and fucoids are important members of temperate seaweed communities, but may be negatively impacted by climate change and non-native species. We used a field experiment to investigate the effect of higher temperatures and a non-native seaweed, *Sargassum muticum*, on the kelp *Saccharina latissima* and furoid *Fucus serratus*. All three are canopy-forming species which may grow together in the infralittoral and upper sublittoral zones in southwestern Norway. Artificial assemblages with different combinations of the species were placed in the shallow sublittoral, and length changes, weight changes and survival of the thalli were measured. This was done over a hot summer and again over a cool summer. The results showed that the species and their competitive interactions were affected by the different thermal conditions. *Saccharina latissima* was the most successful species in the cool summer and had an impact on the other two species, but it was strongly negatively affected by the hot summer. Under these conditions, *Fucus serratus* became the most successful species, gaining the most weight. The effect of *Sargassum muticum* on the native species was no larger than the effect of intraspecific competition within those species. At the end of both summers *S. muticum* was in poor condition, potentially caused by low seawater nutrients resulting in low internal nitrogen.

Keywords: Competition; climate change; non-native; temperature effects; *Sargassum muticum*; *Saccharina latissima*; *Fucus serratus*

INTRODUCTION

Large brown macroalgae (class Phaeophyceae) form the dominant seaweed canopy in many temperate coastal zones (Lüning 1990, Chapman 1995). Kelps and fucoids are the largest groups, and are of vital importance for coastal ecosystems: they have high primary production which enters coastal food webs (Mann 2000, Norderhaug et al. 2003, Golléty et al. 2010), structure diverse and species rich habitats (e.g. Christie et al. 2009), and provide several ecosystem services (Smale et al. 2013).

Worryingly, there are indications that kelps and fucoids are being negatively affected by anthropogenic influences through species introductions and anthropogenic environmental changes (Smale et al. 2013, Strain et al. 2014). Non-native animals may overgrow native seaweeds (Levin et al. 2002), while non-native seaweeds may reduce the abundance of native seaweeds through competition (Scheibling & Gagnon 2006, Thomsen et al. 2016). Kelp and fucoids will also be affected by ocean warming (Brodie et al. 2014), with mean seawater temperatures predicted to rise by 2-3 °C by 2100 in the NE Atlantic (Müller et al. 2009). Already, heat waves have been linked to declines in the abundance of kelps and fucoids, even far from range edges (e.g. Moy & Christie 2012, Smale & Wernberg 2013, Wernberg et al. 2013, Filbee-Dexter et al. 2016). Interactions between stressors may also occur, resulting in a larger effect (Strain et al. 2014). For example, one non-native species may facilitate the spread of another (Levin et al. 2002), and warming and nutrient enrichment may have a synergistic negative impact on growth and survival of canopy algae (e.g. Gerard 1997, Moy & Christie 2012, Andersen et al. 2013, Strain et al. 2014). As coastal sea surface temperatures are predicted to rise (Müller et al. 2009) and the NE Atlantic is one of the most invaded areas of the world by introduced macroalgae (Thomsen et al. 2016), we can expect interactions between temperature and non-native seaweeds in this region.

Sargassum muticum (Yendo) Fensholt is a relatively well-studied non-native seaweed, which is now widespread in the NE Atlantic (Engelen et al. 2015). On the southwest coast of Norway, *S. muticum* is most common in sheltered areas or sounds where it can form locally dominant patches around or below mean low water. In these habitats, it may compete with two native species which also occupy the sublittoral fringe: *Saccharina latissima* (L.) Lane et al. (Laminariales) and *Fucus serratus* (L.) (Fucales), both of which are common and widely distributed in the NE Atlantic. All three species are canopy-forming, but have different

morphologies and growth patterns (Figure 1), suggesting that their competitive relationships might vary depending on environmental conditions. In the sublittoral, *Sargassum muticum* competes for light by forming a floating canopy which can shade other algae below (Ambrose & Nelson 1982, Britton-Simmons 2004, Lang & Buschbaum 2010, Engelen et al. 2015), although its effect on seaweeds in the littoral zone is inconsistent (Sánchez et al. 2005, Harries et al. 2007, Sánchez & Fernández 2005, Olabarria et al. 2009, Smith 2016). Conversely, *S. muticum* can itself be limited by native species through their preemptive use of space and light (Britton-Simmons 2006, Sánchez & Fernández 2006).

As *S. muticum* is close to its northern limit in Europe on the southwestern coast of Norway, its growth may also be limited by temperature. If so, future warming could improve conditions for *S. muticum*; firstly by temperature ranges moving closer to its optimum (Norton 1977), and secondly, by a negative effect on cold-adapted native competitor seaweeds. *Saccharina latissima* is particularly vulnerable to increasing temperatures (Bolton & Lüning 1982, Andersen et al. 2013, Simonson et al. 2015), while fucoids such as *F. serratus* tend to be more tolerant (Lüning 1990). However, even *F. serratus* abundance has declined in parts of its southern range, and the species is predicted to be lost from the warm temperate NE Atlantic by the year 2200 (Duarte et al. 2013, Jueterbock et al. 2013). A decline in their abundances could provide opportunities for *Sargassum muticum* to establish at new sites or increase in abundance, increasing its effects on the ecosystem. The effects of *S. muticum* may vary depending on its density and characteristics of the invaded habitat (Buschbaum et al. 2006, Lang & Buschbaum 2010, White & Shurin 2011), but in some habitats it has affected the composition of seaweed-associated fauna communities (Wernberg et al. 2004, Buschbaum et al. 2006, Harries et al. 2007, Engelen et al. 2013), influenced food webs (Salvaterra et al. 2013) and altered seasonal detritus influx (Pedersen et al. 2005).

We have investigated the competitive relationships between *Saccharina latissima*, *Fucus serratus* and *Sargassum muticum* in a field experiment on the southwest coast of Norway, during two summers with widely different temperatures. The three large brown seaweeds represent very different morphologies and habits of growth, and are predicted to vary in success depending on competitor species and environmental conditions. The aim of the study was to compare the outcome of competition between adult individuals of the three species, when grown together in different combinations at a fixed density. This allowed us to

examine 1) the effect of a warmer than average summer on the growth and survival of the three species; 2) competition between the three species; and 3) how these two factors interact.

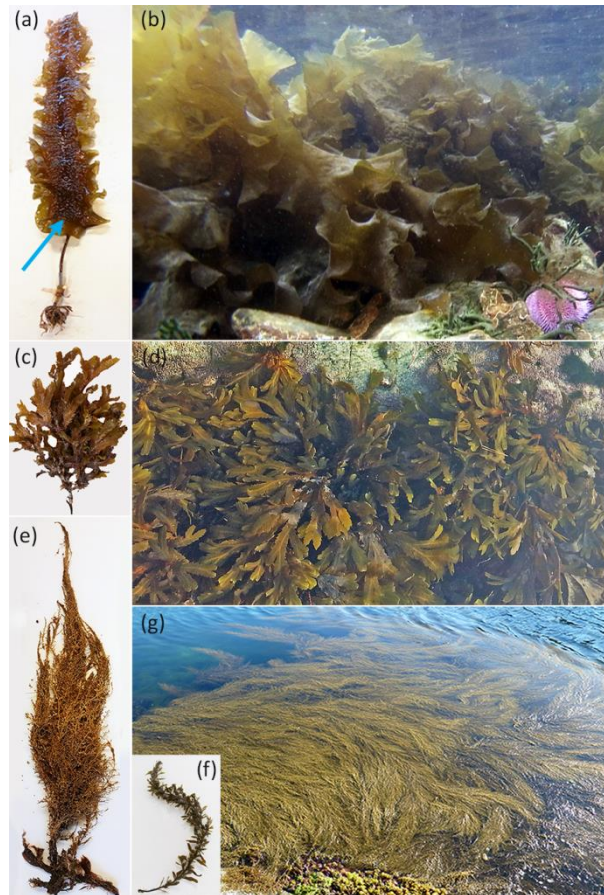


Figure 1 Photographs showing the growth habits of the three seaweeds in southwestern Norway. *Saccharina latissima* forms a broad blade, which grows from the top of the stipe (a; arrow). The blade can increase in length quickly and lies over the substratum (b). *Fucus serratus* has leathery, serrated, dichotomous branches with apical growth, resulting in an increasingly bushy structure over time (c). *F. serratus* tends to spread out in a layer over the substratum (d). *Sargassum muticum* grows rapidly from the apex and can form a long thallus (e; here pictured attached to a piece of rope at the base). The main axis grows from early spring (f), becoming longer and increasingly bushy with more and longer side branches by late summer (e). Gas vesicles allow *S. muticum* to float in the water column (g).

MATERIALS AND METHODS

Experimental design

The experiment was carried out on the southwest coast of Norway, which is in the cold temperate North-East Atlantic biogeographic region (Lüning 1990). The coast is made up of many islands and fjords, resulting in a complex rocky shoreline with many areas sheltered

from the open sea. Mean sea surface temperatures range from around 4.7 °C in February to around 15.6 °C in August (1980-2009 mean, 1 m depth; Institute of Marine Research 2016).

Thalli of *Sargassum muticum*, *Fucus serratus*, and *Saccharina latissima* (hereafter referred to by generic name alone) were collected by hand at low tide, and some *Saccharina* by triangular dredge. Collections were done within 40 km of the study site (60.26836 N, 5.21773 E). Collected thalli were stored in tanks with continuously flowing seawater or on ropes in the sea, and were kept damp during handling. Only thalli which looked healthy were included in the experiment. The collected thalli were assembled into different combinations of the three species by attaching individuals to metal grids in a substitutive design. There were seven assemblage types: (1) *Saccharina* only, (2) *Fucus* only, (3) *Sargassum* only, (4) *Saccharina* x *Fucus* mix, (5) *Saccharina* x *Sargassum* mix, (6) *Fucus* x *Sargassum* mix, and (7) *Saccharina* x *Fucus* x *Sargassum* mix. These may hereafter be referred to by an abbreviation of the species name shortened to two letters (Sl for *Saccharina*, Fs for *Fucus*, Sm for *Sargassum*; for example, “SlxFs” for the *Saccharina* x *Fucus* assemblage). The single-species assemblages exposed the thalli to intraspecific competition, while the mixed-species assemblages also exposed them to different types of interspecific competition; thus the present study is comparing these forms of competition, rather than comparisons to no competition. Two replicates of each assemblage were made in 2014, and three replicates in 2015.

In all treatment types the thallus density was kept constant at 50 thalli per m². In the one-species assemblages (types 1-3), 20 thalli of each species were used (an experimental area of 0.4 m²); in the two-species assemblages (types 4-6), 18 thalli of each species were used (0.72 m²); in the assemblages with all three (7), 16 thalli of each species were used (0.96 m²). This thallus density is higher than the experimental densities of Strong and Dring (2011), but lower than Creed et al. (1998). We consider it realistic from reported densities: mature *Fucus* at 88 - 208 per m² on the Isle of Mann (Creed et al. 1998); *Sargassum* at 57 per m² in California (Ambrose & Nelson 1982), up to 64 per m² in France (Plouguerné et al. 2006) and up to 72 per m² in Ireland (Baer & Stengel 2010); *Saccharina* at 40 per m² in June, close to the study site (Sjøtun 1985).

The thalli were attached so that all had approximately the same starting height (40 cm). *Fucus* thalli were trimmed at the base to avoid damaging the meristematic tips. *Sargassum*

also has apical meristems, but cutting was avoided because *Sargassum* is less robust. Instead, the thalli were attached so they extended up to approximately 40 cm above the grid, with the basal part of the thallus in the space below the grids (which stood slightly raised from the substratum). The mean maximum length of *Sargassum* used was 56 cm, so this excess was normally only around 16 cm. *Saccharina* thalli were cut to the correct length from the distal end of the blade, as growth occurs at the stipe-blade transition (Figure 1). *Saccharina* with stipes ≥ 17 cm were not included in the study; these were excluded to ensure that there was blade tissue left above the meristem for normal growth after trimming. In nature however, *Saccharina* stipes can often be longer than this, varying with environmental conditions and age. Standardising the starting length and thallus density meant that biomass was not standardised across the assemblage types, and varied naturally with species identity.

The length and weight of each thallus was measured before and after the experiment. For *Saccharina*, length change consists of both growth and erosion of the distal end of the blade, so these were estimated separately by punching a hole in the blade, 10 cm above the blade-stipe transition (the location of the meristem). Tracking how far this hole moves from the stipe, in relation to the total length, is an established method for assessing kelp growth and erosion (Creed et al. 1998, Strong & Dring 2011). The age of the *Saccharina* thalli was also estimated at the end of the experiment by counting rings in a cross-section of the stipe (Parke 1948). For all species, survival was recorded for each thallus, with missing or dead individuals classed as non-surviving.

The assemblages were left in the upper subtidal from mid-May to early August, after which the thalli were collected in again for re-measurement. The experimental site was outside Espegrend Marine Biological Station (University of Bergen), on the shorelines of two islands facing each other across a narrow channel sheltered from waves (60.26836 N, 5.21773 E). The substratum was large rounded stones, colonised by turf and filamentous ephemeral algae with some natural populations of *Fucus*, *Saccharina* and *Sargassum* present. In 2014 the western island was used for both replicates, and in 2015 the eastern island was also used for the third replicate. Mean spring low water in this area is around +30 cm relative to chart datum, and the assemblages were placed around -50 cm (the deepest point on any grid was -83 cm, the shallowest point was -18 cm). Water temperature was continuously logged at 1

m depth near to the site (Tinytag aquatic 2, Gemini data loggers, Chichester UK). In 2015, seawater samples were taken to assess the levels of nitrite, nitrate and phosphate (Table 1), and were analysed according to standard methods (Parsons et al. 1992).

Seaweeds samples were also taken to measure their nitrogen and carbon content. Vegetative tissue was sampled mid-blade in *Saccharina*, and from branches in *Sargassum* and *Fucus*. In 2014, 10 *Sargassum* thalli occurring naturally near the experiment, were sampled in mid-June. In 2015, samples were taken from 7 to 10 thalli each of *Saccharina*, *Fucus* and *Sargassum* at the start of the experiment (collected from the same place as the experimental thalli; early May), 5 thalli of each species during the experiment (collected near to the experiment; late June), and 10 to 12 thalli of each species after the experiment (from the experimental thalli, evenly distributed between treatments; mid-August). Samples were analysed in a Flash 2000 elemental analyser (Thermo Fisher Scientific, MA, USA), in nitrogen-carbon configuration: filters, sediments, soils. The measurements were performed with the following parameters: carrier gas (helium) 130 ml/min, reference gas (helium) 100 ml/min, oxygen 250 ml/min; cycle (run time) 450 s, sampling delay: 12 s, oxygen injection end: 10 s (Pella & Colombo 1973).

Analysis

The number of days between start and end measurements of the thalli varied between grids due to practical limitations (from 77 – 92 days), therefore before analysis, the end length and weight measurements of each individual thallus were standardised to the shortest time (77 days), using the formula $Standardised\ end\ x = start\ x + ((change\ in\ x/number\ of\ days)*77)$, where x is length or weight. For *Saccharina* growth and erosion, the formula used was $Standardised\ end\ x = ((x/number\ of\ days)*77)$, where x is growth or erosion.

For each of the three species, analysis was carried out to ascertain how assemblage type and year influenced thallus end length, end weight, and survival, as well as thallus growth and erosion in *Saccharina*. The program R (R Development Core Team 2016) was used to perform the analyses. For continuous response variables (end length, end weight, growth, erosion), linear mixed-effects models (LMMs) were used (R package *nlme*; Pinheiro et al. 2015); for the binary response variable (survival), generalised mixed-effects models (GLMMs) were used with the binomial distribution and Laplace approximation (R package *lme4*; Bates et al. 2015). *Grid* nested in *replicate* was included as a random effect, selected a priori based on

experimental design. Thallus starting length or weight was also included to account for differences in starting size, and age was included for *Saccharina* as this influences growth rates (Sjøtun 1993). Nearly all *Saccharina* in the experiment were estimated to be 0 or 1 years old; four thalli which were 2 years old were excluded.

Model-selection of the fixed effects was done by reducing the most complex model, including all terms and a *year*treatment* interaction, term-by-term, carrying out a likelihood ratio test (LRT) at each stage (Zuur et al. 2009). If the interaction was significant, the single predictors *year* and *treatment* were also retained in the model. Only the end weight of *Saccharina* showed heterogeneity of variance and was square-root transformed. If the LRT p-value was under 0.1, the term was kept in the model, provided that there were significant differences (<0.05) in pairwise comparisons between the different levels. These pairwise differences were assessed by Wald tests on the t-statistic (LMMs) or z-statistic (GLMMs). For the LMMs, an estimate of R^2 was obtained using R package *MuMIn* (Barton 2016), and plots were created using the R base package and *ggplot2* (Wickham 2009). Least-squared means were calculated using package *LSmeans*. Least-squared means are the predictions from the models for each assemblage type and/or year (Lenth 2016), and are provided in Supplementary Material S1-S10.

RESULTS

Environmental conditions

Apart from a 3 week period in late June/early July, daily mean temperatures were higher in the 2014 experiment (Figure 2). The mean difference in monthly averages was 3.2 °C, with overall mean temperatures of 15.1 °C in 2014 versus 12.4 °C in 2015. The temperature difference was most pronounced during the last part of the experiment, when in 2014 there were 17 days with mean daily seawater temperatures of or above 19.4 °C (with a maximum recorded temperature of 21.5 °C), while in 2015, the temperature never exceeded 16.2 °C. The large difference in temperatures means that hereafter 2014 may be referred to as the hot year, and 2015 as the cool year.

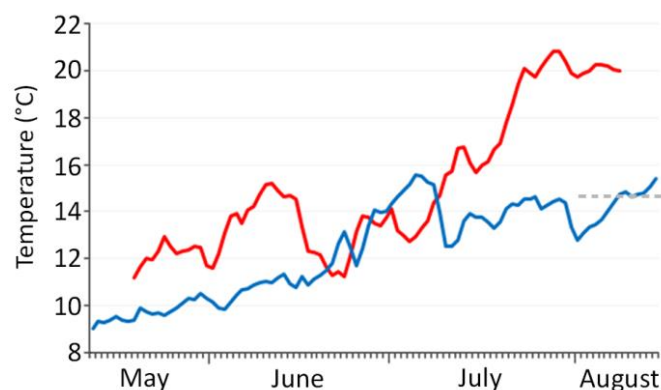


Figure 2 Mean daily seawater temperature (1 m depth) during the experimental period in 2014 (red) and 2015 (blue). The dotted grey line marks the mean August sea surface temperature (1980-2009, 1 m depth) for this region. Note that the y-axis scale does not begin at 0.

Data from the Meteorological institute of Norway (Meteorologisk Institutt 2016) showed that cloud cover was lower in 2014 than 2015. In May, June, July and August, the total number of overcast days (defined as the number of oktas (eighths of the sky covered in cloud) at three measuring times summing to ≥ 20) was 34 in 2014, versus 57 in 2015. Mean cloud cover was similar, with both years having intermediate levels (4.3 oktas in 2014 and 5.7 oktas in 2015). The seawater nutrients were low throughout summer 2015, with no recordings of nitrate, nitrite or phosphate $> 0.6 \mu\text{mol l}^{-1}$ (Table 1).

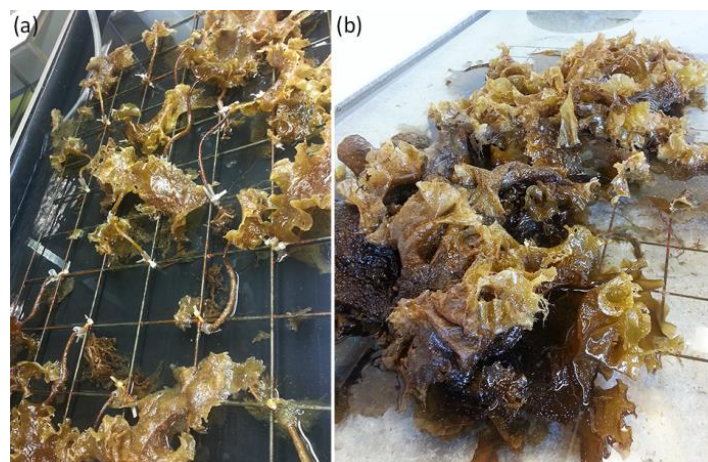
Table 1 Nutrients in seawater during the experimental period in 2015 (range across the samples, given in $\mu\text{mol l}^{-1}$). Date format *dd.mm.yyyy*.

Date	Number of samples	Nitrite	Nitrate	Phosphate
27.05.2015	5	0.10-0.12	<0.4-0.5	<0.06
10.06.2015	4	0.10-0.20	<0.4	<0.06
24.06.2015	6	0.14-0.23	<0.4-0.6	<0.06-0.25
29.07.2015	3	0.19-0.24	<0.4	<0.06-0.12
11.08.2015	6	0.23-0.31	<0.4	<0.06-0.31

Saccharina latissima

There was a large difference in the condition of *Saccharina* between the hot and cool years. In the cool year, *Saccharina* had large positive length and weight changes, higher growth, and low erosion, whereas in the hot year, weight loss and length reduction frequently occurred (Figures 3, 4 and 5). Significant interactions between assemblage type and year were present for both end length and end weight (Table 2). In the cool year, the length and weight gain of *Saccharina* was fairly similar in all assemblage types. However, in the hot year, the length and weight change of *Saccharina* was lower when in combination with *Fucus* (SlxFs) than in some or all of the other assemblage types, being negative changes on average (Figure 4, Supplementary Material S1 and S2). This is likely connected to the patterns in growth and erosion. *Saccharina* growth was always significantly higher in the assemblage with *Fucus* (SlxFs) than the other treatments (Table 2, Figure 5, Supplementary Material S3). However, the effect of treatment on erosion varied by year (Table 2). In the hot year, erosion increased more in the assemblage with *Fucus* (SlxFs) than the other treatments (especially compared to the assemblage with *Sargassum*, SlxSm); however, in the cool year, erosion was low in all assemblage types (Table 2, Figure 5, Supplementary Material S4). Starting length and weight of *Saccharina* were positively related to end length and weight respectively, but age of the thallus was unrelated to both (Table 2).

Figure 3 Photographs of experimental assemblages of *Saccharina latissima*-only, at the end of the experiment in 2014 (a) and 2015 (b).



In 2015, the mean growth of *Saccharina* was 31 ± 12 cm (standard deviation, SD), compared to 20 ± 7 cm in 2014 (Figure 5). The maximum individual growth observed was 70 cm (2015). The age of the thalli had an influence on the growth rate (Table 2), with the mean growth of those less than one year old being higher than those more than one year old (Supplementary Material S3). Because of this, the mean growth rates stated above may be somewhat influenced by the fact that the thalli which could be measured for growth in 2015 contained a higher proportion of age 0+ thalli than in 2014 (2014: 16/74 thalli; 2015: 62/163 thalli). Despite this, there was clearly also an effect of year on growth (Table 2, Figure 5). Starting weight was negatively related to growth and erosion (Table 2).

Saccharina survival was only slightly higher in the cool year, at 83 % compared to 78 % in the hot year. The interaction between year and treatment was not statistically significant according to the likelihood ratio test, but the results of the Wald test indicated that the effect of year on *Saccharina* survival in the assemblage with *Fucus* (SlxFs) was different to the effect in the assemblage with all three species (Table 2). *Saccharina* survival was lower in the hot year than in the cool year in the SlxFs treatment, while it remained similar across both years in the *Saccharina*-only treatment (Figure 6, Supplementary Material S5).

The nitrogen content of the *Saccharina* thalli decreased slightly throughout the summer, from 1.07 ± 0.35 % (SD) in May to 0.83 ± 0.22 % at the end of the experiment in August. On the other hand, the carbon content increased by around 3 % (Figure 7).

Fucus serratus

The majority of *Fucus* showed positive length and weight changes in both years (Figure 4). Its end length was unaffected by treatment, but was significantly higher in the cool year across all assemblages (Table 2), although this was a small difference (Figure 4). Year had little consistent effect on weight, but interactive effects with assemblage type were present (Table 2). In the hot year, the end weight of *Fucus* was relatively similar in all assemblage types, but in the cool year it was lower when grown together with *Saccharina* than in the other assemblage types (Figure 4). This effect was most clear in comparisons with the assemblage with *Sargassum* (FsxSm) (Table 2, Figure 4, Supplementary Material S7). *Fucus* showed the highest overall survival of the three species (94 %). There was a slight but significant reduction in survival from 98 % in 2014 to 91 % in 2015 (Figure 6), but the difference between assemblages was not statistically significant (Table 2). End length and

weight were positively linked to starting length and weight, respectively, but there was no influence of the starting size on survival (Table 2).

The nitrogen content of *Fucus* decreased throughout the summer of 2015, from 1.9 ± 0.31 % (SD) in May to 0.86 ± 0.25 % in August. *Fucus* started with higher nitrogen content than *Saccharina* and *Sargassum*, but this difference decreased with time and by August all three species were quite similar (Figure 7). The carbon content of *Fucus* was much higher than *Sargassum*, and increased throughout the summer (Figure 7).

Sargassum muticum

The *Sargassum* thalli were generally in poor condition at the end of the experiment in both years; many had lost some side branches and air vesicles and were no longer buoyant. We did not observe receptacles as might be expected for this time of year in this area, and the advanced state of the decline suggested that they would not become reproductive at all. To ensure that this was not because of the experimental treatment, we visited naturally occurring *Sargassum* on the surrounding islands, and found it to be in a similar condition.

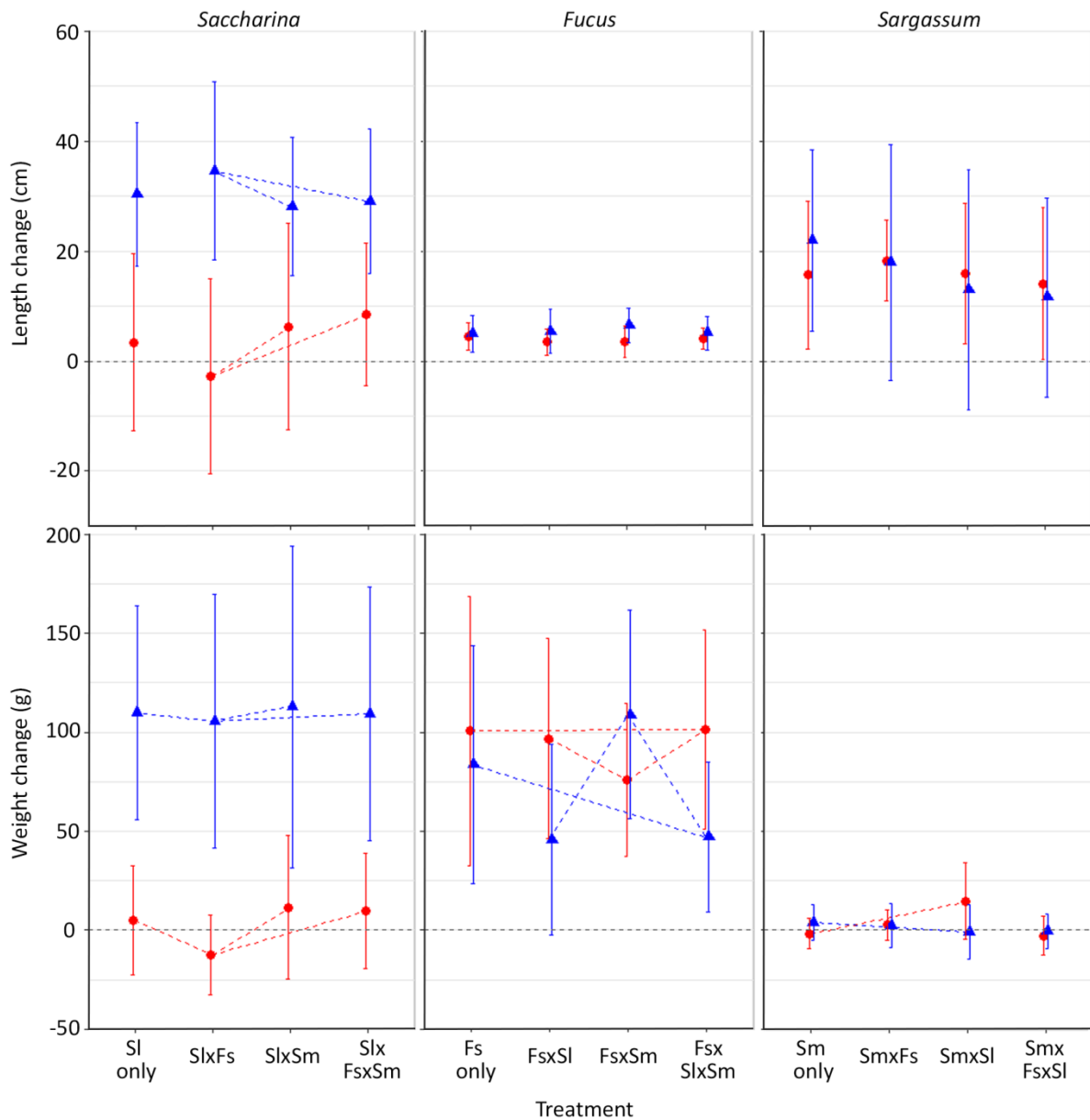
There was no difference in length between the assemblages or years (Table 2), with the thalli usually increasing by around 10-25 cm (but with large variation; Figure 4). Weight change however showed significant interactive effects of year and treatment (Table 2). For the *Sargassum*-only, *Fucus* and 3-species assemblages (Sm-only, SmxFs, SmxFsxSI), weight change was always low, but in the assemblage with *Saccharina* (SmxSI) weight change was higher in the hot year compared to the cool year and other treatments (Figure 4, Supplementary Material S9).

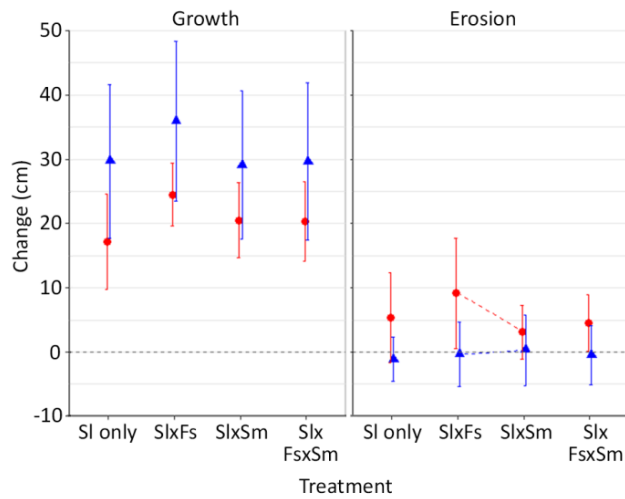
Sargassum survival was significantly higher in the hot year (76 % in 2014 compared to 52 % in 2015; Table 2). It was also always lowest in the assemblage with both native species, significantly lower than the assemblages where *Sargassum* was alone or with *Fucus* only (Table 2, Figure 6). In contrast to the other two species, *Sargassum* survival was positively linked to starting weight (Table 2); the predictions of the model are that in 2015, a thallus in the *Sargassum*-only treatment had a 24 % chance of being lost if weighing 10 g, 33 % if 20 g, and 44 % if 30 g (parameter estimate = 0.046, standard error = 0.017).

In 2015, the mean nitrogen content in *Sargassum* was 1.34 ± 0.17 % (SD) at the start of the experiment in May, but this rapidly decreased by June, and stayed low (Figure 7). The

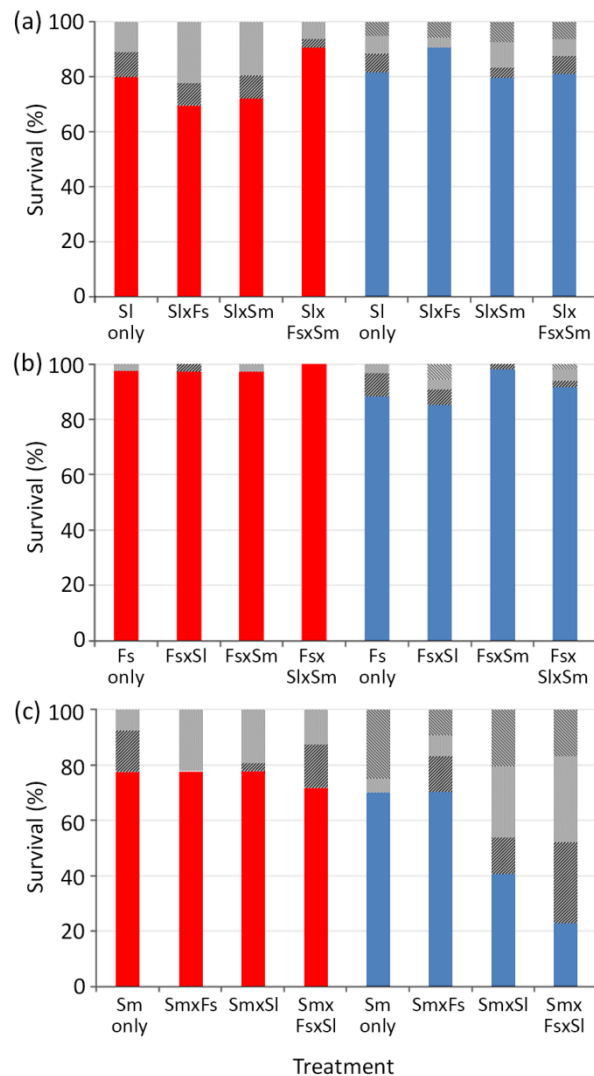
nitrogen content in June 2014 was similar to June 2015 (0.7 ± 0.1 % in 2014 and 0.71 ± 0.18 % in 2015). As with all the species, the carbon content of *Sargassum* increased through the summer, but was consistently 5-7 % lower than *Fucus* and *Saccharina* (Figure 7).

Figure 4 Mean length change (top row) and weight change (bottom row) of *Saccharina latissima* (Sl; n = 133 in 2014, 177 in 2015, left column), *Fucus serratus* (Fs; n = 141 in 2014, 196 in 2015, middle column), and *Sargassum muticum* (Sm; n = 110 in 2014, 112 in 2015, right column) during the experiment in different treatments and years (red circles: 2014, blue triangles: 2015). Note that the order of species in the mixed-species assemblages is not important, and is only arranged so that the species of interest is first (i.e. “SlxFs” is the same as “FsxSl”). Significant interactions (Table 2) are shown as dotted lines between treatment types, and standard deviation of the means displayed as error bars. Length change of *Saccharina* is the result of both growth and erosion of the blade, which are examined separately in Figure 5.





◀ **Figure 5** Mean growth and erosion (± 1 standard deviation) of *Saccharina latissima* during the experiment in different treatments and years (n=74 in 2014, n=163 in 2015). Higher positive numbers on the erosion axis indicate that more of the blade was eroded. Symbols, colours, and abbreviations as in Fig. 4.

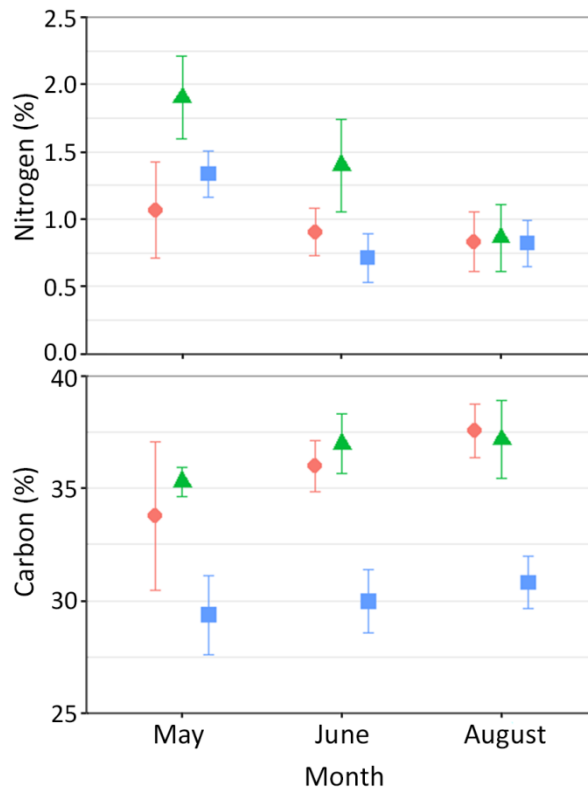


◀ **Figure 6** Total survival of *Saccharina latissima* (plot (a); n = 365), *Fucus serratus* (plot (b); n = 360) and *Sargassum muticum* (plot (c); n = 360) in summer 2014 (red) and summer 2015 (blue). Coloured bars show the percentage of surviving thalli in each treatment, while the grey areas above show the percentage of thalli which died or were lost during the experiment, patterned to show the split between the 2 (2014) or 3 (2015) replicates of each grid. Abbreviations as in Fig. 4.

Table 2 Results of statistical analyses carried out to examine the effect of treatment and year on *Fucus serratus* (Fs), *Saccharina latissima* (Sl) and *Sargassum muticum* (Sm). For each predictor, the likelihood ratio (L) or chi squared value is given, with degrees of freedom in subscript (NS = non-significant and removed from model; + = included in model due to significant interaction). *P* values are shown in italics if over the 0.05 level; all are unadjusted. The R^2 values indicate the proportion of variation explained by the fixed effects in the model, while the values in brackets indicate the variation explained by the model as a whole (including random effects). In cases where ‘treatment’ was significant, contrasts between levels close to significance are shown in the last two columns. Predictions from these models (as least-squares means) are presented in supplementary material.

Species and response	Predictors					R^2	Differences between treatment levels	
	Starting size	Age	Year	Treat	Year* Treat			
<i>Saccharina latissima</i>								
Length	$L_1 = 6.79$, $p = 0.009$	NS	+	+	$L_3 = 12.1$, $p = 0.007$	0.46 (0.47)	Yr*SlxFs - Yr*SlxSm Yr*SlxFs - Yr*SlxFsxSm	$t_9 = -2.70$, $p = 0.024$ $t_9 = -2.87$, $p = 0.019$
Weight	$L_1 = 303$, $p < 0.001$	NS	+	+	$L_3 = 11.4$, $p = 0.010$	0.84 (0.84)	Yr*SlxFs - Yr*Sl Yr*SlxFs - Yr*SlxSm Yr*SlxFs - Yr*SlxFsxSm	$t_9 = -2.52$, $p = 0.033$ $t_9 = -2.98$, $p = 0.016$ $t_9 = -2.56$, $p = 0.031$
Growth	$L_1 = 22.3$, $p < 0.001$	$L_1 = 8.85$, $p = 0.003$	$L_1 = 17.0$, $p < 0.001$	$L_3 = 13.1$, $p = 0.004$	NS	0.34 (0.34)	SlxFs - Sl SlxFs - SlxSm SlxFs - SlxFsxSm	$t_{12} = -3.40$, $p = 0.005$ $t_{12} = -3.36$, $p = 0.006$ $t_{12} = -2.95$, $p = 0.012$
Erosion	$L_1 = 6.80$, $p = 0.009$	NS	+	+	$L_3 = 9.59$, $p = 0.022$	0.26 (0.28)	Yr*SlxF - Yr*SlxSm	$t_9 = 3.13$, $p = 0.012$
Death/Loss	NS	n/a	+	+	$\chi^2_3 = 7.17$, $p = 0.067$	n/a	Yr*SlxFs - Yr*Sl Yr*SlxFs - Yr*SlxFsxSm	$z = 1.79$, $p = 0.073$ $z = 2.47$, $p = 0.014$
<i>Fucus serratus</i>								
Length	$L_1 = 110$, $p < 0.001$	n/a	$L_1 = 6.94$, $p = 0.008$	NS	NS	0.28 (0.35)		
Weight	$L_1 = 296$, $p < 0.001$	n/a	+	+	$L_1 = 17.0$, $p < 0.001$	0.66 (0.68)	Yr*Fs - Yr*FsxSl Yr*Fs - Yr*FsxSlxSm Yr*FsxSm - Yr*FsxSl Yr*FsxSm - Yr*FsxSlxSm	$t_9 = -2.05$, $p = 0.071$ $t_9 = -2.29$, $p = 0.048$ $t_9 = -3.12$, $p = 0.012$ $t_9 = -3.36$, $p = 0.008$
Death/Loss	NS	n/a	$\chi^2_1 = 5.86$, $p = 0.015$	NS	NS	n/a		
<i>Sargassum muticum</i>								
Length	$L_1 = 5.65$, $p = 0.017$	n/a	NS	NS	NS	0.03 (0.05)		
Weight	$L_1 = 45.8$, $p < 0.001$	n/a	+	+	$L_3 = 10.7$, $p = 0.013$	0.37 (0.63)	Yr*SmxSl - Yr*Sm Yr*SmxSl - Yr*SmxFs	$t_9 = 2.97$, $p = 0.016$ $t_9 = 2.15$, $p = 0.060$
Death/Loss	$\chi^2_1 = 7.19$, $p = 0.007$	n/a	$\chi^2_1 = 5.57$, $p = 0.018$	$\chi^2_3 = 6.58$, $p = 0.087$	NS	n/a	SmxFsxSl - Sm SmxFsxSl - SmxF	$z = -2.34$, $p = 0.019$ $z = -2.24$, $p = 0.025$

Figure 7 Seaweed nitrogen (top) and carbon content (bottom) over the experiment during summer 2015. Mean percentage content of dry weight is shown for each species, ± 1 standard deviation. Red circles: *Saccharina latissima* (n = 27), green triangles = *Fucus serratus* (n = 24), blue squares = *Sargassum muticum* (n = 22)



DISCUSSION

Temperature

Relatively short extreme temperature events put acute stress on cold-adapted seaweeds, in addition to the chronic stress of gradual warming (Brodie et al. 2014). If extremely warm summers become more frequent, seaweed ranges and abundances may be affected more severely, more quickly, or over a wider area, than predicted from changes in mean temperature alone (e.g. Smale & Wernberg 2013). In the present study, conditions in 2014 had a substantial negative impact on *Saccharina*, with moderate warming from May and a short hot period later sufficient to reduce *Saccharina* growth and increase blade erosion until there was almost no net gain in weight or length over the summer. We expect that high temperature was the main cause of this, as high temperature alone (20 °C) has been shown to cause tissue deterioration, loss of pigments, and reduced net photosynthesis in *Saccharina* from southwestern Norway (Andersen et al. 2013). Other temperature experiments show a similar negative effect, with blade weakness, tissue loss and mortality

increased at 18-20 °C, and total mortality at 21-23 °C (Bolton & Lüning 1982, Andersen et al. 2013, Simonson et al. 2015). In contrast, average summers in southwestern Norway (such as 2015) provide close to ideal conditions for *Saccharina*, which has optimum growth at 10-15 °C (Lüning 1990, Andersen et al. 2013). The elongation rate for *Saccharina* in 2015 was on average 0.4 cm day⁻¹, which is similar to a former study of tagged individuals (around 0.5 cm day⁻¹) during a normal summer (Sjøtun 1993).

In contrast to *Saccharina*, the different summer conditions did not have a large effect on *Fucus* and *Sargassum*. Regardless of whether it was a cool or hot summer, *Fucus* had net weight gain and high survival. *Fucus* has optimum growth at only slightly higher temperatures than *Saccharina*, 15 °C, but it can survive at temperatures up to 25 °C (Lüning 1990), making it better adapted for surviving summer heatwaves. Intertidal *F. serratus* populations still persist in northern Spain, despite a reduction in abundance associated with warming (Duarte et al. 2013), and in the British Isles, Hawkins and Hartnoll (1985) also reported that intertidal *Fucus* appeared undamaged after a hot summer, while *Saccharina* showed signs of damage or mortality. The slightly lower elongation of *Fucus* observed in the hot year indicates that high temperature had some negative effect, but the elongation rates (around 0.35 cm wk⁻¹ in 2014 and 0.50 cm week⁻¹ in 2015) are comparable to other locations in the NE Atlantic (Knight & Parke 1950 and references therein).

Sargassum was expected to perform better in the warmer year because its distribution in Europe stretches south to Morocco (Engelen et al. 2015) and its growth rate increases with temperature to at least 25 °C (Norton 1977; but also see Sfriso and Facca 2013). Although survival improved under hotter conditions, growth and general condition were similarly poor in both years. Compared to other locations, the change in length was low and senescence was quite advanced by mid-August (Engelen et al. 2015; also compared to some other local sites in Norway). This, along with our field observations, suggests that *Sargassum* is limited by a factor other than temperature at sheltered sites. Possibilities for this include brown filamentous algal epiphytes, which may cover subtidal *Sargassum* in early summer at sheltered sites in Ireland, Scotland and Norway (Baer & Stengel 2014, Engelen et al. 2015, pers. obs.); however, the thalli used in the present experiment were relatively clean. Nutrient limitation is another possible explanation (see later discussion).

Competition

Competitive interactions can be the major determinant of the composition of canopy-forming brown algae on the shore (Hawkins & Hartnoll 1985, Hawkins & Harkin 1985). The results of the present experiment are consistent with the hypothesis that these interspecific competitive interactions may change under higher temperatures. In the cool summer, *Saccharina* was the superior competitor to *Fucus* and *Sargassum*, with the highest length and weight gains. On the other hand, when *Saccharina* was under temperature stress, its growth and ability to maintain its blade were reduced. Under these conditions, *Fucus*, and to a lesser extent *Sargassum*, tended to be more successful in the treatment with *Saccharina* than they were in the cool year, demonstrating that the competitive effect of *Saccharina* was weaker. *Fucus* became the most successful, gaining the most weight. The experiment did not assess which resource was being competed for, but as the thalli already had attachment space and ambient nutrients were low throughout the summer, light is most likely. This is usually the primary resource competed for in the sublittoral (Lüning 1990).

The strongest interactions observed were those between the native seaweeds. *Saccharina* had a strong competitive effect on *Fucus*, with *Fucus* gaining much less weight when *Saccharina* was in good condition. This was expected as *Fucus* is capable of growing deeper than normally observed, but is competitively excluded by kelps (Kain & Jones 1975, Hawkins & Hartnoll 1985). However, *Fucus* also affected *Saccharina* in two ways. The first was temperature dependant, as shown by the differences in erosion, weight and mortality of *Saccharina* between the cool and hot summer in the assemblage with *Fucus*. A possible explanation is interference competition. When water temperatures are maintained at ≥ 18 °C the blade of *Saccharina* becomes considerably more fragile (Simonson et al. 2015), potentially making it more susceptible to abrasion and tearing by leathery serrated *Fucus* branches. The second effect was increased growth of *Saccharina* in the *Saccharina* x *Fucus* assemblages, which was independent of temperature. High biomass of *Fucus* around the *Saccharina* thalli may alter conditions (e.g. light levels), causing the kelp to allocate resources to elongation, rather than thickening or widening of the blade. Field studies have shown that light or wave-exposure can affect blade thickness, wideness, and growth allocation in kelps (Sjøtun & Fredriksen 1995, Wing et al. 2007). The effects of *Fucus* on *Saccharina* were not

evident in the treatment with all three species, possibly due to the inclusion of *Sargassum* lowering the density of *Fucus* and *Saccharina*.

Britton-Simmons (2004) found that *Sargassum* can negatively affect sublittoral macroalgae by exploitative competition for light. However, in the present study, *Sargassum* had no more effect than intraspecific competition in *Fucus* and *Saccharina*. Strong and Dring (2011) also found no effect of *Sargassum* on *Saccharina* growth or erosion, and Vaz-Pinto et al. (2014) found no negative effect of *Sargassum* on growth of the native furoid *Cystoseira humilis*. Poor condition of *Sargassum* at the end of the present experiment may have limited its competitive ability, but this does not apply to the other studies. For *Saccharina*, it may be that adaptation to low light (Fortes & Lüning 1980) makes adult thalli relatively resistant to shading by *Sargassum* when in the upper subtidal. But it may also be that competition between adult thalli is not the critical factor in explaining the success of *Sargassum* (Vaz-Pinto et al. 2014).

The competitive effects of *Fucus* on *Sargassum* were similar to the effects of intraspecific competition in *Sargassum*. Vaz-Pinto et al. (2014) also found no competitive effect of the furoid *Cystoseira humilis* on *Sargassum* growth. However, *Saccharina* appeared to have a negative influence on *Sargassum* survival under average temperatures. This differs to the findings of Strong and Dring (2011), who found no competitive effect of *Saccharina* on *Sargassum* even at high densities, and suggested that the presence of *Saccharina* actually benefitted *Sargassum* by reducing intraspecific competition. This contradiction may be partly explained the poor state of *Sargassum* by the end of the present study, which probably reduced intraspecific competition to low levels. Growth conditions for *Sargassum* vary locally on the southwestern coast of Norway, and its condition seems to be better in places with strong tidal currents. In Ireland it also is less successful at sheltered sites (Baer & Stengel 2010). Repeating the experiment at locations with higher water movement would be useful future work, to clarify how local conditions affect competitive interactions.

Sargassum survival was always lower in the treatment with both native species, suggesting that *Fucus* and *Saccharina* have a combined negative effect on *Sargassum*. Because only the trend in survival was statistically significant, and the difference was relatively small in the hot summer, more work must be done before drawing definitive conclusions. However, it does fit with the idea that diversity may reduce vulnerability to invasion on a local scale (Elton

1958). Theoretically, more native species use resources more completely, instead of leaving them available for non-native species (Stachowicz & Tilman 2005). This may be particularly important if environmental conditions change, making some native species less effective in using resources, as happened with *Saccharina* during this study in the hot summer. If resource availability is the key factor rather than diversity per se, invasion resistance could occur with a smaller number of native species as long as they are efficient at coping with the variability in resources (Dunstan & Johnson 2007).

Nutrients may also play a role in seaweed competitive relationships. The decreasing internal nitrogen content in all three species from May to August reflects the low external nitrogen availability during summer in the area (Strömberg 1986, Pedersen & Borum 1996), with an average nitrogen content of around 0.8 % in August suggesting that all three species were nitrogen limited during this season (Dean & Jacobsen 1986, Duarte 1992, Pedersen & Borum 1996). Internal nitrogen levels were relatively low compared to other published values, such as: in *Fucus*, 2.5 % in May and 1-1.3 % in August (Scotland, Brenchley et al. 1998); in *Saccharina*, 1.6-2.6 % in May and 1-1.6 % in July (Denmark and southwestern Norway, Sjøtun 1993, Nielsen et al. 2014); in *Sargassum*, 1-2 % in June-August (Denmark, Wernberg et al. 2001) and 1.8 % in August (Portugal, Vaz-Pinto et al. 2014).

Low summer nutrients may be particularly limiting for *Sargassum* due to its phenology. *Saccharina* and *Fucus* are perennial and may store nitrogen, so although growth is fastest early in the year when nutrient levels are higher, it can continue for some time in low nutrient conditions during the summer (Strömberg 1986, Sjøtun et al. 1993, Brenchley et al. 1998, Nielsen et al. 2014). On the other hand, *Sargassum* is pseudo-perennial, with thalli growing rapidly from a basal holdfast in February/March until receptacle formation in mid-July, followed by senescence in late August/September (in southwest Norway; timing varies by location (Engelen et al. 2015)). This pseudo-perennial strategy can lead to a competitive advantage in some environments, as rapid growth and air vesicles allow it to form a floating layer, shading algae below (Britton-Simmons 2004). It also allows *Sargassum* to avoid expending energy in maintaining a large thallus over long periods, which may explain its lower carbon content than perennial brown seaweeds (Wernberg et al. 2001; present study). However, in southwestern Norway, this strategy means that *Sargassum* must quickly gain considerable biomass and become reproductive during a period of very low water nutrients.

Fast-growing algae are also more susceptible to nutrient depletion, for example the minimum nitrogen content for growth is 0.71 % in the fast-growing *Ulva lactuca*, compared to 0.55 % in *Fucus vesiculosus* (Pedersen & Borum 1996). A nitrogen content of 0.7 % suggests that *Sargassum* was severely nitrogen-limited by June, which may explain its poor condition, and have led to a competitive disadvantage compared to *Fucus* and *Saccharina*.

Limitations and implications

This experiment only examined competition between adult thalli, as adult competition for light is expected to be important in *Saccharina-Sargassum* interactions (Strong & Dring 2011). However, competition varies depending on the size and life-stage of seaweeds (Olson & Lubchenco 1990). *Saccharina* and *Fucus* tend to recruit in autumn and winter, when *Sargassum* biomass is low and infertile. Presence of *Sargassum* is therefore unlikely to affect recruitment of these species in the NE Atlantic, as it can do in regions where kelp recruitment and *Sargassum* peak-biomass periods coincide (e.g. Ambrose & Nelson 1982). However, *Saccharina* and *Fucus* maintain a perennial canopy which could reduce recruitment of *Sargassum* (Sánchez & Fernández 2006) or survival of recruits through shading (Britton-Simmons 2006, Vaz-Pinto et al. 2012). These effects are also likely to be important in determining the success of *Sargassum* (Vaz-Pinto et al. 2014). Competition can also be influenced by the density of individuals (e.g. Strong and Dring 2011), which was not manipulated in the present study.

The experiment was carried out in the field and took advantage of a natural event where two successive years had contrasting thermal conditions. An advantage of this is that it allowed us to observe effects on the algae in the presence of all their natural interactions; however, a limitation is that factors other than temperature may also have varied between the two years. PAR and UV levels may have been higher during 2014, which can affect macroalgae additively or interactively with temperature (e.g. Tait & Schiel 2013, Xiao et al. 2015). However, the thalli were sublittoral and mean cloud cover was intermediate in both years, which would have reduced the influence of this factor. Since the first year was the year with the highest temperatures, this may also have influenced the results the following year, for example by causing acclimatisation of the seaweeds to higher temperatures, or by influencing the rest of the community, e.g. grazer populations. However, we did not observe large differences in grazers, and the condition of the three species under the different

temperatures was consistent with existing literature, as discussed previously. A final consideration is that *Sargassum* 'survival' in our experiment applied to the laterals, but the holdfast is perennial and may survive to grow again the next year(s) after poor conditions.

Despite these limitations, the observations can be used with existing studies to provide some insight into the effects of hotter summers in the sublittoral fringe. The negative effect on *Saccharina* could lead to reduced abundance in the uppermost subtidal and/or sheltered areas where the water warms more (e.g. Filbee-Dexter et al. 2016), especially if additional stressors are present (Moy & Christie 2012, Andersen et al. 2013). Widespread declines in *Saccharina* have already occurred along the Norwegian coast in a period of hot summers from 1996 - 2002 (Moy & Christie 2012), and marine heatwaves can affect large areas of the NE and NW Atlantic where *Saccharina* is an important component of sheltered seaweed communities (Mills et al. 2013, Joint & Smale 2017). However, temperature ecotypes exist within *Saccharina* (Lüning 1975, Gerard & Du Bois 1988) and it may be able to acclimatise (Andersen et al. 2013), suggesting the effect of temperature may not be uniform. *Fucus* coped well with the hot summer. It can be limited from the subtidal by competitive interactions with kelp (Kain & Jones 1975, Hawkins & Hartnoll 1985), and may therefore become more common in the upper sublittoral where *Saccharina* has declined, as has occurred with warming in Nova Scotia (Filbee-Dexter et al. 2016). It seems unlikely that warming will directly benefit adult *Sargassum* at sheltered sites in this area, as their condition appears to be limited by another factor, but a reduction in *Saccharina* could improve survival of adult *Sargassum* and create physical gaps for *Sargassum* recruitment. However, for a more reliable indication of what may happen with *Sargassum* in this region, research should be conducted examining the causes of its patchy success.

Acknowledgements

We would like to thank the crew of R/V Hans Brattström, exchange students Jessica Field and Leah Strople, and University of Bergen technician Solveig Torkildsen for their practical assistance. Thank you also to Knut Helge Jensen (University of Bergen) and the anonymous reviewers, whose comments improved this manuscript. This work was financially supported by the Research Council of Norway through the project "Towards integrated European marine research strategy and programmes - SEAS-ERA" (ERAC-CT2009-249552) within the framework of the EU ERA-Net initiative (7th Framework Program).

LITERATURE CITED

- Ambrose RF, Nelson BV (1982) Inhibition of giant kelp recruitment by an introduced brown alga. *Bot Mar* 25:265-268
- Andersen GS, Pedersen MF, Nielsen SL (2013) Temperature acclimation and heat tolerance of photosynthesis in Norwegian *Saccharina latissima* (Laminariales, Phaeophyceae). *J Phycol* 49:689-700
- Baer J, Stengel DB (2010) Variability in growth, development and reproduction of the non-native seaweed *Sargassum muticum* (Phaeophyceae) on the Irish west coast. *Estuar Coast Shelf Sci* 90:185-194
- Baer J, Stengel DB (2014) Can native epiphytes affect establishment success of the alien seaweed *Sargassum muticum* (Phaeophyceae)? *Biol Environ* 114B:41-52
- Barton K (2016) MuMIn: Multi-model inference (R package version 1.15.6). <http://CRAN.R-project.org/package=MuMIn> (accessed 25.11.2016)
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw* 67:1-48
- Bolton JJ, Lüning K (1982) Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Mar Biol* 66:89-94
- Brenchley JL, Raven JA, Johnston AM (1998) Carbon and nitrogen allocation patterns in two intertidal fucoids: *Fucus serratus* and *Himantalia elongata* (Phaeophyta). *Eur J Phycol* 33:307-313
- Britton-Simmons KH (2004) Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. *Mar Ecol Prog Ser* 277:61-78
- Britton-Simmons KH (2006) Functional group diversity, resource preemption and the genesis of invasion resistance in a community of marine algae. *Oikos* 113:395-401
- Brodie J, Williamson CJ, Smale DA, Kamenos NA, Mieszkowska N, Santos R, Cunliffe M, Steinke M, Yesson C, Anderson KM, Asnaghi V, Brownlee C, Burdett HL, Burrows MT, Collins S, Donohue PJC, Harvey B, Foggo A, Noisette F, Nunes J, Ragazzola F, Raven JA, Schmidt DN, Suggett D, Teichberg M, Hall-Spencer JM (2014) The future of the northeast Atlantic benthic flora in a high CO₂ world. *Ecol Evol* 4:2787-2798
- Buschbaum C, Chapman A, Saier B (2006) How an introduced seaweed can affect epibiota diversity in different coastal systems. *Mar Biol* 148:743-754
- Chapman ARO (1995) Functional ecology of fucoid algae: twenty-three years of progress. *Phycologia* 34:1-32
- Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. *Mar Ecol Prog Ser* 396:221-233
- Creed JC, Kain JM, Norton TA (1998) An experimental evaluation of density and plant size in two large brown seaweeds. *J Phycol* 34:39-52
- Dean TA, Jacobsen FR (1986) Nutrient-limited growth of juvenile kelp, *Macrocystis pyrifera*, during the 1982–1984 “El Niño” in southern California. *Mar Biol* 90:597-601
- Duarte CM (1992) Nutrient concentration of aquatic plants: Patterns across species. *Limnol Oceanogr* 37:882-889
- Duarte L, Viejo RM, Martínez B, Gómez-Gesteira M, Gallardo T (2013) Recent and historical range shifts of two canopy-forming seaweeds in North Spain and the link with trends in sea surface temperature. *Acta Oecol* 51:1-10
- Dunstan PK, Johnson CR (2007) Mechanisms of invasions: can the recipient community influence invasion rates? *Bot Mar* 50:361-372
- Elton CS (1958) *The ecology of invasions by plants and animals*. Methuen, London
- Engelen AH, Primo AL, Cruz T, Santos R (2013) Faunal differences between the invasive brown macroalga *Sargassum muticum* and competing native macroalgae. *Biol Invasions* 15:171-183
- Engelen AH, Serebryakova A, Ang P, Britton-Simmons K, Mineur F, Pedersen MF, Arenas F, Fernández C, Steen H, Svenson R, Pavia H, Toth G, Viard F, Santos R (2015) Circumglobal invasion by the brown seaweed *Sargassum muticum*. *Oceanogr Mar Biol Annu Rev* 53:81-126
- Filbee-Dexter K, Feehan CJ, Scheibling RE (2016) Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. *Mar Ecol Prog Ser* 543:141-152

- Fortes MD, Lüning K (1980) Growth rates of North Sea macroalgae in relation to temperature, irradiance and photoperiod. *Helgolander Meeresunters* 34:15-29
- Gerard VA (1997) The role of nitrogen nutrition in high-temperature tolerance of the kelp, *Laminaria saccharina* (Chromophyta). *J Phycol* 33:800-810
- Gerard VA, Du Bois KR (1988) Temperature ecotypes near the southern boundary of the kelp *Laminaria saccharina*. *Mar Biol* 97:575-580
- Golléty C, Riera P, Davoult D (2010) Complexity of the food web structure of the *Ascophyllum nodosum* zone evidenced by a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ study. *J Sea Res* 64:304-312
- Harries DB, Harrow S, Wilson JR, Mair JM, Donnan DW (2007) The establishment of the invasive alga *Sargassum muticum* on the west coast of Scotland: a preliminary assessment of community effects. *J Mar Biol Assoc UK* 87:1057-1067
- Hawkins S, Hartnoll R (1985) Factors determining the upper limits of intertidal canopy-forming algae. *Mar Ecol Prog Ser* 20:265-271
- Hawkins SJ, Harkin E (1985) Preliminary canopy removal experiments in algal dominated communities low on the shore and in the shallow subtidal on the Isle of Man. *Bot Mar* 28:223-230
- Institute of Marine Research (Norway) (2016) Forskningsdata. <http://www.imr.no/forskning/forskningsdata/stasjoner/> (accessed 27.10.2016)
- Joint I, Smale DA (2017) Marine heatwaves and optimal temperatures for microbial assemblage activity. *FEMS Microbiol Ecol* 93(2): fiw243
- Jueterbock A, Tyberghein L, Verbruggen H, Coyer JA, Olsen JL, Hoarau G (2013) Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecol Evol* 3:1356-1373
- Kain JM, Jones NS (1975) Algal recolonization of some cleared subtidal areas. *J Ecol* 63:739-765
- Knight M, Parke M (1950) A biological study of *Fucus vesiculosus* L. and *F. serratus* L. *J Mar Biol Assoc UK* 29:439-514
- Lang AC, Buschbaum C (2010) Facilitative effects of introduced Pacific oysters on native macroalgae are limited by a secondary invader, the seaweed *Sargassum muticum*. *J Sea Res* 63:119-128
- Lenth RV (2016) Least-Squares Means: The R Package lsmeans. *J Stat Softw* 69:1-33
- Levin PS, Coyer JA, Petrik R, Good TP (2002) Community-wide effects of nonindigenous species on temperate rocky reefs. *Ecology* 83:3182-3193
- Lüning K (1975) Kreuzungsexperimente an *Laminaria saccharina* von Helgoland und von der Isle of Man. *Helgolander Wiss Meeresunters* 27:108-114
- Lüning K (1990) Seaweeds: their environment, biogeography and ecophysiology. John Wiley & Sons, Inc., New York
- Mann KH (2000) Ecology of coastal waters: with implications for management, 2nd Edition. Wiley-Blackwell, Malden, MA
- Meteorologisk Institutt (Kristiansen S, Tajet HTT, Gangstø R, Mamen J, Szewczyk-Bartnicka H, Heiberg H) (2016) MET info: Været i Norge, Klimatologisk månedsoversikt Mai 2014; Juni 2014; Juli 2014; August 2014; Mai 2015; Juni 2015; Juli 2015; August 2015. http://met.no/Forskning/Publikasjoner/MET_info/ (accessed 18.11.2016)
- Mills KE, Pershing AJ, Brown CJ, Chen Y, Chiang F-S, Holland DS, Lehuta S, Nye JA, Sun JC, Thomas AC, Wahle RA (2013) Fisheries management in a changing climate: lessons from the 2012 ocean heatwave in the Northwest Atlantic. *Oceanography* 26:191-195
- Moy FE, Christie H (2012) Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. *Mar Biol Res* 8:309-321
- Müller R, Laepple T, Bartsch I, Wiencke C (2009) Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. *Bot Mar* 52:617-638
- Nielsen MM, Krause-Jensen D, Olesen B, Thinggaard R, Christensen PB, Bruhn A (2014) Growth dynamics of *Saccharina latissima* (Laminariales, Phaeophyceae) in Aarhus Bay, Denmark, and along the species' distribution range. *Mar Biol* 161:2011-2022

- Norderhaug KM, Fredriksen S, Nygaard K (2003) Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality. *Mar Ecol Prog Ser* 255:135-144
- Norton TA (1977) The growth and development of *Sargassum muticum* (Yendo) Fensholt. *J Exp Mar Biol Ecol* 26:41-53
- Olabarria C, Rodil IF, Incera M, Troncoso JS (2009) Limited impact of *Sargassum muticum* on native algal assemblages from rocky intertidal shores. *Mar Environ Res* 67:153-158
- Olson AM, Lubchenco J (1990) Competition in seaweeds: Linking plant traits to competitive outcomes. *J Phycol* 26:1-6
- Parke M (1948) Studies on British Laminariaceae. I. Growth in *Laminaria Saccharina* (L.) Lamour. *J Mar Biol Assoc UK* 27:651-709
- Parsons TR, Maita Y, Lalli CM (1992) A manual of chemical and biological methods for sea water analysis. Pergamon, New York
- Pedersen MF, Borum J (1996) Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Mar Ecol Prog Ser* 142:261-272
- Pedersen MF, Stæhr PA, Wernberg T, Thomsen MS (2005) Biomass dynamics of exotic *Sargassum muticum* and native *Halidrys siliquosa* in Limfjorden, Denmark—Implications of species replacements on turnover rates. *Aquat Bot* 83:31-47
- Pella E, Colombo B (1973) Study of carbon, hydrogen and nitrogen gas determination by combustion-gas chromatography. *Microchim Acta* 61:697-719
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2015) nlme: Linear and Nonlinear Mixed Effects Models (R package version 3.1-122).
- Plouguerné E, Le Lann K, Connan S, Jechoux G, Deslandes E, Stiger-Pouvreau V (2006) Spatial and seasonal variation in density, reproductive status, length and phenolic content of the invasive brown macroalga *Sargassum muticum* (Yendo) Fensholt along the coast of Western Brittany (France). *Aquat Bot* 85:337-344
- R Development Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Salvaterra T, Green D, Crowe T, O’Gorman E (2013) Impacts of the invasive alga *Sargassum muticum* on ecosystem functioning and food web structure. *Biol Invasions* 15:2563-2576
- Sánchez Í, Fernández C (2005) Impact of the invasive seaweed *Sargassum muticum* (Phaeophyta) on an intertidal macroalgal assemblage. *J Phycol* 41:923-930
- Sánchez Í, Fernández C (2006) Resource availability and invasibility in an intertidal macroalgal assemblage. *Mar Ecol Prog Ser* 313:85-94
- Sánchez Í, Fernández C, Arrontes J (2005) Long-term changes in the structure of intertidal assemblages after invasion by *Sargassum muticum* (Phaeophyta). *J Phycol* 41:942-949
- Scheibling RE, Gagnon P (2006) Competitive interactions between the invasive green alga *Codium fragile* ssp. *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). *Mar Ecol Prog Ser* 325:1-14
- Sfriso A, Facca C (2013) Annual growth and environmental relationships of the invasive species *Sargassum muticum* and *Undaria pinnatifida* in the lagoon of Venice. *Estuar Coast Shelf Sci* 129:162-172
- Simonson EJ, Scheibling RE, Metaxas A (2015) Kelp in hot water: I. Warming seawater temperature induces weakening and loss of kelp tissue. *Mar Ecol Prog Ser* 537:89-104
- Sjøtun K (1985) Ei autøkologisk undersøkjing av *Laminaria saccharina* (L.) Lamour. i Espegrend-området. Cand. real. thesis, University of Bergen, Bergen, Norway
- Sjøtun K (1993) Seasonal lamina growth in two age groups of *Laminaria saccharina* (L.) Lamour. in Western Norway. *Bot Mar* 36:433
- Sjøtun K, Fredriksen S (1995) Growth allocation in *Laminaria hyperborea* (Laminariales, Phaeophyceae) in relation to age and wave exposure. *Mar Ecol Prog Ser* 126:213-222

- Sjøtun K, Fredriksen S, Lein TE, Rueness J, Sivertsen K (1993) Population studies of *Laminaria hyperborea* from its northern range of distribution in Norway. *Hydrobiologia* 260-261:215-221
- Smale DA, Burrows MT, Moore P, O'Connor N, Hawkins SJ (2013) Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecol Evol* 3:4016-4038
- Smale DA, Wernberg T (2013) Extreme climatic event drives range contraction of a habitat-forming species. *Proc R Soc Lond [Biol]* 280: 20122829
- Smith JR (2016) The putative impacts of the non-native seaweed *Sargassum muticum* on native communities in tidepools of Southern California and investigation into the feasibility of local eradication. *Mar Ecol* 37:645-667
- Stachowicz JJ, Tilman D (2005) Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. In: Stachowicz JJ, Tilman D, Gaines, S (eds.) *Species invasions: insights into ecology, evolution, and biogeography*. Sinauer Associates Inc., Sunderland, MA. p 41-64
- Strain EMA, Thomson RJ, Micheli F, Mancuso FP, Airoldi L (2014) Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. *Global Change Biol* 20:3300-3312
- Strong JA, Dring MJ (2011) Macroalgal competition and invasive success: testing competition in mixed canopies of *Sargassum muticum* and *Saccharina latissima*. *Bot Mar* 54:223-229
- Strömgren T (1986) Annual variation in growth rate of perennial littoral furoid algae from the west coast of Norway. *Aquat Bot* 23:361-369
- Tait LW, Schiel DR (2013) Impacts of temperature on primary productivity and respiration in naturally structured macroalgal assemblages. *PLOS ONE* 8:e74413
- Thomsen MS, Wernberg T, South PM, Schiel DR (2016) Non-native seaweeds drive changes in marine coastal communities around the world. In: Hu Z-M, Fraser C (eds) *Seaweed Phylogeography: Adaptation and Evolution of Seaweeds under Environmental Change*. Springer Netherlands, Dordrecht. p 147-185
- Vaz-Pinto F, Olabarria C, Arenas F (2012) Propagule pressure and functional diversity: interactive effects on a macroalgal invasion process. *Mar Ecol Prog Ser* 471:51-60
- Vaz-Pinto F, Martínez B, Olabarria C, Arenas F (2014) Neighbourhood competition in coexisting species: The native *Cystoseira humilis* vs the invasive *Sargassum muticum*. *J Exp Mar Bio Ecol* 454:32-41
- Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux CS (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Clim Change* 3:78-82
- Wernberg T, Thomsen M, Staehr P, Pedersen M (2004) Epibiota communities of the introduced and indigenous macroalgal relatives *Sargassum muticum* and *Halidrys siliquosa* in Limfjorden (Denmark). *Helgol Mar Res* 58:154-161
- Wernberg T, Thomsen M, Stæhr PA, Pedersen M (2001) Comparative phenology of *Sargassum muticum* and *Halidrys siliquosa* (Phaeophyceae: Fucales) in Limfjorden, Denmark. *Bot Mar* 44:31-39
- White LF, Shurin JB (2011) Density dependent effects of an exotic marine macroalga on native community diversity. *J Exp Mar Biol Ecol* 405:111-119
- Wickham H (2009) *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New York
- Wing S, Leichter J, Perrin C, Rutger S, Bowman M, Cornelisen C (2007) Topographic shading and wave exposure influence morphology and ecophysiology of *Ecklonia radiata* (C. Agardh 1817) in Fiordland, New Zealand. *Limnol Oceanogr* 52:1853-1864
- Xiao X, de Bettignies T, Olsen YS, Agusti S, Duarte CM, Wernberg T (2015) Sensitivity and acclimation of three canopy-forming seaweeds to UVB radiation and warming. *PLOS ONE* 10:e0143031
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer-Verlag, New York

Supplementary material

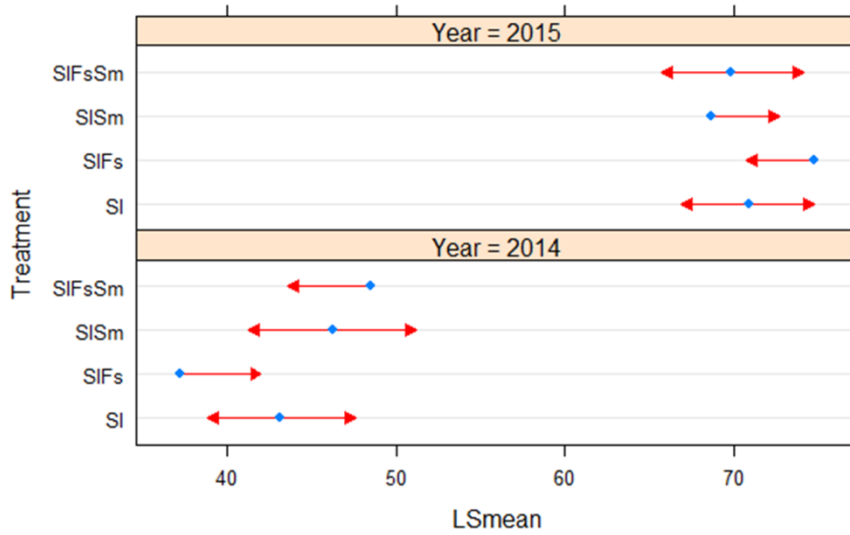


Figure S1. Least-squares means of *Saccharina latissima* end length with comparison arrows (Lenth 2016), by treatment and year, based on a starting length of 40.3 cm. “SI” = *Saccharina latissima*, “Fs” = *Fucus serratus*, “Sm” = *Sargassum muticum*.

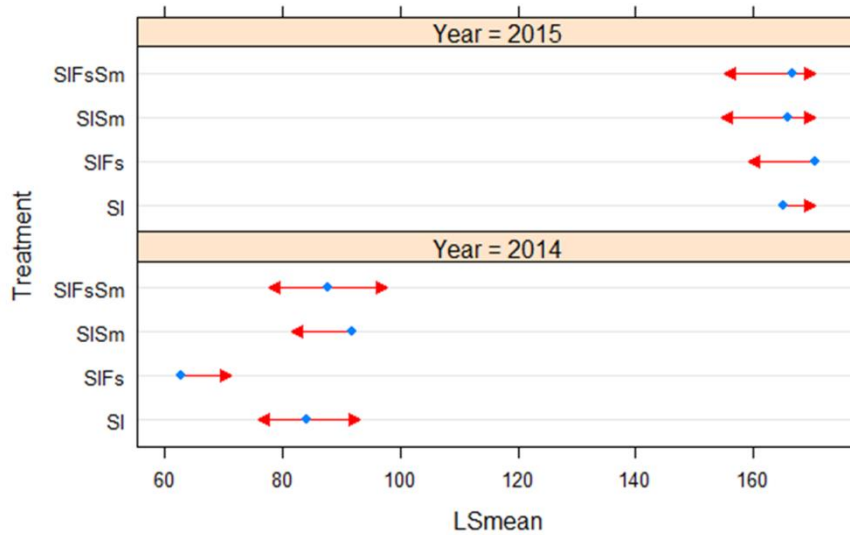


Figure S2. Least-squares means of *Saccharina latissima* end weight with comparison arrows, by treatment and year, based on a starting weight of 84.1 g. Codes and arrows as in Figure S1.

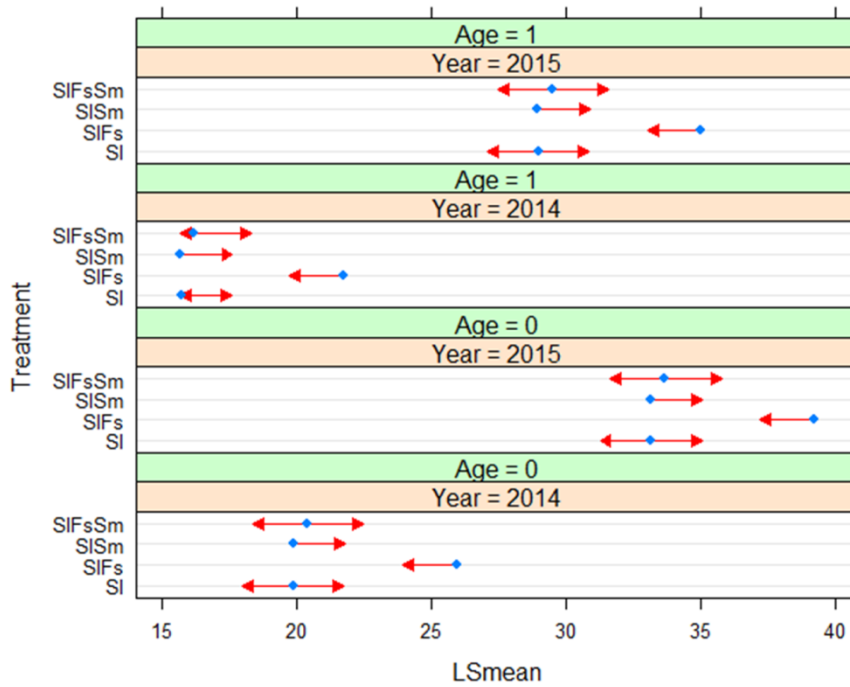


Figure S3. Least-squares means of *Saccharina latissima* growth with comparison arrows by treatment, year and age, based on a starting weight of 90.7 g. Codes and arrows as in Figure S1.

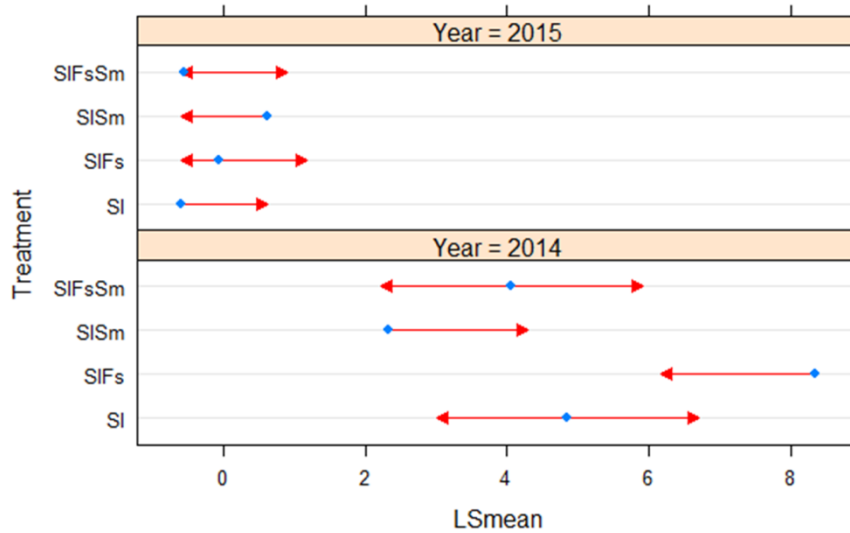


Figure S4. Least-squares means of *Saccharina latissima* erosion with comparison arrows by treatment and year, based on a starting weight of 90.7 g. Codes and arrows as in Figure S1.

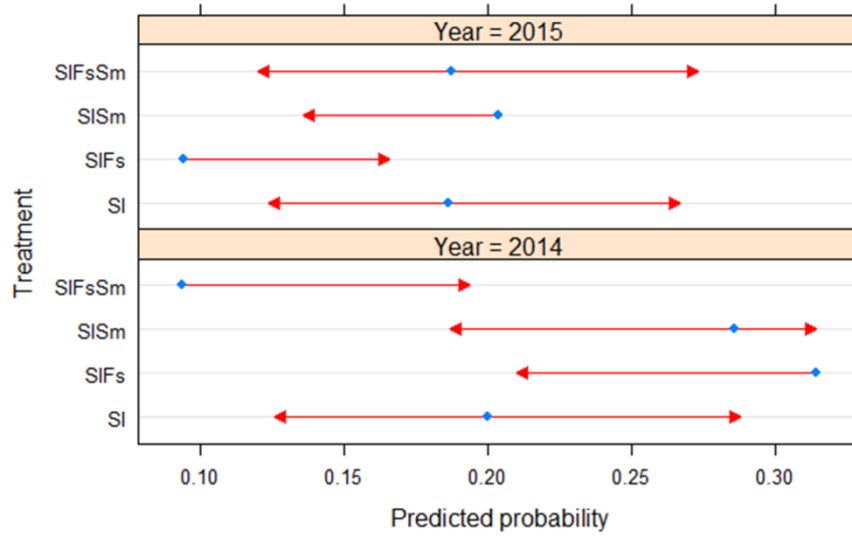


Figure S5. Least-squares means showing the predicted probability of *Saccharina latissima* death/loss with comparison arrows, by treatment and year. Codes and arrows as in Figure S1.

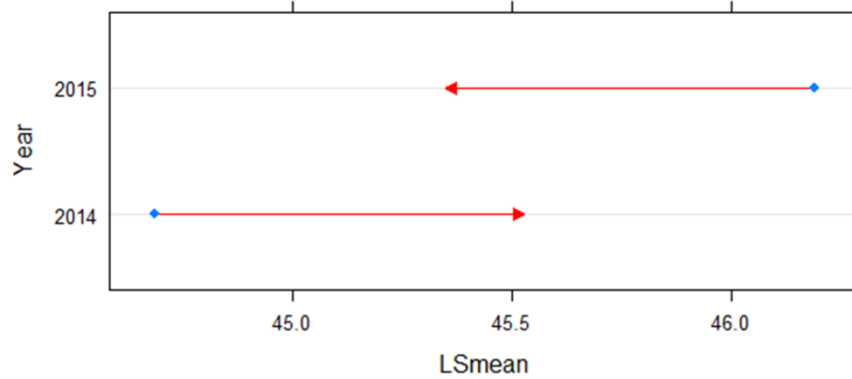


Figure S6. Least-squares means of *Fucus serratus* end length, with comparison arrows, by year, based on a starting length of 40.7 cm. Arrows as in Figure S1.

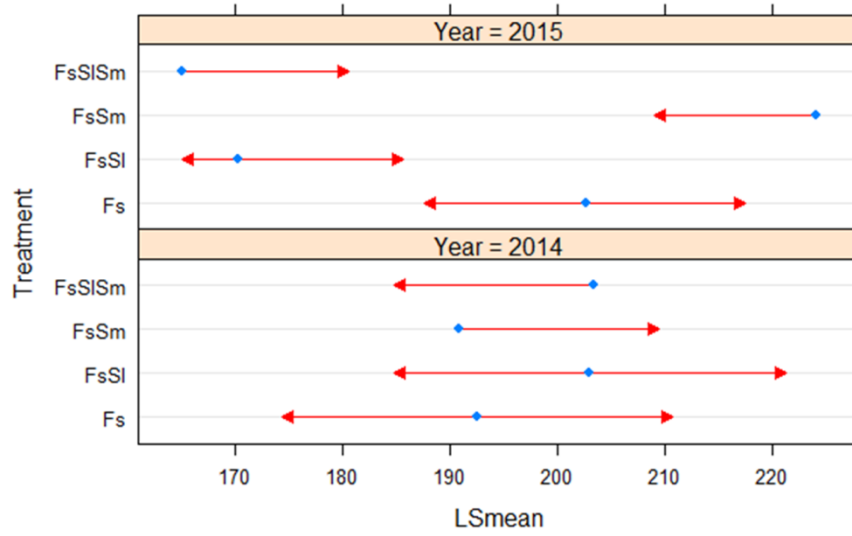


Figure S7. Least-squares means of *Fucus serratus* end weight with comparison arrows, by treatment and year, based on a starting weight of 112.5 g. Codes and arrows as in Figure S1.

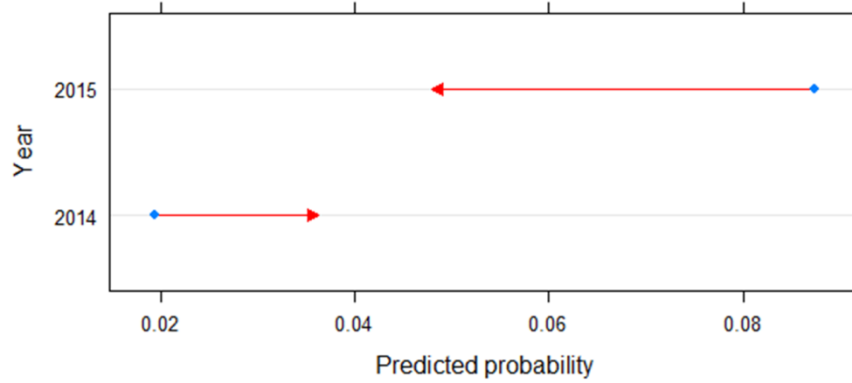


Figure S8. Least-squares means showing the predicted probability of *Fucus serratus* death/loss with comparison arrows, by year. Arrows as in Figure S1.

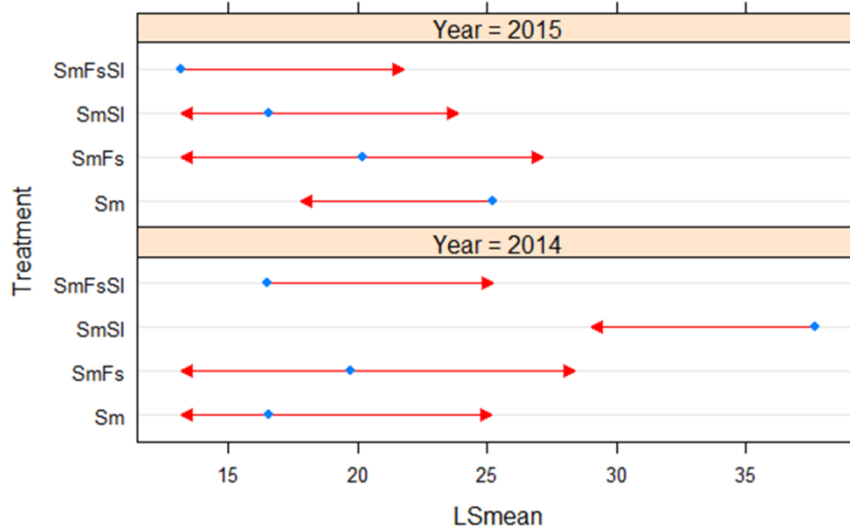


Figure S9. Least-squares means of *Sargassum muticum* end weight with comparison arrows, by treatment and year, based on a starting weight of 18.7 g. Codes and arrows as in Figure S1.

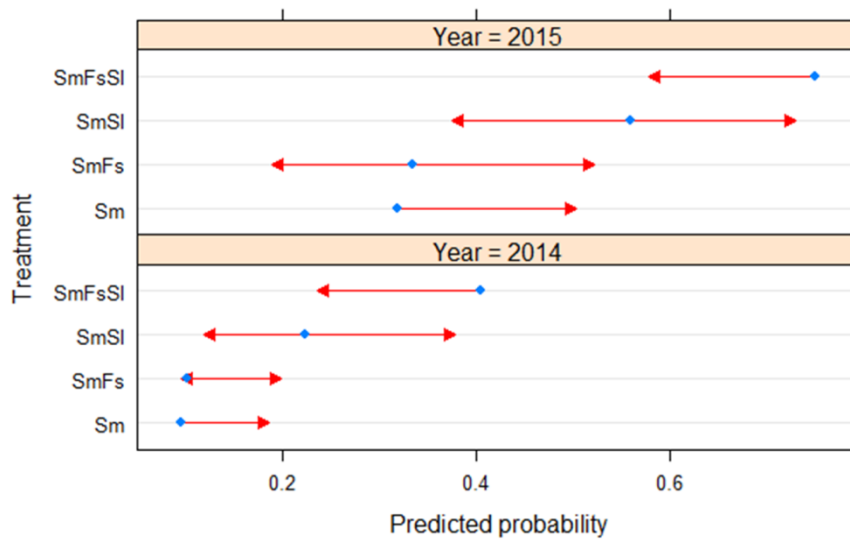


Figure S10. Least-squares means showing the predicted probability of *Sargassum muticum* death/loss with comparison arrows by treatment and year, based on a starting weight of 19.0 g. Codes and arrows as in Figure S1.