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

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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 fucoid *Fucus serratus*. All 3 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 during a hot summer and again during a cool summer. The results showed that the species and their competitive interactions were affected by the different thermal conditions. *S. latissima* was the most successful species in the cool summer and had an impact on the other 2 species, but it was strongly negatively affected by the hot summer. Under these conditions, *F. 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.

KEY WORDS: 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 important 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 to 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, Fil-

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*Corresponding author: caroline.s.armitage@gmail.com bee-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 in 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 2 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 3 species are canopy-forming, but have different morphologies and growth patterns (see Fig. 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 & Fernández 2005, Sánchez et al. 2005, Harries et al. 2007, 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* on the southwestern coast of Norway is close to its European northern limit, 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 the abundance of these species 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 the 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 investigated the competitive relationships between *Saccharina latissima*, *F. serratus* and *Sargassum muticum* in a field experiment on the southwest coast of Norway, during 2 summers with widely different temperatures. The 3 large brown seaweeds represent very different morphologies and growth habits, 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 3 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 3 species; (2) competition between the 3 species; and (3) how these 2 factors interact.

MATERIALS AND METHODS

Experimental design

The experiment was carried out on the southwest coast of Norway, which is in the cold temperate Northeast 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 to 2009 mean, 1 m depth; Institute of Marine Research 2016).

Thalli of *Sargassum muticum*, *Fucus serratus* and *Saccharina latissima* (hereafter referred to by genus alone; *Sargassum*, *Fucus*, and *Saccharina*, respectively) 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 3 species by attaching individuals to metal grids in a substitutive design. There were 7 assemblage types: (1) *Saccharina* only, (2) *Fucus* only, (3) *Sargassum* only, (4) *Saccharina* and *Fucus* mix, (5) *Saccharina* and *Sargassum* mix, (6) *Fucus* and *Sargassum* mix, and (7) *Saccharina* and *Fucus* and *Sargassum* mix. These assemblages will hereafter be referred to by an abbreviation of the species name shortened to 2 letters (*Sl* for *Saccharina*, *Fs* for *Fucus*, *Sm* for *Sargassum*; for example, *SlFs* for the *Saccharina* and *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 compared these forms of competition, rather than comparisons to no competition. Two replicates of each assemblage were made in 2014, and 3 replicates in 2015.

In all treatment types thallus density was kept constant at 50 thalli m^{-2}. In the single-species assemblages (types 1 to 3), 20 thalli of each species were used (an experimental area of 0.4 m^2); in the 2-species assemblages (types 4 to 6), 18 thalli of each species were used (0.72 m^2); and in the assemblages with all 3 (type 7), 16 thalli of each species were used (0.96 m^2). This thallus density is higher than the experimental densities of Strong & Dring (2011), but lower than Creed et al. (1998). We consider it realistic from reported densities: mature *Fucus* at 88 to 208 m^{-2} on the Isle of Mann (Creed et al. 1998); *Sargassum* at 57 m^{-2} in California (Ambrose & Nelson 1982), up to 64 m^{-2} in France (Plouguerné et al. 2006) and up to 72 m^{-2} in Ireland (Baer & Stengel 2010); *Saccharina* at 40 m^{-2} 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 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 (Fig. 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

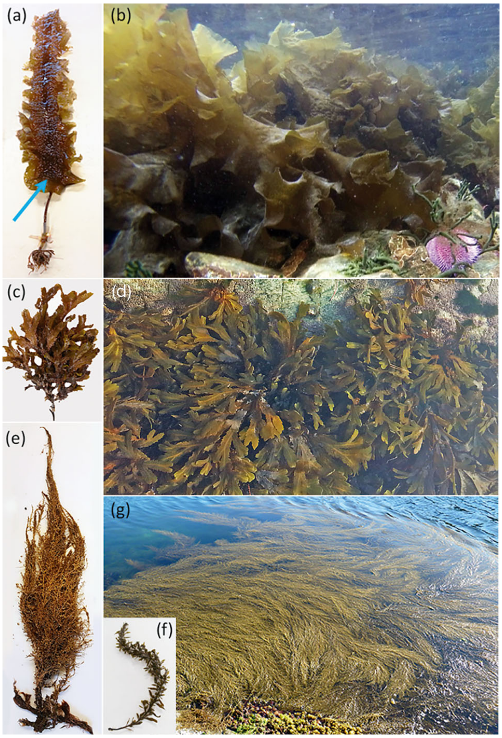

Fig. 1. Growth habits of the 3 seaweeds in southwestern Norway. (a) *Saccharina latissima* forms a broad blade, which grows from the top of the stipe (arrow). (b) The blade can increase in length quickly and lies over the substratum. (c) *Fucus serratus* has leathery, serrated, dichotomous branches with apical growth, resulting in an increasingly bushy structure over time. (d) *F. serratus* tends to spread out in a layer over the substratum. (e) *Sargassum muticum* grows rapidly from the apex and can form a long thallus (here pictured attached to a piece of rope at the base). (f) The main axis grows from early spring, becoming longer and increasingly bushy with more and longer side branches (e) by late summer. (g) Gas vesicles allow *S. muticum* to float in the water column

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 again for re-measurement. The experimental site was outside Espegrend Marine Biological Station (University of Bergen), on the shorelines of 2 islands facing each other across a narrow channel sheltered from waves (60.26836° N, 5.21773° E). The substratum consisted of 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 the site (Tinytag aquatic 2; Gemini data loggers). In 2015, seawater samples were taken to assess levels of nitrite, nitrate and phosphate (see 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), in nitrogen–carbon configuration: filters, sediments, soils. The measurements were performed with the following parameters: carrier gas (helium) 130 ml min^{-1}; reference gas (helium) 100 ml min^{-1}; oxygen 250 ml min^{-1}; 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 among grids due to practical limitations (from 77 to 92 d); therefore, before analysis the end length and weight measurements of each individual thallus were standardised to the shortest time (77 d), 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 3 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 yr old; 4 thalli which were 2 yr 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 less than 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).

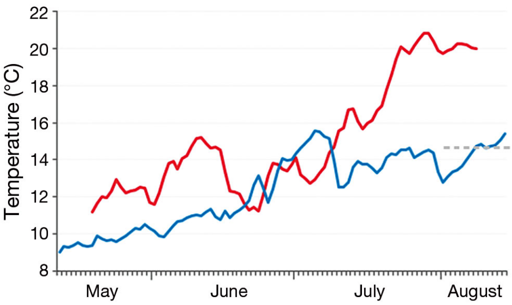

Fig. 2. Mean daily seawater temperature (1 m depth) during the experimental period in 2014 (red) and 2015 (blue). Dotted grey line: mean August sea surface temperature (1980 to 2009, 1 m depth) for this region. Note that the *y*-axis scale does not begin at 0

For the LMMs, an estimate of R^2 was obtained using the R package 'MuMIn' (Barton 2016), and plots were created using the R base package and 'ggplot2' (Wickham 2009). Least-squares means were calculated using package 'LSmeans'. Least-squares means are the predictions from the models for each assemblage type and/or year (Lenth 2016), and are provided in Figs. S1–S10 in the Supplement at www.int-res.com/articles/suppl/m573p085_supp.pdf.

RESULTS

Environmental conditions

Apart from a 3 wk period in late June/early July, daily mean temperatures were higher in the 2014 experiment (Fig. 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 d where mean daily seawater temperatures were at or above 19.4°C (max. recorded temperature: 21.5°C), while in 2015, the temperature never exceeded 16.2°C. The large difference in temperatures means that hereafter 2014 is referred to as the hot year, and 2015 as the cool year.

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 3 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). Seawater nutrients were low throughout summer 2015, with no recordings of nitrate, nitrite or phosphate >0.6 µmol l^{-1} (Table 1).

Table 1. Nutrients in seawater during the experimental period in 2015 (range across samples, given in µmol l^{-1}). Date format = (dd/mm/yyyy)

Date	No. 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

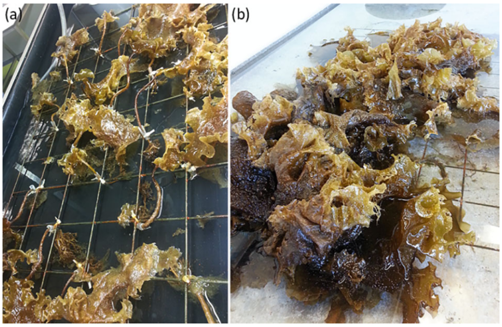

Fig. 3. Experimental assemblages of *Saccharina latissima* only, at the end of the experiment in (a) 2014 and (b) 2015

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 (Figs. 3–5). 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* (*SlFs*) than in some or all of the other assemblage types, with negative changes on average (Fig. 4, Figs. S1 & S2 in the Supplement at www.int-

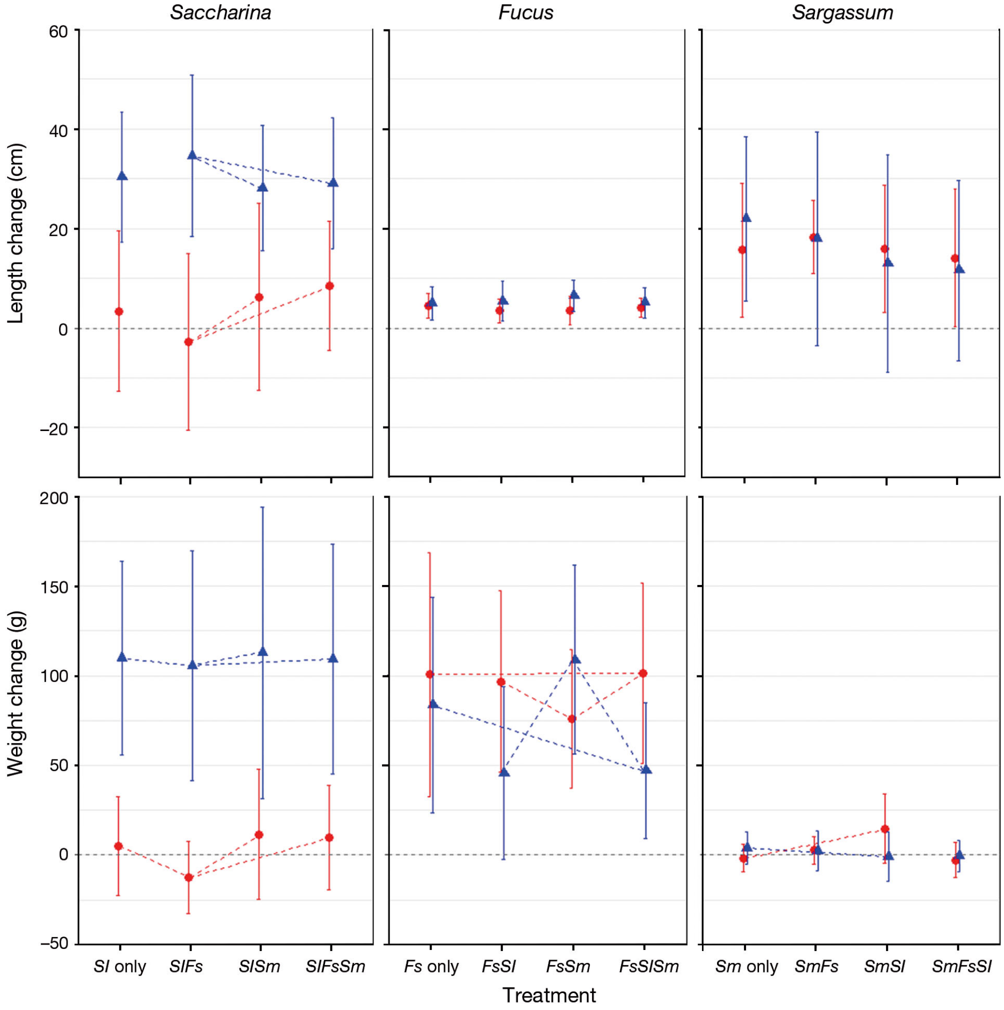

Fig. 4. Mean length change (top row) and weight change (bottom row) of *Saccharina latissima* (*Sl*; n = 133 in 2014, 177 in 2015, left column), *Fucus serratus* (*Fs*; n = 141 in 2014, 196 in 2015, middle column), and *Sargassum muticum* (*Sm*; n = 110 in 2014, 112 in 2015, right column) during the 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. *SlFs* is the same as *FsSl*). Significant interactions (Table 2) are shown as dotted lines between treatment types. Error bars: SD. Length change of *Saccharina* is the result of both growth and erosion of the blade, which are examined separately in Fig. 5

res.com/articles/suppl/m573p085_supp.pdf). This is likely connected to patterns in growth and erosion. *Saccharina* growth was always significantly higher in the assemblage with *Fucus* (*SlFs*) than the other treatments (Table 2, Figs. 5 & 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* (*SlFs*) than the other treatments (especially compared to the assemblage with *Sargassum*; *SlSm*); however, in the cool year, erosion was low in all assemblage types (Table 2, Figs. 5 & S4). Starting length and weight of *Saccharina* were positively related to end length and weight respectively, but thallus age was unrelated to both (Table 2).

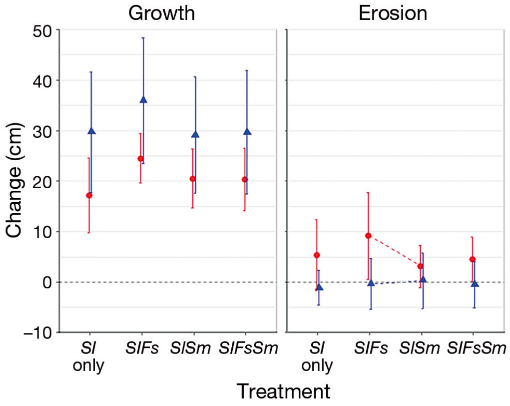

Fig. 5. Mean growth and erosion (±1 SD) of *Saccharina latissima* during the experiment in different treatments and years (n = 74 in 2014, n = 163 in 2015). Higher positive numbers on the erosion axis indicate that more of the blade was eroded. Symbols, colours, and abbreviations as in Fig. 4

In 2015, the mean (±SD) growth of *Saccharina* was 31 ± 12 cm, compared to 20 ± 7 cm in 2014 (Fig. 5). The maximum individual growth observed was 70 cm (2015). The age of the thalli influenced growth rate (Table 2), with mean growth of those that were <1 yr old being higher than those >1 yr old (Fig. 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

Table 2. Results of statistical analyses carried out to examine the effect of treatment and year (Yr) 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 the model; (+) included in the model due to significant interaction. p-values are shown in *italics* if over the 0.05 level; all are unadjusted. R^2 values indicate the proportion of variation explained by the fixed effects in the model; 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 2 columns. Predictions from these models (as least-squares means) are presented in the Supplement at www.int-res.com/articles/suppl/m573p085_supp.pdf. n/a = not applicable

Species and	Predictors					R^2	Differences between treatment levels	
response	Starting size	Age	Year	Treat	Year × Treat			
Saccharina latissima								
Length	$L_1 = 6.79$, p = 0.009	NS	+	+	$L_3 = 12.1$, p = 0.007	0.46 (0.47)	Yr × *SlFs* – Yr × *SlSm* Yr × *SlFs* – Yr × *SlFsSm*	$t_9 = -2.70$, 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 × *SlFs* – Yr × *Sl* Yr × *SlFs* – Yr × *SlSm* Yr × *SlFs* – Yr × *SlFsSm*	$t_9 = -2.52$, 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)	*SlFs* – *Sl* *SlFs* – *SlSm* *SlFs* – *SlFsSm*	$t_{12} = -3.40$, 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 × *SlFs* – Yr × *SlSm*	$t_9 = 3.13$, p = 0.012
Death/loss	NS	n/a	+	+	$\chi^2_3 = 7.17$, p = *0.067*	n/a	Yr × *SlFs* – Yr × *Sl* Yr × *SlFs* – Yr × *SlFsSm*	$z = 1.79$, p = *0.073* $z = 2.47$, p = 0.014
Fucus serratus								
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 × *FsSl* Yr × *Fs* – Yr × *FsSlSm* Yr × *FsSm* – Yr × *FsSl* Yr × *FsSm* – Yr × *FsSlSm*	$t_9 = -2.05$, 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		
Sargassum muticum								
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 × *SmSl* – Yr × *Sm* Yr × *SmSl* – Yr × *SmFs*	$t_9 = 2.97$, 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	*SmFsSl* – *Sm* *SmFsSl* – *SmFs*	$z = -2.34$, p = 0.019 $z = -2.24$, p = 0.025

contained a higher proportion of age 0+ thalli than in 2014 (2014: 16 of 74 thalli; 2015: 62 of 163 thalli). Despite this, there was clearly also an effect of year on growth (Table 2, Fig. 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 LRT, but the results of the Wald test indicated that the effect of year on *Saccharina* survival in the assemblage with *Fucus* (*SlFs*) was different from the effect in the assemblage with all 3 species (Table 2). *Saccharina* survival was lower in the hot year than in the cool year in the *SlFs* treatment, while it remained similar across both years in the *Saccharina*-only treatment (Figs. 6 & S5).

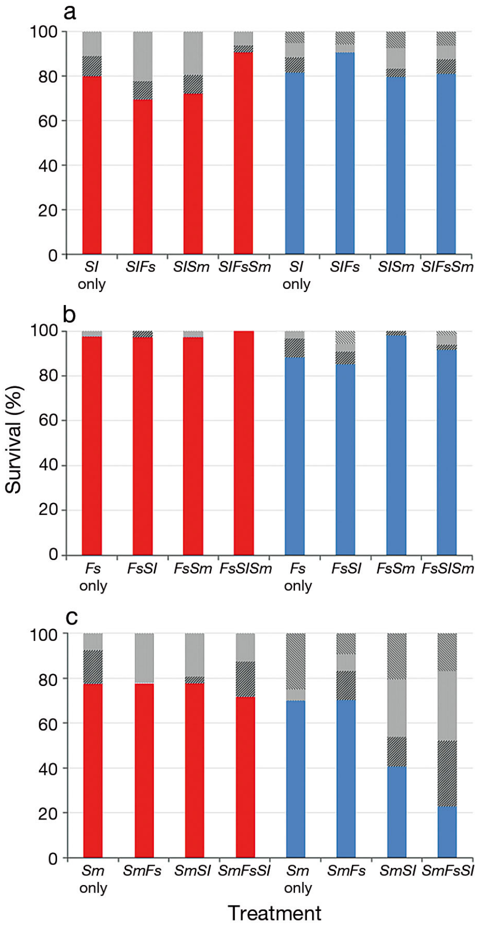

Fig. 6. (a) Total survival of *Saccharina latissima* (n = 365), (b) *Fucus serratus* (n = 360) and (c) *Sargassum muticum* (n = 360) in summer 2014 (red) and summer 2015 (blue). Coloured bars: percentage of surviving thalli in each treatment; grey areas: percentage of thalli which died or were lost during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

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. Conversely, carbon content increased by around 3% (Fig. 7).

Fucus serratus

The majority of *Fucus* showed positive length and weight changes in both years (Fig. 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 (Fig. 4). Year had little consistent effect on weight,

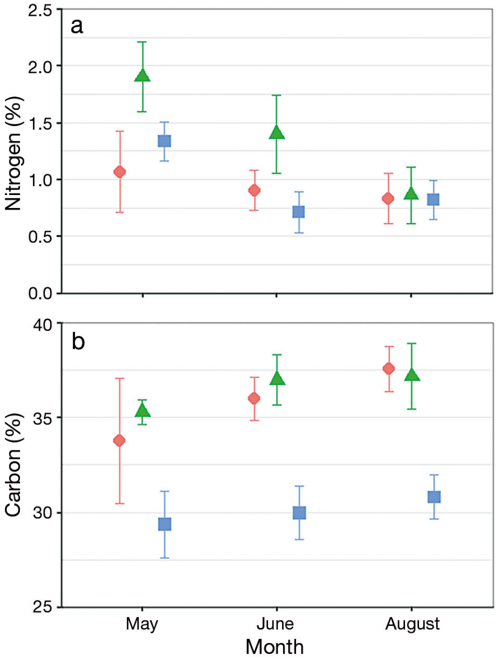

Fig. 7. Seaweed (a) nitrogen and (b) carbon content over the experiment during summer 2015. Mean percentage content of dry weight is shown for each species, ±1 SD. Red circles: *Saccharina latissima* (n = 27), green triangles: *Fucus serratus* (n = 24) and blue squares: *Sargassum muticum* (n = 22)

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 (Fig. 4). This effect was most clear in comparisons with the assemblage with *Sargassum* (*FsSm*) (Table 2, Figs. 4 & S7). *Fucus* showed the highest overall survival of the 3 species (94%). There was a slight but significant reduction in survival from 98% in 2014 to 91% in 2015 (Fig. 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 3 species were similar (Fig. 7). The carbon content of *Fucus* was much higher than *Sargassum*, and increased throughout the summer (Fig. 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 to 25 cm (but with large variation; Fig. 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, *SmFs*, *SmFsSl*), weight change was always low, but in the assemblage with *Saccharina* (*SmSl*), weight change was higher in the hot year compared to the cool year and other treatments (Figs. 4 & 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, Fig. 6). In contrast to the other 2 species, *Sargassum* survival was positively linked with 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, SE = 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 (Fig. 7). The nitrogen content in June 2014 was similar to June 2015 (0.7 ± 0.1% in 2014; 0.71 ± 0.18% in 2015). As with all the species, the carbon content of *Sargassum* increased through the summer, but was consistently 5 to 7% lower than *Fucus* and *Saccharina* (Fig. 7).

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 have shown similar negative effects, with blade weakness, tissue loss and mortality increased at 18 to 20°C, and total mortality at 21 to 23°C (Bolton & Lüning 1982, Andersen et al. 2013, Simonson et al. 2015). In contrast, average summers in southwestern Norway (such as 2015) provide near-ideal conditions for *Saccharina*, which has optimum growth at 10 to 15°C (Lüning 1990, Andersen et al. 2013). The elongation rate for *Saccharina* in 2015 was on average 0.4 cm d^{-1}, which is similar to a former study of tagged individuals (around 0.5 cm d^{-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* exhibits optimum growth at only slightly higher temperatures than *Saccharina* (15°C), but 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 & 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 wk^{-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 & 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, authors' 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 a 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 blades 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 for which competition occurs 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 2 ways. The first was temperature-dependent, as shown by the differences in erosion, weight and mortality of *Saccharina* between the cool and hot summers in the assemblage with *Fucus*. A possible explanation is interference competition. When water temperatures are maintained at ≥18°C, the blades of *Saccharina* become considerably more fragile (Simonson et al. 2015), potentially making it more susceptible to abrasion and tearing by the leathery, serrated *Fucus* branches. The second effect was increased growth of *Saccharina* in the *SlFs* 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, width 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 3 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 between *Fucus* and *Saccharina*. Strong & 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 fucoid *Cystoseira humilis*. The poor condition of *Sargassum* at the end of the present experiment may have limited its competitive ability, but this would 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 a 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 fucoid *C. humilis* on *Sargassum* growth. However, *Saccharina* appeared to have a negative influence on *Sargassum* survival under average temperatures. This differs from the findings of Strong & 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 appears 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* in our study during 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 3 species from May to August reflects low external nitrogen availability during summer in the study area (Strömgren 1986, Pedersen & Borum 1996), with an average nitrogen content of around 0.8% in August suggesting that all 3 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 *Fucus*: 2.5% in May and 1 to 1.3% in August (Scotland; Brenchley et al. 1998); *Saccharina*: 1.6 to 2.6% in May and 1 to 1.6% in July (Denmark and southwestern Norway; Sjøtun 1993, Nielsen et al. 2014); *Sargassum*: 1 to 2% in June through 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 (Strömgren 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 or March until receptacle formation in mid-July, followed by senescence in late August or 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, this 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. The presence of *Sargassum* is therefore unlikely to affect recruitment of these species in the NE Atlantic, as it can 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.

This experiment was carried out in the field and took advantage of a natural event where 2 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 2 years. Photosynthetically active radiation (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 had 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 3 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, our observations can be used with existing studies to provide some insight into the effects of hotter summers in the sublittoral fringe. The negative effects 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 during a period of hot summers from 1996 to 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.

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