Aquatic Botany 133 (2016) 70–78

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Interactive effects of increasing temperature and nutrient loading on the habitat-forming rockweed *Ascophyllum nodosum*

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ARTICLE INFO

Article history:
Received 31 December 2015
Received in revised form 2 June 2016
Accepted 4 June 2016
Available online 6 June 2016

Keywords:
Ascophyllum nodosum
Juvenile growth
Climate warming
Nutrient loading
Interactive effects

ABSTRACT

Perennial seaweeds are dominant primary producers and foundation species along rocky shores, providing essential ecosystem functions and services. Although increasingly affected by various anthropogenic activities, the cumulative effects of multiple stressors are little known. We tested the interactive effects of nutrient enrichment and increased water temperatures on growth, nitrogen retention and carbon storage in juvenile *Ascophyllum nodosum* from Nova Scotia, Canada (44° 29.9′ N, 63° 31.7′ W) using a multi-factorial laboratory experiment. Temperature strongly affected growth, significantly reducing weight and length gain from 16 °C to 20 °C and 24 °C. Medium nutrient enrichment enhanced while high enrichment slowed rockweed growth at lower temperatures, yet these effects disappeared with warming. Nitrogen retention in rockweed tissue significantly increased with nutrient enrichment and decreased with warming, whereas carbon storage remained unaffected. These individual and interactive effects of nutrient loading and climate warming may alter the structure and function of rockweed habitats with potentially far-reaching ecological and economic consequences.

1. Introduction

Perennial seaweeds play critical roles in coastal ecosystems (Worm and Lotze, 2006). Laminarians (kelps) and fucoids are foundation species that form canopies, providing important ecological services: they are involved in nutrient cycling; store nitrogen and carbon; and add energy to food webs (Worm et al., 2000; Schmidt et al., 2011; Seeley and Schlesinger, 2012). Additionally, they provide essential habitat and shelter for invertebrate, vertebrate and algal communities (Thompson et al., 2002; Schmidt et al., 2011; Tuya et al., 2011; Wernberg et al., 2011).

The fucoid rockweed *Ascophyllum nodosum* (L.) Le Jolis (hereafter *Ascophyllum*) is found along rocky shores of the temperate North Atlantic Ocean as well as parts of the Arctic Ocean (Sharp, 1987). In the northwest Atlantic, it ranges from New Jersey to Baffin Island in the Canadian Arctic; in the northeast Atlantic, it extends from northern Portugal to the White Sea in the Russian Arctic (Sharp, 1987; Kerin, 1998). Given the diversity and importance of the ecological services rockweed provides, it is listed as a “high-priority” species for protection in the United States and Canada (Wippelhauser, 1996), a “priority species” in Northern Ireland (Morton, 2011) and a “high-sensitivity species” in the UK (Hill and White, 2008). However, rockweed is also economically important with commercial harvests increasing in recent decades (Seeley and Schlesinger, 2012).

Like other ecologically important coastal ecosystems, rockweed habitats are exposed to increasing anthropogenic impacts, including nutrient loading, climate change and direct harvesting (Lotze et al., 2006; Worm and Lotze, 2006; Schmidt et al., 2011). On a global scale, humans have doubled nitrogen loading to coastal waters in post-industrial times (Millennium Ecosystem Assessment, 2005), whereas on local scales, nitrogen and phosphorus loading has increased up to 10-fold (Lotze et al., 2006). Rockweeds and other vegetation, such as seagrass meadows and wetlands, contribute to nutrient cycling and storage thereby diminishing the effects of land-derived nutrient export to the open ocean (Lotze et al., 2006). *Ascophyllum* can also store nitrogen and phosphorus in its tissues to accommodate seasonal changes in nutrient supply (Fletcher, 1996; Chopin et al., 1996, 1997). However, increased nutrient loading can change the species composition and abundance of primary producers (Duarte, 1995) and alter a coastal ecosystem’s ability to store and cycle nutrients (Worm et al., 2000). Although slight increases in nutrient levels have been shown to enhance rockweed growth, high nutrient levels can result in overgrowth by ephemeral algae (Kraberg and Norton, 2007). In some areas, *Ascophyllum* has been

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http://dx.doi.org/10.1016/j.aquabot.2016.06.002
0304-3770/

declining because of overgrowth and replacement by ephemeral algae (Rueness, 1973; Fletcher, 1996; Worm and Lotze, 2006).

Anthropogenic greenhouse gas emissions have also increased exponentially in the post-industrial era resulting in a net warming effect (Solomon, 2007). Surface seawater temperature (SST) has increased in the Canadian Maritimes since 2000 (Ugarte et al., 2009) and in Eastern North America is predicted to rise by 3 °C in the 21st century (Solomon, 2007). The growth rate of *Ascophyllum* is sensitive to changes in water temperature (Vadas et al., 1976, 1978; Wilce et al., 1978; Keser et al., 1998). Moderate increases in temperature can lead to faster apical growth and extend the season of optimal growth. With greater increases in temperature, however, growth slows or stops and high temperatures can be lethal for *Ascophyllum* (Keser et al., 1998; Wilson et al., 2015). Thus, increasing temperature is predicted to shift the distribution range of rockweed northward (Jueterbock et al., 2013) and shift the composition of *Ascophyllum*-dominated habitats to mixed fucoid beds by favouring more opportunistic fucoid species like *Fucus vesiculosus* (Ugarte et al., 2010).

While more attention has been devoted to the cumulative and interactive effects of environmental or anthropogenic factors on aquatic ecosystems in recent years (see review by Crain et al., 2008), significant gaps remain in our understanding of the effects of multiple stressors on species' growth and function (Wernberg et al., 2012). For annual green algae, rising temperatures and nutrient loading have shown strong synergistic effects on growth (Lotze and Worm, 2002). In the case of *Ascophyllum*, the interactive effects of nutrient loading and a warming climate are so far unknown. In Norway, however, the combined effects of eutrophication and warming have been shown to cause the collapse of kelp forest (Moy and Christie, 2012). Thus, we could expect potentially strong cumulative effects on rockweed growth and nutrient storage with potential consequences on the ecosystem structure, function and the services it provides. Therefore, the aim of this study was to investigate the individual and interactive effects of rising temperatures and nutrient loading on rockweed growth and carbon and nutrient storage. To do so, we performed a multi-factorial laboratory experiment with juvenile rockweed plants exposed to three levels of temperature and four levels of nutrient enrichment in a fully crossed design. Our results provide insight into this seaweed's response to nutrient enrichment, climate change and their interaction, which can help predict the future role that *Ascophyllum* may play in coastal community structure, ecosystem services as well as the viability of expanding rockweed harvests.

2. Materials and methods

2.1. Collection of Ascophyllum plants

On June 29th, 2011, *Ascophyllum* plants of approximately the same length and age were harvested from the intertidal zone at Duncan's Cove, Nova Scotia, Canada (44° 29.9′ N, 63° 31.7′ W). This site is a small embayment on the open Atlantic coast and protected from wave exposure. At low tide, plants with their holdfast were scraped from rocks; intact fronds were removed from the holdfast and stored in glass jars filled with seawater in a cooler overnight. Fronds were then sorted; all those selected for the experiment were between 5 and 9 cm in length and had not yet laid down the first air vesicle. This ensured that all fronds were sexually immature and, therefore, somatic growth could be examined in the absence of reproductive tissue growth.

2.2. Nutrient and temperature treatments

Four nutrient concentrations and three temperatures were chosen to represent different nutrient enrichment and climate warming scenarios. Nutrient treatments were prepared using stock solutions of sodium nitrate and sodium phosphate and contained nitrate (NO_3) and phosphate (PO_4) in a 10:1 ratio, which is comparable to ratios observed in the field (Lotze and Worm, 2002). The four treatment levels represented ambient (control), low, medium and high levels of nutrient enrichment (NO_3/PO_4 at 0/0, 4/0.4, 20/2 and 100/10 μmol L^{-1} respectively). These four levels correspond to background summer (0/0) and winter (4/0.4) concentrations seen in open coastal waters off Nova Scotia, concentrations in nutrient-loaded Atlantic Canadian estuaries (20/2) and concentrations in highly eutrophic regions, such as areas in the Baltic and North Seas (100/10) (Lotze and Worm, 2002).

For the three temperature treatments, the lowest temperature (16 °C) was chosen to represent early summer (May–June) and 20 °C to represent late summer (August–September) seawater conditions in protected coastal areas of Nova Scotia, Canada (Lotze and Worm, 2002; Wilson et al., 2015). The upper temperature of 24 °C was selected because a warming of Eastern North America by ~3 °C during the 21st century is predicted by Multi-Model Data (MMD) models (Solomon, 2007). The large number of experimental units made it logistically necessary to incubate replicates in three adjacent temperature controlled chambers set at 16, 20 and 24 °C (Lotze and Worm, 2002; Clark et al., 2013). However, each plant was held in its own 1-L microcosm, which was supplied with seawater and air from a common source, and exposed to the same light treatment. A control experiment (see below) confirmed that *Ascophyllum* growth did not differ among chambers when set at the same temperature, therefore eliminating the potential effects of pseudo-replication. Temperature within microcosms was monitored throughout the experiment using HOBO® Pendant Temp/Light Data Loggers as well as verified daily with a VWR™ QUARTZ digi-thermo, revealing consistent variation of ±1 °C. All microcosms were exposed to a 14:10 h light:dark cycle with fluorescent light tubes (Coralife 50/50) providing ambient irradiance. Irradiance was monitored daily with a light meter (LI-COR Inc. LI-250A) as well as continuously using HOBO® Pendant Temp/Light Data Loggers and kept constant at 100–120 μmol m^{-2} s^{-1}.

2.3. Laboratory experiment

The experiment ran for nine weeks in July and August 2011 since the main growth period for *Ascophyllum* in the north Atlantic falls between summer and early fall (Peckol et al., 1988; Åberg, 1992; Vadas et al., 2004). Until the start of the experiment, fronds were acclimated to and kept at 16 °C and ambient nutrient concentrations for twelve days. Then, all fronds were towel dried and weighed (wet weight), photographed and the length was measured to the nearest mm. Each frond was then housed in a 1 l glass jar containing 900 ml of filtered (0.1 μm) seawater sourced from Halifax Harbour, enriched with different levels of nutrients according to their treatment group. Five replicates were used for each temperature x nutrient treatment for a total of 60 experimental units. Fronds were tied to stainless steel nuts to anchor them at the base of the jars so that they stood erect. Air stones continually supplied air to each jar to ensure water movement. The jars in the 24 °C chamber were placed in water baths in order to dissipate excess heat that built up more quickly in these experimental units.

Nutrients were replaced from stock solutions every three days. At the same time, each glass jar was cleaned and each frond gently scrubbed to remove bacterial growth and epiphytes. Since our main interest was to quantify the direct effects of temperature and nutrients on the growth of *Ascophyllum*, epiphytes were continually removed to eliminate any confounding effects of shading or nutrient competition.

The weight and length of each frond was measured at 16-day intervals. For each interval, the changes were calculated by subtracting the initial from final lengths and weights and standardized by dividing by the initial length or weight of each frond. Average changes were then calculated for each treatment group. Fronds were also visually inspected every 16 days and a photograph of each frond was taken to quantify the number of branches and their elongation over time.

To control the nutrient levels derived from stock solutions in the different treatments and to verify that *Ascophyllum* was absorbing nutrients, water samples (10 ml) were taken during the second week of the experiment, after allowing the plants to adapt to experimental treatments. Samples were taken from three replicates of each treatment group (48 measurements in all) immediately after the addition of new nutrients and again three days later before the next water change. Samples were filtered through 0.7 μm Whatman GF/F filters and stored at −20 °C in the freezer. Water nutrient concentrations of nitrate, ammonia and phosphate were then measured using a nutrient auto-analyzer (Bran and Luebbe, AutoAnalyzer 3). This provided a satisfactory control measurement of our nutrient treatment.

To ensure differences in growth were due to differences in experimental parameters rather than to a climate chamber effect or due to the use of water baths in the 24 °C chamber, a separate experiment was performed in which *Ascophyllum* was grown at 20 °C with no nutrient enrichment in all settings. Jars were placed both directly on the shelves (n = 5), and in water baths (n = 5) in the three chambers. The culturing conditions were the same as for the main experiment described above. This additional experiment found no differences in the growth rate for standardized length (ANOVA, $F_{(5.24)} = 0.53$, $P = 0.71$) or weight ($F_{(5.24)} = 0.96$, $P = 0.45$) between the climate chambers with and without water bath as described by Wilson et al. (2015).

At the end of the nine weeks, all fronds were dried at 80 °C for 48 h, ground to a course powder and the dry weight of each frond was measured. Percent tissue carbon (C), percent tissue nitrogen (N) and the Carbon:Nitrogen (CN) ratio of each plant was determined using a CN analyzer (Costech CHNS-O instrument, model ECS 4010).

2.4. Statistical analysis

Initially, two-way fixed-factor analysis of variance (ANOVA) was used to test for significant effects of nutrient level, temperature and their interaction on overall growth rate ((final − initial)/initial weight and length), lateral branching, and on C and N tissue content of *Ascophyllum* over the 9 week period. However, a repeated measures ANOVA was also used in order to track changes in growth rate over time for each treatment combination. The repeated measures ANOVA proved more sensitive to detecting the varying effects of nutrient level and temperature on changes in standardized length and weight over time; thus, only the results of the repeated measures ANOVA and post hoc tests are presented for *Ascophyllum* growth.

Before the analysis, percent tissue N and C data were arcsine transformed. Normality was checked using the Ryan-Joiner test and two further transformations were performed to normalize the data distribution: the arcsine percent tissue N data was logged to the base ten and the square root of the change in weight was taken. Homogeneity of variances was verified using Levene's test, and Mauchy's test of sphericity was used to validate the repeated measures ANOVA. The percent variance explained by each factor was calculated as a measure of relative effect size (Howell, 2002). Tukey's post hoc test was used to make single comparisons of each response variable at the four nutrient enrichment levels across the three temperatures. The statistical environment R (Venables and Ripley, 2002) was used to run all statistical tests.

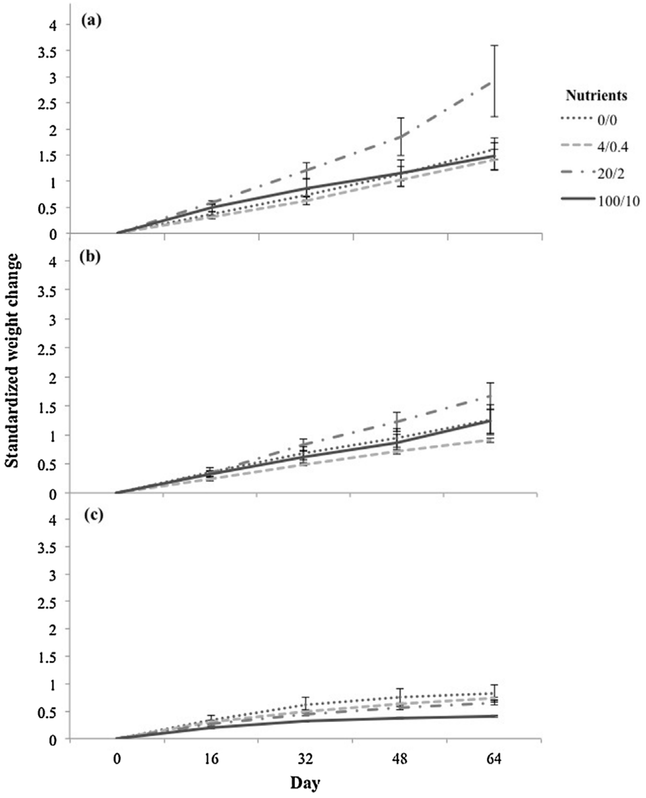

Fig. 1. Change in standardized wet weight (mean ± SE, n = 5) of *Ascophyllum nodosum* exposed to four nutrient levels ($\mu mol\ L^{-1}$ NO_3/PO_4) at (a) 16 °C, (b) 20 °C and (c) 24 °C.

3. Results

3.1. Nutrient concentrations and uptake

The experimental enrichment of nitrate and phosphate at three levels on top of seawater background levels worked well (Table 1), as expected from previous experiments (Lotze and Worm, 2002). After three days in culture with the fronds, immediately before the next water exchange and renewed enrichment, almost all of the nutrients were depleted from the water column except in the 24 °C high (100/10) nutrient treatment where relatively high nutrient levels remained (Table 1).

3.2. Growth of Ascophyllum

In all experimental treatments, fronds of *Ascophyllum* gained weight (Fig. 1) and grew longer (Fig. 2) over the course of 9 weeks, but growth rates differed among treatment combinations. Average weight gain was greatest at 16 °C and lowest at 24 °C. Standardized weight gain over the 9-week period was linear at 16 °C (Fig. 1a) and 20 °C (Fig. 1b) whereas it slowed over time at 24 °C (Fig. 1c), resulting in a significant temperature x time interaction (Table 2).

Compared to temperature, nutrient enrichment had a weaker, yet also significant effect on weight gain (Table 2). Medium nutrient enrichment (20/2 $\mu mol\ L^{-1}$ NO_3/PO_4) enhanced growth relative to no enrichment (0/0) and low enrichment (4/0.4) at 16 °C and 20 °C, respectively (all $P < 0.02$). In contrast, high enrichment (100/10) slowed growth relative to medium enrichment at 16 °C ($P < 0.0001$), especially in the second half of the experiment (Fig. 1a). These effects weakened at 20 °C and disappeared at 24 °C (Fig. 1b and c).

Overall, temperature had the strongest effect on weight gain, explaining 35.1% of the variance compared to the interaction of

Table 1
Mean (±SE; n = 3) nutrient concentrations in seawater with four nutrient enrichment levels prepared for a water change (initial) and concentrations in experimental treatments (16, 20 and 24 °C) three days later (final).

Nutrient level (μmol L^{-1} NO_3/PO_4)	Initial phosphate (μmol L^{-1})	Final phosphate (μmol L^{-1})		
		16 °C	20 °C	24 °C
0/0	1.41 ± 0.17	0.20 ± 0.04	0.24 ± 0.21	0.36 ± 0.11
4/0.4	1.61 ± 0.03	0.20 ± 0.05	0.05 ± 0.05	0.18 ± 0.05
20/2	3.17 ± 0.05	0.30 ± 0.13	0.00 ± 0.00	1.05 ± 0.07
100/10	10.25 ± 0.17	1.29 ± 0.35	0.01 ± 0.01	8.16 ± 0.65
	Initial nitrate (μmol L^{-1})	Final nitrate (μmol L^{-1})		
		16 °C	20 °C	24 °C
0/0	9.03 ± 1.15	0.16 ± 0.03	1.01 ± 0.93	0.29 ± 0.03
4/0.4	11.47 ± 0.04	0.20 ± 0.03	0.13 ± 0.02	0.29 ± 0.10
20/2	27.03 ± 0.13	0.22 ± 0.04	0.12 ± 0.04	2.46 ± 1.40
100/10	104.36 ± 0.95	0.16 ± 0.02	0.12 ± 0.01	78.64 ± 4.59

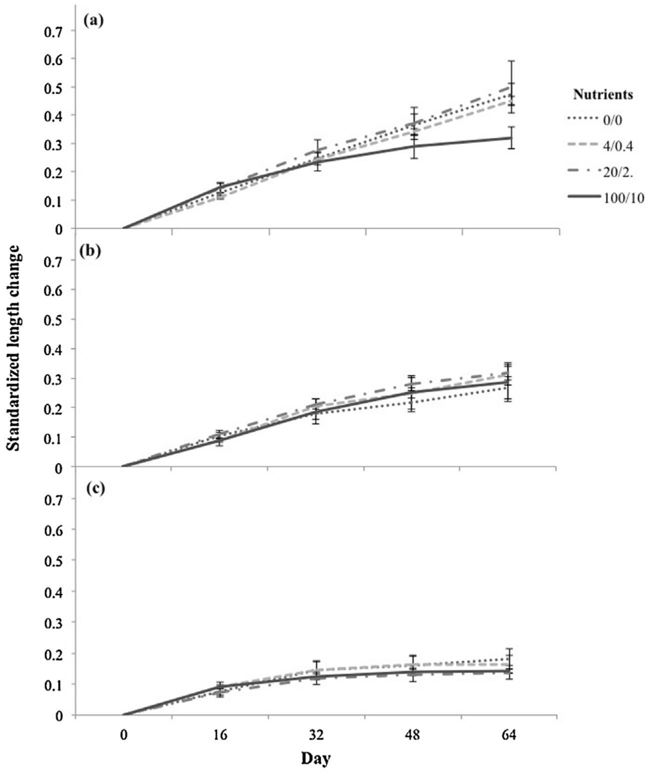

Fig. 2. Change in standardized length (mean ± SE, n = 5) of *Ascophyllum nodosum* exposed to four nutrient levels (μmol L^{-1} NO_3/PO_4) at (a) 16 °C, (b) 20 °C and (c) 24 °C.

Table 2
Results of a repeated measures ANOVA on the main and interactive effects of nutrient, temperature and time on standardized weight and length change for *Ascophyllum nodosum* over the 9-week experiment. Significant effects ($P < 0.05$) are indicated in bold.

Source	df	MS	F	P	Explained variance (%)
Standardized Weight Change					
Nutrient	3	0.241	5.902	0.002	7.3
Temperature	2	1.744	42.767	**<0.001**	35.1
Nutrient:Temperature	6	0.082	2.018	0.082	
Residuals	48	0.041			
Time	3	0.108	8.943	**<0.001**	3.2
Nutrient:Time	9	0.016	1.325	0.229	
Temperature:Time	6	0.143	11.840	**<0.001**	8.6
Nutrient:Temperature:Time	18	0.012	1.001	0.462	
Residuals	144	0.012			
Standardized Length Change					
Nutrient	3	0.004	1.626	0.196	
Temperature	2	0.098	43.680	**<0.001**	32.4
Nutrient:Temperature	6	0.003	0.315	0.315	
Residuals	48	0.002			
Time	3	0.130	67.236	**<0.001**	21.6
Nutrient:Time	9	0.001	2.206	**0.025**	2.1
Temperature:Time	6	0.002	2.997	**0.009**	1.9
Nutrient:Temperature:Time	18	0.001	2.221	**0.005**	4.3
Residuals	144	0.001			

temperature and time (8.6%) and nutrients (7.3%). Tukey's post-hoc tests confirmed that weight changes at each nutrient level were significantly higher at 16 °C than at 24 °C (all $P < 0.001$). Additionally, at medium nutrient enrichment, weight changes at 16 °C were significantly higher than at 20 °C ($P = 0.002$) and at both medium and high enrichment, weight changes at 20 °C were significantly higher than at 24 °C ($P < 0.001$). Averaged across all nutrient levels, standardized weight gain was reduced by 71.3% from 16 °C to 24 °C, by 38.2% from 16 °C to 20 °C, and by 53.5% from 20 °C to 24 °C.

Repeated measures ANOVA revealed a significant interaction between temperature, nutrient level, and time on standardized length change (Table 2). This interaction only accounted for 4.3% of the variation, however, and temperature and time as main effects accounted for 32.4% and 21.6% of the variation respectively. Similar to weight, increase in length was greatest at 16 °C and lowest at 24 °C. Tukey's post-hoc tests confirmed that length changes were significantly higher at 16 °C than at 24 °C at all levels of nutrient enrichment (all $P < 0.001$). Length changes were also significantly higher at 16 °C than 20 °C in both no and medium nutrient enrichment (both $P < 0.01$), as well as at 20 °C than 24 °C in low, medium, and high enrichment (all $P < 0.05$). At 16 °C, length gain was also significantly higher in no and medium nutrient enrichment than under high enrichment (all $P < 0.02$). Lastly, length change decreased over the nine-week period in all nutrient treatments, except in no, low, and medium enrichment at 16 °C (Table 2, Fig. 2). Averaged across all nutrient levels, standardized length gain was reduced by 35.0% from 16 °C to 24 °C, by 9.2% from 16 °C to 20 °C, and by 28.4% from 20 °C to 24 °C.

Overall, absolute weight gain averaged across all nutrient levels was highest at 16 °C (0.126 g $month^{-1}$) and lowest at 24 °C (0.098 g $month^{-1}$). Absolute length change averaged across all nutrient levels was likewise highest at 16 °C (1.4 cm $month^{-1}$), intermediate at 20 °C (1.0 cm $month^{-1}$) and lowest at 24 °C (0.5 cm $month^{-1}$).

Changes in weight resulted from both the increased length of the fronds but also lateral branching. Over the 9-week period, the number of lateral branches was significantly affected by nutrient enrichment (Table 3) and tended to first increase but then decrease at high enrichment levels, especially at 24 °C (Fig. 3). However, the temperature by nutrient interaction was marginally non-significant (Table 3). Post-hoc tests revealed that branching was significantly higher at medium than no nutrient enrichment

Table 3
Output from a two way ANOVA on the lateral branching of *Ascophyllum nodosum*. Significant effects ($P < 0.05$) are indicated in bold.

Source	df	MS	F	P	Explained variance (%)
Nutrient	3	34.356	2.934	**0.043**	12.6
Temperature	2	0.350	0.030	0.971	
Nutrient:Temperature	6	25.039	2.139	0.066	
Residuals	48	11.708			

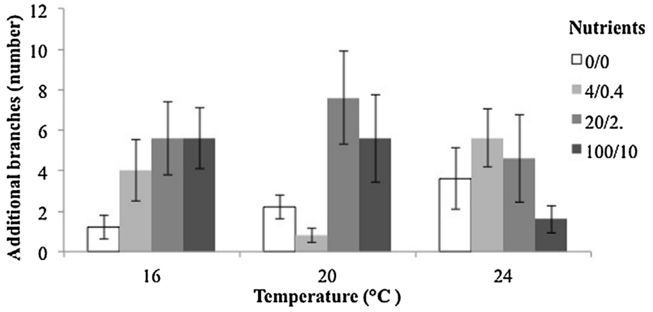

Fig. 3. Changes in (a) tissue nitrogen content (%), (b) tissue carbon content (%), and (c) carbon:nitrogen ratio of *Ascophyllum nodosum* after nine weeks under different temperature and nutrient treatments (μmol L^{-1} NO_3/PO_4). All data are mean ± SE ($n = 5$). Lower case letters reflect significant differences ($P > 0.05$) among nutrient levels within each temperature treatment as well as among temperature treatments within each nutrient level.

($P = 0.029$), however, none of the nutrient enhancement levels within each temperature group were significantly different (Fig. 3).

3.3. Tissue nutrient content

The percent tissue nitrogen (N) in rockweed fronds increased with increasing nutrient enrichment levels during the experiment, with the strongest enrichment at 16 °C (Fig. 4a). Two-way ANOVA revealed a significant interaction between nutrient and temperature on percent tissue nitrogen (Table 3), which explained 7.9% of the variance, compared to 67.2% of the variance explained by the main effect of nutrient. Post-hoc tests showed that ambient (0/0) and low (4/0.4) nutrient levels did not lead to significantly different nitrogen content at each temperature; however, nitrogen content was significantly enhanced at high nutrient enrichment relative to no enrichment (all $P < 0.015$) at each temperature (Fig. 4a). Also, nitrogen content within nutrient enrichment levels was not significantly different across temperature (all $P > 0.05$).

The experimental treatments had no discernible effects on tissue carbon (Fig. 4b, Table 4). In general, tissue carbon showed a decreasing trend with nutrient enhancement, except the lower tissue carbon seen at no enrichment at 16 °C and 24 °C; however, there was no statistically significant difference among treatment groups. The CN ratio showed the reverse trend of that for tissue nitrogen; the ratio decreased with increasing nutrient enrichment, and this was strongest at 16 °C (Fig. 4c). This significant interaction of nutrient level and temperature explained 11.6% of the variance (Table 4), compared to 64.0% explained by the main effects of nutrient enrichment and 7.1% by temperature. Post-hoc tests showed that within each temperature level there was no significant difference between CN ratios for no and nutrient enrichment ($P > 0.8$), whereas CN ratios were significantly reduced towards medium (except at 20 °C) and high nutrient enrichment (Fig. 4c). Moreover, CN ratios were significantly higher at 16 °C than at 20 °C for both no and low (all $P < 0.02$) levels of nutrient enrichment, and also significantly higher at 16 °C than at 24 °C at low nutrient enrichment ($P < 0.005$).

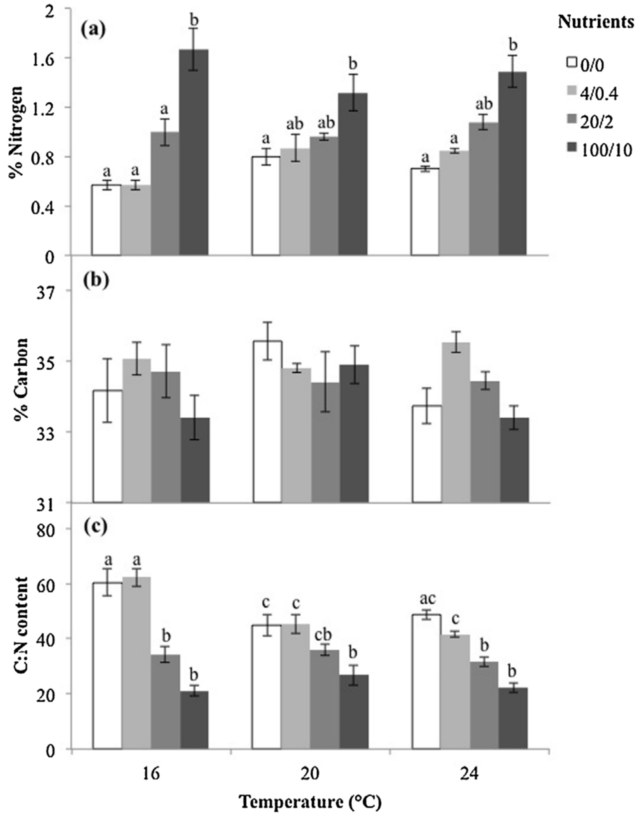

Fig. 4. Additional lateral branches (mean number ± SE, $n = 5$) formed on *Ascophyllum nodosum* over nine weeks using different temperature and nutrient treatments (μmol L^{-1} NO_3/PO_4).

Table 4
Results of a two-way ANOVA on the effects of nutrients and temperature on tissue nitrogen and carbon content and the C:N ratio for *Ascophyllum nodosum*. Significant effects ($P < 0.05$) are indicated in bold.

Source	df	MS	F	P	Explained variance (%)
Tissue nitrogen					
Nutrient	3	1.961	44.466	<0.001	67.2
Temperature	2	0.031	0.694	0.505	
Nutrient:Temperature	6	0.115	2.600	**0.029**	7.9
Residuals	48	0.044			
Tissue carbon					
Nutrient	3	2.587	1.619	0.197	
Temperature	2	2.086	1.306	0.280	
Nutrient:Temperature	6	2.064	1.292	0.279	
Residuals	48	1.597			
C:N ratio					
Nutrient	3	2511.090	58.968	**<0.001**	64.0
Temperature	2	415.110	9.748	**<0.001**	7.1
Nutrient:Temperature	6	227.740	5.348	**<0.001**	11.6
Residuals	48	42.580			

4. Discussion

Our study was designed to examine the interactive effects of four nutrient enrichment levels mimicking realistic levels of low to high nutrient enrichment and three temperatures reflecting normal summer temperatures and predicted levels of climate warming on growth, nitrogen retention and carbon storage in the rockweed *Ascophyllum nodosum*. Overall, increasing temperature slowed *Ascophyllum's* growth rate suggesting that the predicted 3 °C increase in temperature in Eastern North America in the 21st century (Solomon, 2007) could have considerable negative effects on rockweed itself and on the structure, functions and services it provides. The effect of nutrient enrichment was less pronounced but, significantly affected weight change and, for change in length, significantly interacted with temperature and time. Interestingly, at low temperatures, medium nutrient enrichment enhanced growth rates yet high enrichment reduced them. Yet these effects weakened at 20 °C and even more at 24 °C, probably overshadowed by the strong negative effect of warming. Still, with increasing enrichment, rockweed did incorporate higher levels of nitrogen into its tissue, whereas no effects were detected on carbon storage. These results indicate that both rising temperature and increased nutrient loading can have direct negative consequences on rockweed plants and the habitats they form.

4.1. *Direct effects of temperature on growth of* Ascophyllum

In this study, increasing temperature from 16 °C to 20 °C and 24 °C slowed growth in *Ascophyllum*, which can be clearly seen in the breakdown of standardized weight and length change (Figs. 1 and 2). Weight gain at 24 °C was reduced by 71% compared to 16 °C and 50% compared to 20 °C. These results are consistent with findings from previous field and laboratory studies as well as with the natural temperature range of *Ascophyllum*. It is worth noting, however, that populations examined in the field may be locally adapted temperature ecotypes and, as intertidal species, tolerant to high temperatures during low tide. For example, a Norwegian population of *Ascophyllum* tolerates air temperatures ranging from −20 °C to roughly 25 °C during exposure at low tide (Stromgren, 1977) and grows in water up to a mean maximum temperature of 22 °C in the western Atlantic Ocean (Setchell, 1922). Our findings are more consistent with older laboratory studies where *Ascophyllum* from Norway and New England had the highest apical growth at temperatures below 17 °C (Stromgren, 1977; Chock and Mathieson, 1983), which was supported by field observations of optimal growth in moderate temperatures (6–10 °C; Mathieson et al., 1976). In addition, reduced *Ascophyllum* growth and mortality at higher temperatures was observed near thermal effluents in Maine and Massachusetts (Vadas et al., 1976, 1978; Wilce et al., 1978). Our findings are also supported by a more recent experiment that found that *Ascophyllum* from Atlantic Canada grew well in climate chambers at temperatures between 12 and 20 °C, with reduced growth at 23 °C and no growth and eventual mortality at 26 °C and higher (Wilson et al., 2015). This suggests that *Ascophyllum* may tolerate higher temperature for a few weeks before survival is reduced. Interestingly, when exposed to artificially increased temperatures in field in Long Island Sound, *Ascophyllum* continued to grow up until 25 °C with mortality occurring at 27–28 °C (Keser et al., 2005). These results may reflect local adaptations to warmer environments as well as potential adaptations to increasing water temperatures since the 1970s (Harley et al., 2012).

Overall, values of non-standardized length change in rockweed from our experiment, averaged across all nutrient levels for each temperature (0.5–1.4 cm month^{-1}), fall within the range of reported intertidal growth rates from other locations and studies (Table 5). Highest growth rates generally occur in intertidal rockweeds during the hours at low tide when *Ascophyllum* is exposed to warm air and higher levels of irradiance (Brinkhuis and Jones, 1976). Daily exposure was not replicated in our study, but would be interesting to study in a future experiment, particularly exposure to increasing air temperatures.

Along the Atlantic coast of Nova Scotia, summer seawater temperatures in protected coastal areas have so far rarely exceeded 20 °C (Keizer et al., 1996; Lotze and Worm, 2002; Wilson et al., 2015). Since *Ascophyllum*'s main growth period is during the summer, our 24 °C treatment represents a realistic level of warming and our high temperature findings should reflect responses in natural populations in coming years. It should be noted that, while annual mean sea surface temperature may increase by 4 °C on North Atlantic rocky shores by the end of the 21st century (Müller et al., 2009), more severe temperature increases are expected during winter months, which do not correspond with *Ascophyllum*'s main growth period. Our high temperature of 24 °C, therefore, represents the higher limit of predicted temperatures. By compromising *Ascophyllum's* growth and potentially survival (Wilson et al., 2015), rising temperature has the potential to alter the distribution and structure of rockweed habitat, as well as its functions, such as productivity, biomass and energy provision (Svensson et al., 2009). The range of *Ascophyllum* and other foundation macroalgae (*Fucus serratus, F. vesiculosus*) in the temperate north Atlantic is predicted to shift northward to the extent that these species will be found in the Canadian Arctic by 2100 while the coastline south of 45° North will no longer be suitable by 2200 (Jueterbock et al., 2013). Relatedly, a shift in the composition of rocky shore *Ascophyllum*-dominated habitats to mixed fucoid beds is expected with increasing water temperature (Ugarte et al., 2010); this change might be due to reduction of *Ascophyllum* biomass that would result from restricted growth and increased competitiveness of more opportunistic fucoids, sessile invertebrates or grazers (Davies et al., 2007; Ugarte et al., 2010; Harley et al., 2012). In 2003, changes in commercially harvested rockweed beds in Nova Scotia were already apparent; an increase in *F. vesiculosus* was seen in some areas (Ugarte et al., 2009). In harvested areas of New Brunswick, large recruitment events of the blue mussel *Mytilus edulis* were seen in the rockweed beds. Ugarte et al. (2009) suspect these changes are due to air and water temperature rises in the region; however, no direct correlation has been shown yet. On the Northeast Atlantic coast, increased mortality and increasing reproductive output at the expense of growth have been noted in southern edge populations of *Ascophyllum* in response to climate change (Araùjo et al., 2011).

Plastic and adaptive responses can lessen the loss and migration of species in response to warming climate (Lavergne et al., 2010). Southern edge populations of *Ascophyllum* and *Fucus* spp. have long persisted in ancient glacial refugia and are, consequently, generally populations with high genetic diversity with higher potential for adaptation (Maggs et al., 2008). In a warming climate, these southern edge populations will be under greatest pressure; unfortunately the adaptive potential of *Ascophyllum* and patterns of local adaptation are not well enough understood to predict whether southern populations will adapt or become extinct (Jueterbock et al., 2013).

4.2. *Direct effects of nutrients on growth of* Ascophyllum, *nitrogen retention and carbon storage*

Overall, the effects of nutrient enrichment were less pronounced than those of warming, but significantly affected weight gain and interacted with temperature and time to affect length gain. At 16 °C, medium nutrient enrichment significantly enhanced whereas high enrichment slowed growth. This combination of medium nutrient level and low temperature may represent optimal conditions for *Ascophyllum* growth. For example, higher growth of *Ascophyllum* exposed to land-based fish farm effluent has been documented in southwestern Nova Scotia (White et al., 2011, Table 5), and their documented tissue nitrogen levels were comparable to our medium enrichment levels. In our study, fronds at high nutrient enrichment levels stored higher amounts of nitrogen in their tissue, but this did not directly translate into higher growth. The most obvious effect of high enrichment in our experiment was a darkening of the frond colour, a characteristic change seen in environments with high nutrient levels (Department of Fisheries and Oceans, 1997; Hurd et al., 2014), as well as some reduction in weight and length gain (Stromgren, 1977). Both seagrasses and

Table 5
Comparison of growth rates (elongation) from different field and laboratory growth studies with *Ascophyllum nodosum*.

Growth Rate (length increase)	Field Location or Treatment	Temperature (°C)	Duration	Reference
0.3–1.2 cm month^{-1}	Intertidal; Nova Scotia	–	–	MacFarlane, 1932
1.9–2.5 cm month^{-1}	Intertidal; New England	–	Growth in 1973 and 1974	Mathieson et al., 1976
2.2 cm month^{-1}	Intertidal; Maine	Spring maximum	Spring season	Normandeau Associates, 1977
1.2 cm month^{-1}	Intertidal; Maine	Winter minimum	Winter season	Normandeau Associates, 1977
9.0 cm year^{-1}	Intertidal, harvested stocks; Nova Scotia	–	–	Sharp, 1981
6.0–10.0 cm year^{-1}	Intertidal; New England	–	–	Vadas and Wright, 1986
25.0 cm year^{-1}	Intertidal; New England	3–24 (winter to summer)	Previous year's growth	Peckol et al., 1988
2.0 cm year^{-1}	Subtidal; New England	3–24	Previous year's growth	Peckol et al., 1988
10.1 cm year^{-1}	High shore; Southwestern Nova Scotia	–	Harvested in September 2010 (previous year's growth)	White et al., 2011
10.5 cm year^{-1}	Low shore; Southwestern Nova Scotia	–	Harvested in September 2010	White et al., 2011
7.6 cm year^{-1}	Ambient nutrient control sites; Southwestern Nova Scotia	–	Harvested in September 2010	White et al., 2011
13.1 cm year^{-1}	High nutrients fish farm sites (effluent stream contains 300 μM NO3^{-}); Southwestern Nova Scotia	–	Harvested in September 2010	White et al., 2011
0.2 cm year^{-1}	Norway; Germlings, first year	–	–	Sundene, 1973
1.5 cm year^{-1}	Norway; second year	–	–	Sundene, 1973
1.4 cm month^{-1}	Lab cultured, averaged across 4 nutrient enrichment levels	16	9 weeks	This study
1.0 cm month^{-1}	Lab cultured, averaged across 4 nutrient enrichment levels	20	9 weeks	This study
0.5 cm month^{-1}	Lab cultured, averaged across 4 nutrient enrichment levels	24	9 weeks	This study

freshwater macrophytes exposed to high nutrient stress have been shown to upregulate their nitrogen metabolism in order to contend with accumulating nitrogen and this, furthermore, requires the catabolism of carbohydrate stores (e.g. Invers et al., 2004; Zhang et al., 2010). The increased use of carbon stores and other metabolic shifts that occur under nitrogen loading stress compromise the plants' ability to grow, which may explain why seagrass growth rates did not respond to nutrient enrichment (Invers et al., 2004). If a similar shift in metabolism occurred during our study, it could account for lower percent tissue carbon present at high enrichment relative to medium enrichment as well as slowed growth at high nutrient enrichment.

Increasing nutrient enrichment levels resulted in higher amounts of nitrogen stored in rockweed tissue. Similarly, the decrease in the CN ratio largely reflected the change in nitrogen since there was no significant change in carbon content. Although nutrient level and temperature had a significant interactive effect on tissue nitrogen content, nutrient level accounted for more than 86% of the variance and was therefore the primary driver of changes in tissue nitrogen concentration. This is not surprising since in the field, tissue nitrogen reflects the seasonal cycle of ambient dissolved nitrogen (Hardwick-Witman and Mathieson, 1986). The yellowing of apices in both ambient and low nutrient levels together with the potential to take up as much as ten times the available concentration of nutrients in the high enrichment level (Table 1) suggests nutrient deficient conditions at these low enrichment levels (Hurd et al., 2014), although this did not result in reduced growth rates. On the other hand, the fronds did not take up all nutrient at the high enrichment level at 24 °C, indicated by the remaining higher nutrient concentrations in the water (Table 1). This suggests that the uptake saturation point for nitrogen and phosphorus species at this temperature had been reached or that the enzymes responsible for uptake cannot function optimally at 24 °C (Topinka, 1978). The most notable external sign of tissue nutrient content was the gradient in frond colour from light green at low enrichment to dark green at high as seen in natural *Ascophyllum* populations in Nova Scotia associated with a gradient in nutrient supply (Department of Fisheries and Oceans, 1997).

5. Interactive effects of nutrient loading and climate warming

The importance of understanding the cumulative and interactive effects of multiple, co-occurring anthropogenic and environmental stressors is increasingly being recognized (e.g. Crain et al., 2008; Moy and Christie, 2012). Thus a growing number of studies aim at uncovering the interactive effects of diverse stressors such as ultraviolet radiation and nutrient loading on a microphytobenthic community (Wulff et al., 2000), radiation, temperature, and salinity on the kelp *Alaria esculenta* (Fredersdorf et al., 2009), and ultraviolet radiation and warming on juveniles of three canopy-forming subtidal seaweeds (Xiao et al., 2015). In a previous laboratory experiment, Lotze and Worm (2002) showed that both nutrient enrichment and rising temperatures synergistically enhanced the recruitment and growth of annual green algae. Interestingly, in our experiment the positive and negative effects of medium and high nutrient enrichment, respectively on rockweed growth observed at 16 °C weakened at 20 °C and 24 °C. Similarly, the higher degree of branching seen at medium compared to no nutrient enrichment diminished as temperature increased to 24 °C (Fig. 4). This was probably caused by the strong negative effect of warming and may suggest that the direct effects of nutrient loading on rockweed will not necessarily increase in a warming climate.

Although not quantified in this study, it is well-documented that added nutrients may cause indirect effects on macrophytes, such as the growth of epiphytes causing shading. A study by Fletcher (1996) showed that *Ascophyllum* in sewage-polluted areas became laden with epiphytic algae. Epiphytic algae can shade perennial seaweeds from the sun; *Ectocarpus* sp. in particular can form a turf over the surface of the frond and can decrease *Ascophyllum*'s ability to photosynthesize (Davison and Hughes, 1998). In some regions in North America, high nutrient levels in coastal waters have led to overgrowth of *Ascophyllum* by ephemeral algae and some populations are declining because of eutrophication (Fletcher (1996); Worm and Lotze, 2006). Since rockweed growth rates in our study did not substantially differ among nutrient enrichment levels the negative effect of nutrient loading on *Ascophyllum* observed in the field may be primarily indirect through epiphytic algae overgrowth and shading.

Temperature has also been shown to have indirect effects on seaweeds, mainly through enhanced grazing rates (Lotze and Worm, 2002; Davies et al., 2007; Hawkins et al., 2008; Harley et al., 2012). Herbivory by several gastropods does not affect survival or breakage of *Ascophyllum* (Lazo et al., 1994), however, the limpet *Patella vulgata* has been shown to destructively graze *Ascophyllum* monocultures the northeast Atlantic (Davies et al., 2007; Lorenzen, 2007). Additionally, through reduction in recruitment, grazing of germlings may directly affect the abundance of *Ascophyllum*; however, given the generation time of *Ascophyllum* (50–70 years) and its current low annual recruitment, it is unclear how vulnerable *Ascophyllum* would be to increased grazing of germlings (Davies et al., 2007; Olsen et al., 2010; Jueterbock et al., 2013).

5.1. *Ecological implications*

The results of our study suggest that growth of *Ascophyllum* could slow considerably with increasing ocean temperatures. Nutrient loading showed the greatest direct effects on rockweed growth at lower temperatures, with medium loading having a slightly positive effect, yet high loading having a negative effect on rockweed growth. Although these direct effects of nutrient enrichment disappeared with warming, indirect effects, such as epiphyte growth, may be expected to increase. Thus, the effects of nutrient enrichment and climate warming are likely interactive and need to be managed in this context. The synergy of eutrophication and warming, for example, caused the shift of kelp forests (*Saccharina latissima*) to ephemeral algae along the south and west coasts of Norway (Moy and Christie, 2012).

Although the increased tissue nitrogen did not affect rockweed growth, it does suggest that rockweed plays an important role in taking up and retaining nitrogen in coastal waters (Schmidt et al., 2011). Both carbon storage and nitrogen retention are important ecosystem services provided by rockweed beds and other coastal vegetated habitats (Worm et al., 2000; Schmidt et al., 2011). Rockweed habitats in Atlantic Canada store 14 times the amount of carbon per unit area stored by eelgrass beds—the other significant coastal vegetated habitat in Atlantic Canada—and retain eight times as much nitrogen (Schmidt et al., 2011). However, our results indicate that *Ascophyllum* stores nitrogen less efficiently at 24 °C, which could have consequences in warming eutrophic coastal ecosystems. Additionally, with the weight gain of *Ascophyllum* reduced as temperature increases, the potential for nitrogen retention per unit area of rockweed habitat could become further limited. Similarly, while our results do not show that tissue carbon is directly affected by warming, reduced weight gain at higher temperatures could also diminish the carbon storage capacity of rockweed habitats.

Finally, *Ascophyllum* is an ecologically important species that provides essential habitat for a wide range of species (Lotze et al., 2006; Schmidt et al., 2011; Seeley and Schlesinger, 2012). Rockweed is also economically important in Atlantic Canada (Chopin et al., 1996), and the rockweed processing industry in Atlantic Canada and the United States of America (Maine) continues to grow (Seeley and Schlesinger, 2012). Our study suggests that both *Ascophyllum*'s habitat provision and economic importance could be affected in a warmer climate. Future field studies to assess and monitor the cumulative and interactive effects of several anthropogenic impacts on rockweed beds are needed to inform long-term sustainable and ecosystem-based management of Atlantic Canada's rockweed harvesting and the integrated management of multiple human activities in the coastal zone.

Acknowledgments

We would like to thank Audrey Barnett and Claire Normandeau for processing water samples and CN analysis, respectively. This work was funded by the Natural Sciences and Engineering Research Council (NSERC) of Canada with a Discovery grant to H.K.L., NSERC PGSD and Killam Pre-Doctoral Scholarships to A.L.S. and a Sarah Lawson Research Scholarship and NSERC USRA to L.M.K.

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