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Effects of increasing water temperatures on survival and growth of ecologically and economically important seaweeds in Atlantic Canada: implications for climate change

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Abstract Rising temperatures are changing the distribution and abundance of species worldwide, yet the magnitude of warming varies regionally. Atlantic Canada lies in a zone of significant warming and harbors many cold-adapted seaweeds of ecological and economic importance. Using a factorial laboratory experiment, we tested the effects of increasing water temperature on the survival, growth, and nutrient content of rockweeds (*Ascophyllum nodosum*, *Fucus vesiculosus*), Irish moss (*Chondrus crispus*), kelp (*Laminaria digitata*), and the invasive *Codium fragile* ssp. *tomentosoides* from Nova Scotia (44°29.9′N, 63°31.7′W). In June 2014, species were exposed to typical spring–summer water temperatures (12, 16, 20 °C), a predicted increase in summer temperature (23 °C), and potential heat wave temperatures in shallow waters (26, 29 °C) for 9 weeks. *Chondrus crispus* and *L. digitata* experienced highest growth at 12 °C, *F. vesiculosus* and *Codium* at 16 °C, and *A. nodosum* at 20 °C. Survival was lowest in *L. digitata* with no survival above 20 °C, followed by rockweeds with low survival above 23 °C, while *C. crispus* and *Codium* exhibited high survival at all temperatures. There was some evidence for temporary acclimation and short-term survival at higher temperatures. Temperature stress did not affect carbon content but some species showed increased tissue nitrogen, potentially changing nutritional quality and the ability to store and cycle nutrients. These species-specific responses to increasing water temperature will result in shifts in species composition along Atlantic Canada's rocky shore, altering seaweed canopies, their ecosystem structure and function, and the services they provide.

Introduction

Marine macroalgae are dominant and essential components of coastal ecosystems around the world (Gattuso et al. 1998; Harley et al. 2012). They are highly productive, form vast amounts of primary producer biomass, and store and cycle significant quantities of carbon and nitrogen (Smith 1981; Pedersen et al. 2004; Schmidt et al. 2011). As autogenic ecosystem engineers (Jones et al. 1994), they also create spatially complex three-dimensional habitats, which provide shelter and food to a wide range of marine species, including commercially important fish and invertebrates (Dean and Connell 1987; Worm et al. 2000; Schmidt et al. 2011). Yet, they are threatened by a multitude of anthropogenic impacts, including nutrient loading, harvesting, invasive species, food web alterations, and increasingly climate change (Worm and Lotze 2006; Schmidt and Scheibling 2006, 2007; Harley et al. 2006, 2012).

Greenhouse gas emissions have exponentially increased since 1750, resulting in increasing water temperatures, rising sea level, and ocean acidification (IPCC 2013). Between 1980 and 2011, the Northwest (NW) Atlantic Ocean had warmed by 0.8–1.6 °C, with significant warming trends north of 42°N (Baumann and Doherty 2013). Thus, Atlantic Canada lies within the zone of significant

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warming and can expect another 3 °C increase in SST over the current century (IPCC 2007, 2013). This has important implications for marine ecosystems along the Atlantic coast because water temperature is a major factor affecting the survival and growth of macroalgae (Lüning 1990). Therefore, increasing sea surface temperature (SST) can strongly influence macroalgal abundance and distribution, with many species likely experiencing poleward shifts in distribution, and extinction at their southern limits (Wernberg et al. 2011; Jueterbock et al. 2013). However, this trend is not entirely consistent as some cold water species of macroalgae have shifted their distribution further south (Lima et al. 2007). Such shifts will consequently lead to changes in the structure, functions, and services that these ecosystems provide (Harley et al. 2006, 2012; Wernberg et al. 2010, 2011).

In Atlantic Canada, the rocky coastline is dominated by perennial canopy-forming macroalgae. Within the mid-intertidal zone, fucoid rockweeds dominate as a thick band (Stephenson and Stephenson 1954). In moderate to fully sheltered areas, this band is dominated by *Ascophyllum nodosum*, whereas on ice-scoured or wave-exposed areas it is dominated by *Fucus* species, specifically by *Fucus vesiculosus* and *Fucus distichus*. The low-intertidal zone is covered by the red alga *Chondrus crispus* or Irish moss in all but the most exposed sites, and *C. crispus* is also observed in the understory of the fucoid and laminarian zones. The subtidal zone is dominated by laminarian kelps such as *Alaria esculenta*, *Laminaria digitata*, and *Saccharina latissima*. All these species are of high ecological importance as they form perennial canopies that provide substrate and habitat for a wide range of species, in addition to storing and cycling nutrients (Schmidt et al. 2011; DFO 2013). Moreover, both *A. nodosum* and *C. crispus* are also commercially important in Atlantic Canada, and have been harvested for several decades (DFO 2013). Occasionally harvest licenses have also been issued for *L. digitata* and *S. latissima*. Increasing SST may shift the distribution, dominance, and abundance of these seaweeds with potential ecological and economic consequences.

In 1989, the invasive green algae *Codium fragile* ssp. *tomentosoides* (hereafter *Codium*) was first observed on the Atlantic coast of Nova Scotia (Bird et al. 1993). Originally from Japan (Goff et al. 1992), *Codium* has successfully colonized intertidal to subtidal areas (Schmidt and Scheibling 2005, 2006, 2007), outcompeting some native species, particularly along sheltered coasts of the NW Atlantic (Levin et al. 2002; Scheibling and Gagnon 2006). Native kelp species are typically able to inhibit and outcompete *Codium*. However, when disturbed by colonization of the invasive bryozoan *Membranipora membranacea* (Scheibling and Gagnon 2006), or destructive grazing by the urchin *Strongylocentrotus droebachiensis* (Scheibling 1986), kelp canopy cover is reduced, allowing *Codium* to quickly settle the exposed substrate and inhibit kelp recruitment (Scheibling and Gagnon 2006). Rising SST may further affect cold-adapted kelp species and potentially benefit *Codium*.

The overall goal of this study was to determine the effects of increasing water temperatures and potential heat waves, including response to heat shock, on the growth and survival of five ecologically and economically important seaweeds in Atlantic Canada: *A. nodosum*, a representative *Fucus* species (*F. vesiculosus*), *C. crispus*, *Codium,* and a representative kelp species (*L. digitata*). In addition, we were interested in the effects of rising water temperature on nitrogen and carbon content in the seaweeds' tissue, as temperature can influence the uptake and storage of nutrients (Asare and Harlin 1983; Lüning 1990; Nygård and Dring 2008). This could affect the seaweeds' growth, as well as carbon and nitrogen cycling and storage in coastal ecosystems. To answer these questions, we performed a fully crossed factorial laboratory experiment with six temperature levels and five species. We hypothesized that following temperature stress, growth, survival, and nutrient uptake would be reduced at warmer temperatures, but that the magnitude of effects would be species-specific. This work has implications for predicting shifts in the distribution, dominance, and canopy cover of macroalgae in the Northwest Atlantic in response to continued climate change, as well as potential impacts on the ecosystem services and economic benefits they provide.

Materials and methods

In May 2014, individual thalli of all five species were collected from Duncan's Cove, Nova Scotia, a small semi-sheltered inlet close to Halifax Harbour (44°29.9′N, 63°31.7′W). Juvenile specimens of *Laminaria digitata* and *Codium* of a standard size of (10–15 cm) were haphazardly collected by divers from a depth of ~6 m, whereas juveniles of *Fucus vesiculosus*, *Chondrus crispus*, and *A. nodosum* (also 10–15 cm) were collected from the intertidal zone. Seawater temperature at the time of sampling was 6 °C. We collected juveniles so we could use the entire plants in our experiment. The seaweeds were immediately transferred in a cooler to the laboratory, where any epiphytes were gently scraped off before placing the thalli separated by species in 2.43-L tanks with filtered (4 µm) seawater at 6 ± 1 °C for the acclimation period (see below).

Experimental design

Six temperatures were used to simulate an increase in water temperature. Cooler water temperatures (12, 16, and 20 °C) represented typical cool and warm summer temperatures along the Nova Scotian coastline (Fig. 1a). Warmer water temperatures (23 °C) represented the predicted 3 °C increase in SST in the western North Atlantic by 2100 (IPCC 2007, 2013), as well as potential heat wave temperatures (26 and 29 °C) that might be lethal for some species in tide pools and the shallow intertidal zone. Using a fully crossed experimental design with the factors species (5 levels) and temperature (6 levels), five replicates per species resulted in a total of 150 experimental units.

After holding the specimens at 6 °C for 4 days, the acclimation period began which occurred over the course of 3 weeks. To acclimate samples to experimental temperatures, the water temperature was increased at a rate of 2 °C increase every 2 days up to 12, 16, and 20 °C, respectively. This acclimation protocol was chosen to expose the algae slowly to experimental temperatures, yet not keeping them too long under laboratory conditions before starting the experiment itself. The increase of 2 °C every 2 days had proven to be successful in a previous pilot experiment, and is much less than what these seaweeds experience in their natural environment due to tidal changes and upwelling (Petrie et al. 1987; Ugarte et al. 2010). After another 4 days, replicates for treatments above that temperature were transferred directly from 20 °C seawater to 23 °C as the increased summer temperature, and directly into 26 or 29 °C to mimic the effects of potential heat waves, including the response of heat shock. At this point the experiment started.

To culture the seaweeds, the same methods were performed during the acclimation period, and the duration of the 9 weeks experiment. Each tank had an air stone, was maintained under a 14:10 h light/dark cycle, and the seawater inside the tanks was changed every 3 days using local, filtered (4 μm) seawater. With every water change, the tanks were wiped cleaned, any epiphytes were removed from the seaweeds, and tanks were systematically rotated around the laboratory. In accordance with their natural subtidal–intertidal zonation (Lüning 1990), *L. digitata* was placed at a lower irradiance (75–85 μmol m^{-2} s^{-1} of photosynthetically active radiation, PAR), *Codium and C. crispus* at a mid-irradiance (85–95 μmol m^{-2} s^{-1} PAR), and *F. vesiculosus* and *A. nodosum* at a high irradiance (100–110 μmol m^{-2} s^{-1} PAR) under a radiation range of 260–750 nm. We chose these light levels to ensure that each species would receive their respective optimal light levels for growth, that light was not limiting growth in our experiment, and that we could compare growth at optimal light levels across species. To maintain different irradiance levels, the seaweeds were placed at varying distances from the irradiance source to allow growth under optimal irradiance. Water temperature in all tanks was monitored daily with an analog thermometer, and one tank per temperature treatment had continual logging every 30 min with a HOBO pendant data logger (Onset Computer Corp.). The data loggers were randomly moved around the five different tanks per temperature treatment ($n = 5$). Irradiance levels were also monitored throughout the experiment with a light meter (LI-COR Inc. LI-250A), and continual logging with a HOBO pendant data logger (Onset Computer Corp.).

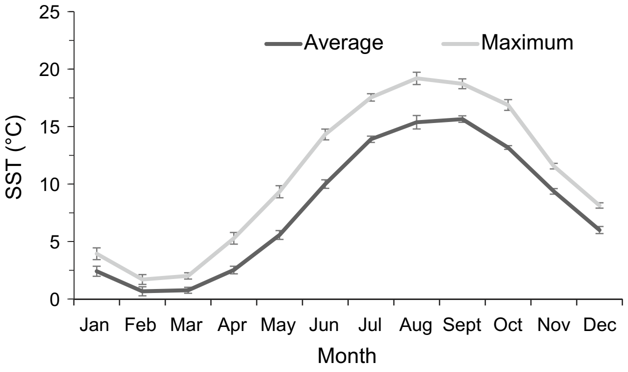


Fig. 1 Monthly average and maximum sea surface temperature (SST ± SE, $n = 12$ years) from a buoy on the approach to Halifax Harbour, Nova Scotia (Station 44.5N 63.4W; Fisheries and Oceans Canada, Marine Environmental Data Service; www.meds-sdmm.dfo-mpo.gc.ca)

During the experiment, individual plants were cultured in separate 1-L mason jars and were kept fully submerged by zip tying on a stainless steel washer to weigh them down to the bottom. Replicates at 12 and 16 °C were placed into climate chambers set to the experimental temperatures (±1 °C). Replicates at 20, 23, 26, and 29 °C were maintained in water baths (±2.3 °C for 20 °C, and ±1 °C for 23–29 °C) in a separate laboratory. For each of the warmer temperatures, five replicate water baths were maintained with each water bath containing one replicate of each species (five jars per tank). To ensure differences in growth were due to temperature manipulation, and not differences in laboratory settings of the water bath method and cooled climate chambers, a pilot experiment was performed prior to the start of the experiment with one species *A. nodosum* grown at 20 °C in all settings. Jars ($n = 5$ each) were placed directly on the shelves and in a water bath in the three laboratory rooms. Using the same culture conditions listed above, the pilot experiment found no differences in the growth rate for length [ANOVA, $F(5,24) = 0.53$, $P = 0.71$] and weight [$F(5,24) = 0.96$, $P = 0.45$] between the two climate chambers with and without water bath and the water bath method in the adjacent laboratory (Kay and Wilson unpubl. data).

The experiment began in June 2014, when the initial length and wet weight of each specimen was recorded. For length, the longest frond of each specimen of *Codium*, *F. vesiculosus*, *C. crispus*, and *A. nodosum* was measured to the nearest mm. As *L. digitata* grows from the meristem at the bottom of the blade and disintegrates at the top of the blade (Lüning 1979), some specimens were slightly cut so all had similar lengths of the stipe (5 cm) and blade (5 cm) at the start of the experiment. Blades were hole-punched, and length was measured from the stipe blade interface to the lowest point of the hole (Lüning 1979). For weight, each specimen was patted dry with paper towel prior to weighing the whole plant to the nearest mg. Every 7–10 days, length and wet weight of each specimen was recorded. After 27 days, a climate chamber malfunction resulted in the loss of all replicates at 16 °C. For these replicates, only three data points over the first 20 days were collected. For the other treatments, the experiment ran for 56 days with seven data points in total. Jars were checked daily to monitor the health of all replicates. When a replicate died prior to the conclusion of the experiment, the final weight and length were recorded to be used in the last growth rate. Mortality was assumed for *L. digitata* when the blade became severely perforated and bleached (Andersen et al. 2013). *Chondrus crispus* mortality was assumed when the algae bleached (turned green) and the fronds were disintegrating. For *A. nodosum* and *F. vesiculosus,* mortality was assumed when the fronds darkened and tips/fronds easily broke off (Stengel and Dring 1997). *Codium* did not experience mortality during the length of the experiment.

At the end of the 56-day experiment, three replicates for each species per temperature that had survived were also analyzed for their carbon and nitrogen content. Replicates were dried (80 °C; 48 h), ground to a powder, and analyzed by the UC Davis Stable Isotope Facility at the University of California for percent (%) tissue N and C.

Statistical analysis

To test differences in survivorship across species and temperatures, the percent survival for each species per temperature was calculated. Survivorship was analyzed using contingency tables and the one-tailed Fisher's exact test due to the low sample size in each cell ($n = 5$; Campbell 2007). Survivorship was compared between temperatures for each species (H_0: no difference in survival; H_A: cooler temperature has higher survival), and between species for each temperature (H_0: no difference in survival; H_A: different species have different survival). Comparisons for 16 °C were done at 27 days, and all other comparisons were done at the end of the experiment (56 days). A significance level of $P < 0.05$ was used for all analyses.

For each specimen, a standardized relative growth rate per day (%/day) was calculated by the equation:

$$(\text{Final Weight} - \text{Initial Weight}) / (\text{Initial Weight} \times \text{Number of Days}) \times 100\ \%$$

This relative growth rate was calculated for every measuring interval of 7–10 days, as well as over the 20- and 56-day periods. Length measurements were not used in the growth rate analysis as weight gave a better indicator of growth due to the lateral branching of many species. To test for differences between temperatures and species on the relative weight growth rate, a permutational statistical approach, using PERMANOVA+ (Anderson et al. 2008), was chosen as mortality of individual samples resulted in an unbalanced design. First, a univariate permutational ANOVA (perANOVA) was performed on the average growth rate for the first 20 days (weight at day 20 minus initial weight), and for the average growth rate over the 56 days (weight at day 56 minus initial weight) using temperature and species as fixed factors. The 20-day period was used so the growth rates at 16 °C could be included in the analysis. This was followed with post hoc tests to determine differences in growth between different temperature treatments within each species. Next, to test whether growth rates changed over the course of the experiment, a repeated measures perANOVA was performed for each species, with temperature and time as fixed factors, and plant number (random factor) nested in temperature (Anderson et al. 2008). This was done for the 56-day period excluding all 16 °C data. To determine changes in tissue %N and C, another perANOVA was performed with temperature and species as factors, followed by post hoc tests to determine differences between temperature treatments within each species.

Finally, an average absolute growth rate was determined for each species at their optimal growth temperature determined by this study to compare against literature values of optimal growth rates. To be more comparable to published absolute growth rates, weight and length were not standardized. As the repeated measures perANOVA found time to be influencing the growth, an average absolute growth for each interval was derived by subtracting final weight from initial weight using the following formula:

$$\left(\text{Weight at Day}_\text{f} - \text{Weight at Day}_\text{i}\right) / \#\ \text{days in the measuring interval;}$$

with f = final and i = initial day of the measuring interval. This was repeated for all measuring intervals ($n = 6$ at 20 °C or $n = 2$ at 16 °C), which were then averaged to determine the average optimal absolute growth rate. The same procedure was performed with the length measurements. In this study, a threshold temperature was defined as a temperature where growth was significantly reduced from all cooler temperature, and this trend remained for all temperatures warmer than the threshold temperature.

Results

The average seawater temperature [±standard error (SE)] for each experimental treatment was 12.7, 16.4, 20.6,

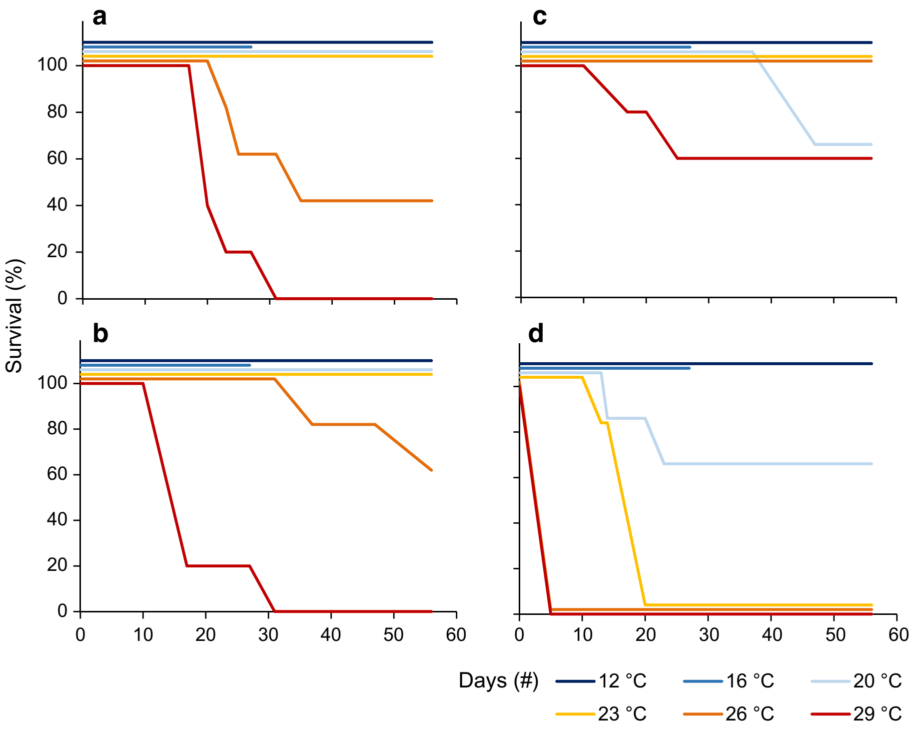


Fig. 2 Percent survival (%) across all temperatures over the course of the experiment ($n = 5$) for **a** *Ascophyllum nodosum*, **b** *Fucus vesiculosus*, **c** *Chondrus crispus*, *and* **d** *Laminaria digitata. Codium* is not shown as it exhibited 100 % survival across all temperatures. To avoid overlap of lines, each data series is offset by 2 %. The 16 °C treatments ended after 20 days due to a climate chamber malfunction

23.1, 25.8, and 28.8 (±0.01 °C for 12 °C, ±0.02 °C for 16–29 °C; $n = 780$ for 16 °C, $n = 1894$ for all other temperatures) based on the data loggers.

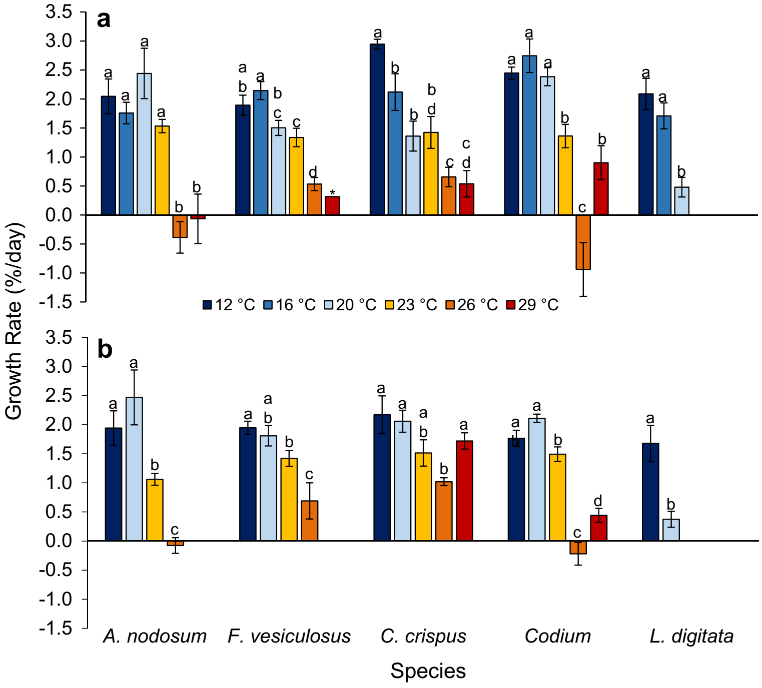
Survivorship

Survivorship curves (Fig. 2) and Fisher's exact tests (Online Resources 1 Table S1) showed distinct differences in survival among species and temperatures. *Codium* was the only species that showed 100 % survival at all temperatures, which was significantly higher survivorship than *Laminaria digitata* at 23–29 °C and all other species except *Chondrus crispus* at 29 °C (Table S1). *Chondrus crispus* also showed high survival rates over the course of the experiment (Fig. 2) with no significant differences among temperatures. Between species, *C. crispus* had significantly higher survival than *L. digitata* at 23 and 26 °C, where *C. crispus* had 100 % survival and *L. digitata* had 0 % survival after 3 weeks. *Ascophyllum nodosum* and *Fucus vesiculosus* both had similar survivorship and showed 100 % survival at 12–23 °C, decreased survival at 26 °C after 3 weeks with only 40 % of individuals of *A. nodosum* and 60 % of *F. vesiculosus* surviving the whole experiment, and 0 % survival at 29 °C after 2 weeks (Fig. 2). Survival at 29 °C was significantly less than survival at 12–23 °C for both species (Table S1). Compared to other species, *A. nodosum* and *F. vesiculosus* had significantly lower survival at 29 °C than *Codium,* but significantly higher survival at 23 °C than *L. digitata*. Lastly, *L. digitata* had the lowest survivorship of all species with 100 % mortality within 1 week at 26 and 29 °C, within 2 weeks at 23 °C, and partial mortality at 20 °C between weeks 2 and 3 (Fig. 2). Survival at 23 through to 29 °C was significantly less than survival at 12 and 16 °C (Table S1).

Growth rates

After 20 days, relative growth rates significantly differed between species [two-way perANOVA, *pseudo-F*(4100) = 64.45, *P* = 0.0001], temperatures [*pseudo-F*(5100) = 11.41, *P* = 0.0001], and their interaction [*pseudo-F*(18,100) = 4.70, *P* = 0.0001]. Growth rates were highest at 12 °C for *L. digitata* and *C. crispus*, at 16 °C for *F. vesiculosus* and *Codium*, and at 20 °C for *A. nodosum* (Fig. 3a). Post hoc tests indicated that *A. nodosum* had similar growth rates at 12–23 °C with significantly lower growth (by >100 % from peak growth) at 26 and 29 °C. *Fucus vesiculosus* had similar growth between 12 and 16 °C, and significantly reduced growth at 20, 23 and 26 °C (by 29, 38, and 75 %, respectively) relative to its peak growth at 16 °C. *Chondrus crispus* grew best at 12 °C and had significantly reduced growth (by 28, 53, 52, 78 and 82 %, respectively) at the five warmer temperatures. There was no difference in growth between 20 and 23 °C; however, growth was significantly reduced at 26 and 29 °C compared to 16 and 20 °C. *Codium* grew best at 20 °C which was not significantly different from 12 and 16 °C; however, growth was significantly reduced at 23 °C

Fig. 3 Average standardized growth rate (%/day ± SE) for all surviving samples after **a** 20 days for all six temperatures and **b** 56 days without 16 °C due to a climate chamber breakdown. *Letters* indicate perANOVA post hoc results among temperatures within each species. *Asterisk* indicates non-significant post hoc test due to small sample size



and warmer temperatures (by 43, 140, and 62 %, respectively from 20 °C). *Laminaria digitata* had comparable growth rates at 12 and 16 °C with a significant decrease (by 77 % from 12 °C) in growth rates at 20 °C. Consequently, after 20 days of growth, 26 °C appeared to be a threshold value for *A. nodosum*, *F. vesiculosus*, where growth significantly decreased at this temperature from all cooler temperature. A similar threshold occurred at 23 °C for *Codium*, and 20 °C for *L. digitata*. *Chondrus crispus* experiences a reduction in growth at 26 °C; however, growth at 29 °C does not differ from 23 °C, so 26 °C cannot be considered a threshold based on our definition.

Similar results were found after 56 days, at the end of the experiment but excluding the 16 °C treatment, with significant differences in relative growth rates between species [two-way perANOVA, *pseudo-F*(4,70) = 33.96, *P* = 0.0001], temperatures, [*pseudo-F*(4,70) = 10.70, *P* = 0.0001], and their interaction [*pseudo-F*(11,70) = 3.68, *P* = 0.0004]. Again, *C. crispus* and *L. digitata* experienced their highest growth rate at 12 °C, while *A. nodosum* grew best at 20 °C (Fig. 3b). In contrast to 20 days, *F. vesiculosus* grew best at 12 °C while *Codium* grew best at 20 °C, although this difference may be due to the absence of 16 °C treatment in these comparisons. After 56 days, *A. nodosum* growth patterns had slightly changed as it had significantly reduced growth above 20 °C, instead of 23 °C after 20 days (by 57 and 103 % from 20 to 23 and 26 °C, respectively). *Fucus vesiculosus* showed the opposite pattern where growth rates at 20 and 23 °C became more similar to 12 °C; still, growth was significantly reduced at 26 °C by 65 % from 12 °C. *Chondrus crispus* growth became more similar across temperatures, with lowest growth at 26 °C. Interestingly, *C. crispus* was able to grow well at 29 °C, where growth rates were not statistically different from even 12 °C. *Codium* experienced significant decreases in growth above 20 °C (by 29, 110, and 79 % at 23, 26, and 29 °C, respectively from 20 °C); however, different from after 20 days it also had a comparable growth rate at 12 and 23 °C. Similar to after 20 days, *L. digitata* growth still significantly decreased above 12 °C by 78 % at 20 °C. Consequently after 56 days of growth, *F. vesiculosus* and *L. digitata* exhibited the same threshold temperatures as after 20 days at 26 and 20 °C, respectively. The threshold temperature dropped from 26 to 23 °C for *A. nodosum* while *Codium's* threshold temperature increased to 26 °C, possibly indicating some acclimation to experimental temperatures. *Chondrus crispus* was also able to acclimate to the warmer temperatures by the end of the experiment, with growth across all temperatures being comparable to one another. A summary of optimal growth temperatures, growth reduction, and mortality timelines is shown in Table 1, and optimal absolute growth rates after 20 and 56 days is shown in Table 2.

Over the course of the 56 days, a repeated measures perANOVA found significant differences between the interaction of temperature and time on relative growth rates for *A. nodosum* [perANOVA, *pseudo-F*(18,70) = 3.09, *P* = 0.0011], *F. vesiculosus* [*pseudo-F*(17,78) = 4.10, *P* = 0.0001], *Codium* [*pseudo-F*(20,100) = 6.82, *P* = 0.0001], *C. crispus* [*pseudo-F*(20,89) = 6.72,

Table 1 Response to temperature *a* after 20 days, and *b* after 56 days

	12 °C	16 °C	20 °C	23 °C	26 °C	29 °C
a						
L. digitata	++	+	~/− (14)	(20)*	(5)*	(5)*
A. nodosum	+	+	++	+	~	~/− (20)
F. vesiculosus	+	++	+	+	~	~/− (17)
C. crispus	++	+	+	+	+	− (17)
Codium	+	++	+	~	~	~
b						
L. digitata	++	Na	~/− (14)	(20)*	(5)*	(5)*
A. nodosum	+	Na	++	~	~/− (23)	(27)*
F. vesiculosus	++	Na	+	+	~/− (37)	(31)*
C. crispus	++	Na	− (47)	+	+	− (17)
Codium	+	Na	++	+	~	~

Symbols represent: growth (+), highest growth (++), growth reduction (~), partial mortality (−), reduced growth with partial mortality (~/−), and completemortality (*). Numbers in brackets represent the day when partial mortalitybegan or when 100 % mortality occurred

Table 2 Average absolute growth rates ± SE for weight (mg/week) and length (mm/week) at their optimal temperature (°C) for each species calculated over *a* 20 days to include 16 °C, and *b* 56 days at the end of the experiment

	A. nodosum	*F. vesiculosus*	*C. crispus*	*Codium*	*L. digitata*
a					
Temperature	20	16	12	16	12
Weight	23 ± 1.6	89 ± 15.7	160 ± 0.04	1228 ± 91.1	139 ± 19
Length	5.0 ± 1.1	4.5 ± 0.1	Na	9.7 ± 0.1	5.1 ± 0.5
b					
Temperature	20	12	12	20	12
Weight	22 ± 0.9	88 ± 6.7	107 ± 19.3	1070 ± 214.2	103 ± 1.9
Length	3.9 ± 0.5	3.3 ± 0.2	Na	5.5 ± 1.6	4.6 ± 0.4

$P = 0.0001$], and *L. digitata* [*pseudo-F*(6,32) = 7.10, $P = 0.0002$]. Thus, time is important to consider when determining and comparing growth rates among and across species as it typically decreased with time. Across the typical water temperatures occurring in Nova Scotia (12–20 °C), growth peaked sometime in the first 20–27 days before decreasing for all species (Online Resources 2 Fig. S1–S5). At the warmer temperatures, there was variation across species, where there was some evidence of temporary acclimation to warmer temperatures. *Ascophyllum nodosum* showed a sharp increase in growth at 26 °C after 2 weeks, followed by a sharp decrease for the rest of the experiment. *Fucus vesiculosus* showed a peak in growth over the first week at 29 °C, followed by a sharp decline over the rest of the experiment. *Chondrus crispus* had a significant increase in growth after 1 month at 29 °C, before declining to original growth rates. *Codium* displayed increases in growth at 26 °C after 4 weeks, and *L. digitata* had low, similar growth rates at 20 °C during the whole experiment.

Carbon and nitrogen content

At the end of the experiment, tissue %N significantly differed between species [two-way perANOVA, *pseudo-F*(4,38) = 52.63, $P = 0.0001$] and temperatures [*pseudo-F*(4,38) = 11.81, $P = 0.0001$], but not their interaction [*pseudo-F*(10,38) = 1.94, $P = 0.06$]. The species-specific differences in %N were expected due to taxonomic and functional differences among species. Interestingly, %N also significantly varied across temperatures. Whereas *A. nodosum* showed no change in %N across temperatures (Fig. 4a), %N increased by 50 % in *F. vesiculosus* and by 72 % in *L. digitata* from the lowest (12 °C) to the highest temperature at which they still survived (26 and 20 °C, respectively). In *C. crispus* and *Codium*, %N increased by 87 and 55 %, respectively, with temperature from 12 to 26 °C, but slightly decreased toward 29 °C. With the exception of *Codium*, %C changed very little across temperatures (Fig. 4b). Thus, %C significantly differed across species [two-way perANOVA, *pseudo-F*(4,38) = 94.44,

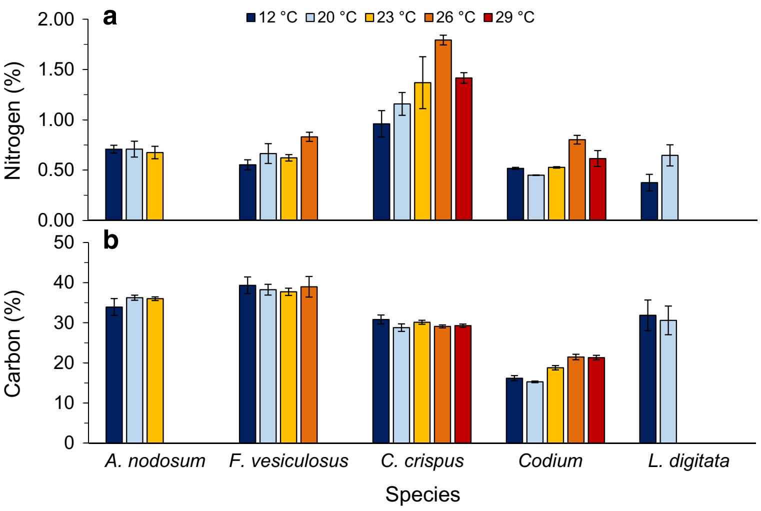


Fig. 4 Percent tissue **a** nitrogen (%N) and **b** carbon (%C; average ± SE) at the end of the experiment for surviving replicates ($n = 3$)

$P = 0.0001$] but not across temperatures [*pseudo-F*(4,38) = 1.05, $P = 0.39$].

Discussion

This study examined the effects of increasing water temperature on the growth, survival, and nitrogen and carbon contents of five seaweeds that are common and important along the rocky shores of Atlantic Canada. There were significant differences in growth, survival, and nitrogen content between current typical spring–summer SST (12 through 20 °C), and higher SST (23 through 29 °C) within and across species. These differences were most pronounced in the two most abundant species: intertidal rockweed *A. nodosum* and subtidal kelp *Laminaria digitata*, suggesting potential shifts in species composition on Atlantic Canada's rocky shores with future climate warming. Consequently, the following discussion is divided by the main interacting species in the intertidal zone (*A. nodosum* and *Fucus vesiculosus*), the subtidal zone (*L. digitata* and *Codium*), and then *Chondrus crispus* which occupies the low intertidal and the understory of the other species. Changes in carbon and nitrogen content are discussed in a separate section across all five species. Finally, we discuss the overall implications of potential shifts in species composition and performance for coastal ecosystems along the Atlantic shore and the benefits they provide to humans.

Effects of increased water temperature on intertidal rockweeds

Fucoids, including *A. nodosum* and *Fucus* species, dominate the mid-intertidal zone of the rocky shores in Atlantic Canada (Stephenson and Stephenson 1954). In this study, *A. nodosum* and *F. vesiculosus* both grew well at typical spring and summer temperatures between 12 and 20 °C, similar to the growth optima observed for laboratory culture of North Sea and New England populations for both species (15 °C; Niemeck and Mathieson 1978; Lüning 1990). This is slightly lower than the growth optima of 24 °C observed by Keser et al. (2005) for *A. nodosum* in field studies in Connecticut, which may be related to the local adaptation (Harley et al. 2012) of *A. nodosum* to warmer waters.

Differences between *A. nodosum* and *F. vesiculosus* became more pronounced at 23 °C, which may be the new sustained summer temperature in shallow coastal waters following the predicted 3 °C increase in SST over this century (IPCC 2007, 2013). At 23 °C after 56 days, *A. nodosum* growth was significantly reduced by 57 % from 20 °C. At 26 °C, the only positive growth occurred during the first 10 days, with decreased survivorship after 20 days. Therefore, should maximum summer SST reach averages of 23 °C, then *A. nodosum* beds will likely be negatively impacted, with reduced growth rates, and thus reduced canopy cover. It has been suggested that mean maximum SST should not be greater than 22 °C in the NW Atlantic for there to be no impacts on *A. nodosum* growth (Setchell 1922). In comparison, *F. vesiculosus* survivorship did not decrease until after 1 month at 26 °C. There was a 65 % reduction in growth rate at 26 °C compared to 12 °C, with no significant reduction in growth at 23 °C. Furthermore, *F. vesiculosus* exhibited a 25 and 110 % higher growth rate at 23 and 26 °C, respectively, relative to *A. nodosum*. Consequently, *F. vesiculosus* displayed a higher tolerance to increasing water temperatures.

Along the southwestern shores of Nova Scotia, the abundance of *F. vesiculosus* has been increasing in *A. nodosum* beds since 2003, which has been correlated with increasing SST, and a high *A. nodosum* harvesting intensity (Ugarte et al. 2010; Vandermeulen 2013). *Fucus vesiculosus* is a more opportunistic species, with shorter life spans (David

1943; Knight and Parke 1950), faster recruitment (Choi and Norton 2005), and higher growth rates (Table 2) in relation to *A. nodosum*. When *A. nodosum* beds are heavily harvested, space is created for *Fucus* species to settle (Vandermeulen 2013). Clearing experiments have found that once *A. nodosum* was removed, *Fucus* species replaced it, and after 10 years *A. nodosum* had not yet returned (Thomas 1994). Consequently, the additive effects of increasing SST and commercial harvesting of *A. nodosum* may further change the abundance of these two species. If SST increases as predicted, the dominance of *A. nodosum* may decrease allowing for the abundance of *F. vesiculosus* to possibly increase. Should this happen, the commercial *A. nodosum* harvest in the Canadian Maritimes may be impacted (Ugarte et al. 2010). Interestingly, in Northern Britain, significant increases in the abundance of both species have been observed in the field during a time of increasing SST from 1974 to 2010, with mean summer SST increasing from 10 to 11 °C in the north and 13 to 14 °C in the south (Yesson et al. 2015). Thus, well below their growth optima and these increases in SST likely allowed for increased growth during the summer. In the NW Atlantic, summer SST come much closer to the thermal growth optima for these two species (Fig. 1). Ecological niche models have predicted that with continued climate change *A. nodosum* and *F. vesiculosus* will shift northwards as an assemblage (Jueterbock et al. 2013). Yet, in contrast to our experimental findings, and field observations by Ugarte et al. (2010), *A. nodosum* was the only species predicted to survive south of Halifax, Nova Scotia, by 2200 in response to increased SST (Jueterbock et al. 2013). The caveat of that prediction is, however, that the present day model predicted a southern boundary for *A. nodosum* much further south than observed (e.g., 36°N versus 40°N), and may thus underestimate the northward shift, whereas the model correctly predicted the southern boundary for *F. vesiculosus*.

In our experiment, both fucoids exhibited significantly reduced survival at 29 °C, where no replicates survived after 1 month, with low (*F. vesiculosus*) or negative (*A. nodosum*) growth rates during this time. Previous studies in the North Atlantic found the upper thermal limit for survival of both these species is 28 °C, above which mortality occurs (Lüning 1990; Keser et al. 2005). However, our study demonstrated that mortality is not immediate above this thermal limit. Therefore, only if SST persists for more than 1 month at 29 °C will this likely denote the southern distribution limit forcing the seaweeds to face local extinction or retreat northwards to cooler waters (Jueterbock et al. 2013). Over the past 50 years, the southern distribution limit of *A. nodosum* has moved northward, where Taylor (1957) had observed *A. nodosum* in New Jersey in the 1950s, but by the 1970s it had moved north and has remained at Long Island Sound (Gosner 1979), where maximum summer SST reach 23 °C (Keser et al. 2005). In the Northeast Atlantic, fucoids reach their southern boundary in Portugal with SST of 18 °C (Chapman 1995). Consequently, as both these temperatures are much below 29 °C, some other factor may be influencing the southern distribution limit for these two species. Thus, the new predicted summer SST of 23 °C in Atlantic Canada may denote the new southern limit for fucoids with continued warming, with the potential for fucoids acclimating to exist at similar abundances as presently observed.

This study only examined the effects of increased water temperature during emersion. With continued climate change there will also be continued increases in air temperature (IPCC 2007, 2013) which would affect the rate of dehydration during low tide. Fucoids are drought tolerant species, meaning they do not have mechanisms to retain water during air exposure (Chapman 1995). Thus, these algae are frequently stressed from desiccation (Davison and Pearson 1996). Desiccation may increase or decrease the effect of warmer temperatures, yet this response is species-specific (Harley et al. 2012). The desiccation tolerance in fucoids increases during the summer (Lüning 1990), suggesting that increasing air temperatures may only have a minimal effect on desiccation.

Effects of increased water temperature on subtidal kelp and *Codium*

The canopy cover of kelp beds in the Northwest Atlantic has been in decline since the introduction of the invasive bryozoan *Membranipora membranacea* in 1992 (Scheibling et al. 1999), and the green alga *Codium* in 1989 (Bird et al. 1993; Scheibling and Gagnon 2006). As SST continues to increase, warmer water temperatures may also likely play a role in the decline of kelp (Levin et al. 2002). Our study found that *L. digitata* grew well at 12–16 °C, with a significant reduction in growth at 20 °C. This is in accordance with previous work on *L. digitata* from Nova Scotia, which found that growth peaked at 10 °C, and became reduced at 15 °C (Bolton and Lüning 1982). At warmer temperatures, we found that in less than 1 week, *L. digitata* experienced rapid mortality at 26 and 29 °C, and after 3 weeks all replicates died at 23 °C. This is not surprising as previous work on Nova Scotian *L. digitata* populations found mortality to occur at 23–24 °C (Bolton and Lüning 1982). Therefore, should maximum average SST increase to 23 °C as predicted, it can be expected that the canopy cover of *L. digitata* would be reduced, if not eliminated, in the shallow subtidal. This would not be restricted to *L. digitata* alone, the survivorship threshold of other common kelp species (*Saccharina latissima* and *Alaria esculenta*) is similar to that of *L. digitata,* and all three species exhibit growth optima at 10–15 °C (Bolton and Lüning 1982).

Surprisingly, although there has been a significant warming trend in the NW Atlantic over the past 30 years (Baumann and Doherty 2013), so far no distributional shifts have been recorded for several species of kelp in Atlantic Canada since 1850 (Merzouk and Johnson 2011). This has been attributed to a lack of baseline knowledge. In Britain, increases in SST, listed above, from 1974 to 2010 have resulted in species-specific and location-specific responses in several kelp species, including *L. digitata*, *S. latissima*, *Chorda filum*, and *A. esculenta* (Yesson et al. 2015). Some populations are declining, typically in southern regions (e.g., *C. filum* in the English Channel), while other populations are increasing, typically in northern regions (e.g., *L. digitata* in the North Sea). This poleward migration has been well documented globally (Wernberg et al. 2011; Tanaka et al. 2012; Gallon et al. 2014; Yesson et al. 2015), and is expected to occur in Atlantic Canada as well (Jueterbock et al. 2013).

In contrast to kelp, no *Codium* replicates experienced any mortality over the 9 weeks of our experiment. This was not surprising as the recorded mortality temperature for this species is 33 °C (Hanisak 1979). *Codium's* growth peaked at 16 °C, but was similar to 12 and 20 °C, with significant growth reductions of 29, 110, and 79 % at 23, 26, and 29 °C, respectively, compared to 20 °C. This peak growth occurred at a lower temperature than expected. Laboratory culture of Rhode Island populations of *Codium* found maximum growth occurred at 24 °C (Hanisak 1979). These differences in optimal growth temperature may be a result of each population exhibiting local adaptations (Harley et al. 2012; e.g., max. summertime SST: Rhode Island 24 °C, Atlantic Canada ~20 °C).

As SST continues to increase the switch from kelp beds to *Codium* meadows may shift to more northern waters. *Codium*'s distribution has been increasing northwards in Atlantic Canada, where it was first observed in Nova Scotia in 1989 (Bird et al. 1993). In 2012, wrack was first observed in Newfoundland, and by 2013 established *Codium* meadows were discovered (Matheson et al. 2014). In typical healthy kelp beds, laminarian kelps are able to inhibit the growth of *Codium* (Scheibling and Gagnon 2006). However, following removal of the kelp canopy cover from urchin grazing, or colonization by *Membranipora membranacea*, and possibly temperature stress, *Codium* is able to colonize the exposed substrate. Once present, *Codium* can inhibit the recruitment and decrease the survival of remaining kelps (Levin et al. 2002). This turnover from a healthy kelp bed to a *Codium* meadow can occur in as little as 2 years (Scheibling and Gagnon 2006). Furthermore, increasing SST decreases the resilience of kelp beds, making them more susceptible to disturbances such as shifts in herbivore abundance, reduced water quality, increasing intensity of storms, as well as decreasing the performance of kelp recruits (Wernberg et al. 2010). Therefore, as SST continues to increase there may be rapid turnover in subtidal canopy cover from kelp to *Codium*, as *Codium* was minimally impacted by warmer water temperatures, and exhibited a higher thermal tolerance than *L. digitata*. This would have severe impacts on the diversity and abundance of associated epiphytic and benthic flora and fauna found in the canopy and understory of subtidal kelp beds along the rocky shores of Nova Scotia (Schmidt and Scheibling 2006, 2007).

Effects of increased water temperature on Irish moss

Chondrus crispus, commonly known as Irish moss, has been commercially important in Atlantic Canada since the late 1940s (Chopin and Ugarte 2006). This perennial red alga forms dense canopies in a distinct band in the low-intertidal zone along the rocky shores, and occurs in the understory of rockweed and kelp (Stephenson and Stephenson 1954). Interestingly, *C. crispus* was able to survive and in fact grow, at even the warmest temperatures in our experiment. Over the first 3 weeks, growth was significantly higher at 12 °C than at all warmer temperatures; however, after 56 days growth became similar across most temperatures. This broad temperature optimum has been established in the literature. In the North Sea, *C. crispus* exhibits optimal growth between 10 and 15 °C (Fortes and Lüning 1980), while North American (Massachusetts, Maine, and Nova Scotia) samples exhibit optimal growth between 15 and 20 °C (Prince and Kingsbury 1973a; Neish et al. 1977; Kübler and Davison 1993; Kübler and Dudgeon 1996).

Should SST continue to increase, our results suggest that *C. crispus* may be able to tolerate water temperature up to 29 °C, with only partial mortality and growth reductions. An earlier study showed that *C. crispus* was able to tolerate warmer water temperatures after an acclimation period (Kübler and Davison 1993), which is also demonstrated in this study with temporarily increased growth rates at both 26 and 29 °C. This is particularly interesting as mortality temperature for Nova Scotian populations has previously been observed at 29 °C, occurring within 2 weeks (Lüning et al. 1986). Since these studies are over 30 years old, our results indicate that *C. crispus* may be demonstrating an increasing tolerance to thermal stress. This is further corroborated by the lack of growth reduction at 23 °C in our study, compared to growth reductions being observed in Massachusetts populations in the 1970s at water temperatures above 21.1 °C (Prince and Kingsbury 1973b). Therefore, if average maximum SST in Atlantic Canada would reach 23 °C, the direct effect on *C. crispus* will likely be minimal. Supporting this across the Atlantic in Brittany, a comparison of *C. crispus* distribution following significant increases in SST from 1992–1998 to 2010–2012 found an increasing prevalence of

C. crispus (Gallon et al. 2014). Although, as climate change is not the only stressor these seaweeds face, other impacts such as harvesting must be considered. When *C. crispus* beds are over-harvested, space is created, allowing for successive colonization of ephemeral algae, barnacle growth, then overgrowth of *Fucus* species, as well as an increase in the abundance of coralline algae (Vandermeulen 2013). Recovery of beds back to dominance of *C. crispus* can take up to 4 years. So far, it is unknown how the cumulative impacts of overharvesting and climate change will affect the abundance of *C. crispus* in Atlantic Canada (DFO 2013).

Tissue carbon and nitrogen content

Macroalgae play an important role cycling and storing nutrients in coastal waters (Smith 1981; Pedersen et al. 2004; Schmidt et al. 2011). As such, tissue nutrient concentrations of macroalgae give good indication of ambient nutrient conditions within the water column (Savage and Elmgren 2004). As all species in our study were collected in the same location, at the same time, and exposed to the same filtered seawater, it can be assumed that significant differences in nutrient content reflect differences in nutrient uptake or usage across experimental temperatures. The tissue dry weight (DW) %C values for all species fell within the range reported in the literature (*A. nodosum*: Schmidt et al. 2011; *F. vesiculosus*: Thompson and Valiela 1999; *L. digitata*: Brady-Campbell et al. 1984; *C. crispus* and *Codium*: Lapointe and Littler 1992). Previous work on eelgrass (*Zostera marina*), a marine angiosperm, showed that temperature can increase DW %C content while DW %N remains the same (Touchette et al. 2003). In contrast, previous work on the kelp *S. latissima* found following temperature increase from 12 to 22 °C that at high and low N enrichment, DW %C decreased, while the decrease of DW %N was only significant at high N enrichment (Gerard 1997). However, our results did not find that increased temperature had a significant effect on C content. Yet, if some seaweed canopies decline or disappear with increasing SST, the storage of carbon in seaweed habitats will be reduced (Schmidt et al. 2011), unless other species are able to fill the gap.

In contrast, we did find increased nitrogen content with increasing temperature. Macroalgae can store extra N during periods of high nutrient availability (e.g., winter) and save it for periods of growth in unfavorable conditions (e.g., summer; Asare and Harlin 1983). Generally, macroalgae require tissue DW %N of ~1.5 % to sustain maximum growth (Fujita et al. 1989), with the minimum requirements (subsistence growth) being dependent on the species, temperature, light, and other conditions, but ranging around 0.52–0.55 % (Lobban and Harrison 1994; Pedersen and Borum 1997). In our experiment, most samples were above these minimum requirements, although only *C. crispus* showed optimal %N levels at higher temperatures. When subjected to increased temperatures, all species, except *A. nodosum*, showed increased DW %N. Perhaps in stressful environments, macroalgae may be storing N to be used later for growth in less stressful conditions. Alternatively, the higher DW %N may indicate that these seaweeds were unable to use up their previously stored N (e.g., from high winter seawater nutrient content) at the warmer temperatures to be used for growth, since growth was reduced. As we used the entire plant in our experiments, we could not take pre-manipulation tissue samples to test this. However, we did measure other specimens of the same species collected in the field at the same time, which showed similar (*A. nodosum*) or higher (*L. digitata*, *F. vesilous*, *C. crispus*, and *Codium*) %N (Wilson et al. unpubl. data), which would corroborate the latter hypothesis. Previous work found evidence of decreased nutrient uptake with increasing temperature from 5 to 15 °C in *F. spiralis* and from 12 to 22 °C in *S. latissima* (Topinka 1978; Gerard 1997). Whichever the mechanism, the combination of increased tissue N with reduced growth may not alter the overall storage of N in the seaweed canopies, unless mortality occurs and the canopies decline.

Changes in nutrient uptake will also affect the nutritional quality of the seaweeds. The level of herbivory by grazers on seaweeds depends on the seaweeds nutritional qualities, as well as the amount of chemical defense within the seaweed (Harley et al. 2012). Since grazer palatability is known to increase with increased nitrogen content (Hemmi and Jormalainen 2002; Van Alstyne et al. 2009), grazing pressure might be altered with increasing SST. More research on the effect of temperature on nutrient uptake and usage in different macroalgal species would be essential in identifying the mechanism(s) driving the higher nitrogen content observed in our study and their broader implications.

Conclusion and implications

As sensitive indicators of local climate change, alterations in the growth and survival of macroalgae can indicate changes in ambient environmental conditions (Merzouk and Johnson 2011). If ambient water temperature is below the growth optima, climate change may benefit macroalgae (Harley et al. 2012). However, for individuals at the southern end of their niche, increasing SST may begin to lead to poleward shifts and local extinctions (Jueterbock et al. 2013). The distributions of seaweeds have been changing globally, with increasing SST being one important driver behind these shifts (Wernberg et al. 2011; Tanaka et al. 2012; Gallon et al. 2014; Yesson et al. 2015). However, increasing SST is only one impact that marine ecosystems are facing today and in the future. Biological invasions, commercial harvesting, ocean acidification, and eutrophication of coastal waters also affect the growth and survival of seaweed communities in the Northwest Atlantic; yet, the cumulative effects of these multiple stressors on seaweeds are not well understood.

This study was unique in that we examined the physiological response of the dominant habitat-forming seaweed species found in Atlantic Canada in relation to predicted increases in SST due to warming temperatures. The dominant native habitat-forming species (intertidal *A. nodosum* and subtidal *L. digitata*) experienced reduced survival at simulated heat wave temperatures (26, 29 °C). Moreover, *A. nodosum* exhibited reduced growth at the predicted future summer maximum SST (23 °C) and all replicates of *L. digitata* died at this temperature. In contrast, the invasive alga *Codium* survived and grew at all experimental temperatures and the more opportunistic *F. vesiculosus* only exhibited growth reductions and mortality above 23 °C. Consequently, continued increases in SST may lead to a shift in dominant canopy-forming species to *Fucus*-dominated beds in the intertidal and *Codium*-dominated meadows in the subtidal zone along the rocky shores of Atlantic Canada. In Nova Scotia, increasing SST and harvesting have already been linked to an increase in *F. vesiculosus* in *A. nodosum* beds (Ugarte et al. 2010), yet the actual effects of increasing SST on kelp and *C. crispus* beds in the field are so far unknown (Merzouk and Johnson 2011; DFO 2013). *Chondrus crispus* coverage will likely not change as a direct result of increasing SST, yet it is important to consider the cumulative impact of harvesting with increasing SST. These potential shifts will affect the commercial importance and ecological services provided by these habitat-forming macroalgae, particularly in the subtidal zone due to the strong differences in associated species composition in kelp beds compared to *Codium* meadows (Schmidt and Scheibling 2006, 2007).

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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