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Coastal ocean acidification and nitrogen loading facilitate invasions of the non-indigenous red macroalga, *Dasysiphonia japonica*

Craig S. Young · Christopher J. Gobler

Abstract Coastal ecosystems are prone to multiple anthropogenic and natural stressors including eutrophication, acidification, and invasive species. While the growth of some macroalgae can be promoted by excessive nutrient loading and/or elevated pCO_2, responses differ among species and ecosystems. Native to the western Pacific Ocean, the filamentous, turf-forming rhodophyte, *Dasysiphonia japonica,* appeared in estuaries of the northeastern Atlantic Ocean during the 1980s and the northwestern Atlantic Ocean during the late 2000s. Here, we report on the southernmost expansion of the *D. japonica* in North America and the effects of elevated nutrients and elevated pCO_2 on the growth of *D. japonica* over an annual cycle in Long Island, New York, USA. Growth limitation of the macroalga varied seasonally. During winter and spring, when water temperatures were < 15 °C, growth was significantly enhanced by elevated pCO_2 ($p < 0.05$). During summer and fall, when the water temperature was 15–24 °C, growth was significantly higher under elevated nutrient treatments ($p < 0.05$). When temperatures reached 28 °C, the macroalga grew poorly and was unaffected by nutrients or pCO_2. The $\delta^{13}C$ content of regional populations of *D. japonica* was −30‰, indicating the macroalga is an obligate CO_2-user. This result, coupled with significantly increased growth under elevated pCO_2 when temperatures were < 15 °C, indicates this macroalga is carbon-limited during colder months, when in situ pCO_2 was significantly lower in Long Island estuaries compared to warmer months when estuaries are enriched in metabolically derived CO_2. The $\delta^{15}N$ content of this macroalga (9‰) indicated it utilized wastewater-derived N and its N limitation during warmer months coincided with lower concentrations of dissolved inorganic N in the water column. Given the stimulatory effect of nutrients on this macroalga and that eutrophication can promote seasonally elevated pCO_2, this study suggests that eutrophic estuaries subject to peak annual temperatures < 28 °C may be particularly vulnerable to future invasions of *D. japonica* as ocean acidification intensifies. Conversely, nutrient reductions would serve as a management approach that would make coastal regions more resilient to invasions by this macroalga.

C. S. Young · C. J. Gobler (✉)
School of Marine and Atmospheric Sciences, Stony Brook University, Southampton, NY 11968, USA
e-mail: Christopher.gobler@stonybrook.edu

Introduction

The continued anthropogenic delivery of carbon dioxide (CO_2) into surface oceans is changing the carbonate chemistry of the ocean, yielding reductions in pH and CO_3^{2-} levels and increases in CO_2 and HCO_3^- levels (Meehl et al. 2007). Beyond the combustion of fossil fuels, eutrophication-enhanced microbial respiration can also be a strong regional source of CO_2 and acidification that can result in the seasonal accumulation of respiratory CO_2 to levels that can exceed end of century projections of pCO_2 for the open ocean (> 1000 µatm; Cai et al. 2011; Melzner et al. 2013; Wallace et al. 2014). While ocean acidification can have negative consequences for calcifying organisms (Gazeau et al. 2007; Ries et al. 2009; Talmage and Gobler 2011; Young et al. 2019) elevated pCO_2 can benefit some, but not all, photosynthetic organisms (Hattenrath-Lehmann et al. 2015; Koch et al. 2013; Palacios and Zimmerman 2007), such as macroalgae (Gao et al. 1993; Hepburn et al. 2011; Young and Gobler 2016; Young et al. 2018). However, elevated pCO_2 may also benefit invasive macroalgae and provide them an advantage over their native counterparts (Hall-Spencer et al. 2008).

Invasive macroalgae can be a significant ecosystem threat. Invasive species often tolerate a wide range of abiotic conditions and may be less palatable to grazers than native species (Hayes and Barry 2008; Low et al. 2015; Theoharides and Dukes 2007). The filamentous, turf-forming rhodophyte *Dasysiphonia* (formerly *Heterosiphonia*) *japonica* (henceforth *Dasysiphonia*) is native to the western Pacific Ocean (Chihara 1970; Choi et al. 2009; Okamura 1936) but was introduced into European waters in 1984 (Sjøtun et al. 2008). Since then, this macroalga has spread throughout the eastern Atlantic Ocean from France north to Norway and Sweden (Husa et al. 2004; Lein 1999), south into the Mediterranean Sea (Sagerman et al. 2015; Sjøtun et al. 2008), and as far west as Scotland (Moore and Harries 2009; Supplementary Fig. S1). Following this introduction, the macroalga spread to the western Atlantic Ocean. In North America, the macroalga has been found as far south as Rhode Island and eastern Long Island Sound (USA) (Newton et al. 2013; Ramsay-Newton et al. 2017; Schneider 2010) and as far north as Maine and Nova Scotia, Canada (Idlebrook 2012; Savoie and Saunders 2013; Supplementary Fig. S1). While the species appears to be a cold-water alga, Bjærke and Rueness (2004) found that the macroalga's temperature range for growth is 0–30 °C and that the optimal temperature for growth is 19–25 °C. Given this, it is possible this macroalga will continue to invade the North American East Coast (Bjærke and Rueness 2004). The role of anthropogenic processes, including ocean acidification and nutrient loading, in facilitating the spread of *Dasysiphonia,* is unknown.

Excessive nutrient loading can promote the overgrowth of larger indigenous macroalgae (Conley et al. 2009; Valiela et al. 1997) by smaller morphologically simpler species that are capable of rapid growth in the presence of high nutrient concentrations and have a high assimilative capacity for nutrients (Neori et al. 2003; Valiela et al. 1997). Despite the great diversity of macroalgae, eutrophic conditions often lead to dominance by opportunistic chlorophytes and several branching or filamentous genera of rhodophytes such as *Gracilaria* (Valiela et al. 1997). To date, it has been generally concluded that such macroalgae can dominate estuaries with high nutrient loads and shorter residence times due to their ability to attach to the benthos and form dense beds (MacIntyre et al. 2004; Valiela et al. 1997). The extent to which invasions of *Dasysiphonia* are related to eutrophication is presently unknown.

Beyond nutrients, elevated pCO_2 has been shown to benefit multiple marine macroalgae, including a variety of non-calcifying chlorophytes (Björk et al. 1993; Holmer et al. 2005; Olischläger et al. 2013; Young and Gobler 2016), phaeophytes (Hepburn et al. 2011), and rhodophytes (Gao et al. 1993; Hofmann et al. 2012; Xu et al. 2010). Of these three divisions, Rhodophyta has the largest number of species that are obligate CO_2 users with a high affinity for CO_2 and thus may respond more positively as CO_2 levels increase compared to species that rely exclusively on HCO_3^- or use both forms of inorganic carbon (Badger et al. 1998; Johnson et al. 1992; Koch et al. 2013). The extent to which a macroalga may benefit from elevated pCO_2 is partly dependent on whether inorganic uptake of the macroalga is substrate-saturated at modern day pCO_2 levels (Koch et al. 2013). To date, no study has explored the effects of elevated pCO_2 on the growth of *Dasysiphonia*.

The objective of this study was to assess how elevated nutrients and pCO_2 levels may individually and collectively affect the growth rate of the invasive

rhodophyte *Dasysiphonia* for the entirety of its growing season (Newton et al. 2013; Ramsay-Newton et al. 2017; Schneider 2010). Surveys of *Dasysiphonia* were performed across the south shore of Long Island (New York, USA) during which $\delta^{13}C$ and $\delta^{15}N$ content of macroalgal tissue were quantified to evaluate C and N sources. Laboratory experiments were performed monthly over an annual cycle, exposing the macroalga to ambient and elevated pCO_2 levels with and without nutrient enrichment with each experiment performed at ambient water temperatures (4–28 °C). Given the invasive nature of *Dasysiphonia*, further experiments were performed to assess the growth response of co-occurring native macroalgae to elevated pCO_2 and nutrients in both the presence and absence of *Dasysiphonia* (*details below*). For those experiments, the foliose rhodophyte *Porphyra purpurea* (henchforth *Porphyra*) and cylindrical, branching rhodophyte *Agardhiella subulata* (henchforth *Agardhiella*) were examined. Both species are common in estuaries across Long Island (Pedersen et al. 2008; Stewart Van Patten and Yarish 2009; Tang et al. 2015). For all experiments, growth rates, $\delta^{13}C$ signatures, and elemental composition were evaluated and analyzed.

Methods

Experimental design and set-up

During spring, summer, and fall 2018, and winter 2019, ten experiments were performed to assess the effects of elevated pCO_2, nutrients, and temperature on the growth rates of *Dasysiphonia*. All experiments were performed following previously published methods (Young and Gobler 2016, 2017; Young et al. 2018) in 1-L polycarbonate vessels, which were acid-washed (10% HCl) and liberally rinsed with deionized water prior to use. Seven parallel experiments were performed with *Porphyra* during summer and fall 2018. Vessels were placed in an environmental control chamber set to a constant temperature consistent with ambient water temperatures (4–28 °C), light intensity (~ 250 μmol photons $m^{-2} s^{-1}$), and duration (i.e. light: dark cycle) at the macroalgal collection site. The light intensity and temperature measurements were made with a LI-COR LI-1500 light sensor logger and a YSI Pro Series sonde at collections sites (*see below*)

and were obtained via regional monitoring buoys. Vessels were filled with filtered (0.2 μm polysulfone filter capsule, Pall©) seawater collected from the macroalgal collection sites and were randomly assigned, in quadruplicate, to one of four treatments: a control with ambient pCO_2 (~ 400 μatm) and ambient nutrients ($\sim 1–5$ μM nitrate, $\sim 0.1–1$ μM phosphate), a treatment with ambient pCO_2 and elevated nutrients (50 μM nitrate, 3 μM phosphate), a treatment with elevated pCO_2 (~ 1800 μatm) without nutrient additions, and a treatment with elevated pCO_2 ($\sim 1,800$ μatm) and elevated nutrients (50 μM nitrate, 3 μM phosphate), resulting in 16 experimental vessels per experiment. The pCO_2 and nutrient levels used during experiments were within the range of levels of US East Coast estuaries (Baumann and Smith 2017; Baumann et al. 2015; Wallace et al. 2014; Wallace and Gobler 2015) and were used during prior experiments that involved macroalgae from Shinnecock Bay, New York, USA (Young and Gobler 2016, 2017; Young et al. 2018).

A 3.8×1.3 cm air diffuser (Pentair) connected with Tygon tubing to 1-mL polystyrene serological pipettes inserted into the bottom of each vessel was used to deliver dissolved gases to vessels. Vessels were subjected to ambient (400 μatm) and elevated (~ 2000 μatm) pCO_2 via a gas proportionator system (Cole Parmer® flowmeter system, multi-tube frame) that mixed ambient air from an air source with 5% CO_2 gas (Talmage and Gobler 2010). Gases were mixed and delivered at a flow rate of 2500 ± 5 mL min^{-1}, which turned over the volume of the vessels $> 1,000$ times daily. Bubbling was initiated 2–3 days prior to the beginning of each experiment to allow pCO_2 levels and pH to reach a state of equilibrium. All experiments lasted approximately one week, a duration consistent with prior studies that yielded significant changes in the growth of macroalgae (Young and Gobler 2016, 2017). Measurements of pH within experimental vessels were made daily with a Honeywell Durafet III ion-sensitive field-effect transistor-based (ISFET) solid-state pH sensor (± 0.01 pH unit, pH unit, total scale), which was calibrated with a seawater pH standard (Dickson 1993). Measurements of pH made with the Durafet were compared to measurements made spectrophotometrically using *m*-cresol purple (Dickson et al. 2007) and were found to be nearly identical and never significantly different.

Discrete seawater samples were collected at the beginning and conclusion of all experiments to directly measure DIC within each experimental vessel in each treatment ($n = 4$ per treatment). DIC samples were preserved using a saturated mercuric chloride ($HgCl_2$) solution and stored at $\sim$ 4 °C until analysis. DIC samples were analyzed by a VINDTA 3-D (versatile instrument for the determination of total inorganic carbon) delivery system coupled with a UIC Inc. coulometer (model CM5017O) as per Young and Gobler (2018). Final total alkalinity, pCO_2, and levels of HCO_3^- (Supplementary Table S1) were calculated from measured DIC levels, pH, temperature, and salinity, as well as the first and second dissociation constants of carbonic acid in seawater (Millero 2010) using the program CO2SYS (http://cdiac.ess-dive.lbl.gov/ftp/co2sys/, last access: 23-November-2019). For quality assurance, DIC levels and pH within certified reference material (provided by Andrew Dickson of the University of California, San Diego, Scripps Institution of Oceanography; batches 159 and 173 = 2027.14 and 2042.41 µmol DIC kg seawater^{-1}, respectively) were measured during analyses of every set of samples. The analysis of samples only continued after complete recovery (99.8 $\pm$ 0.2%) of certified reference material was attained. Actual mean pH and pCO_2 were 7.99 and 408 µatm, respectively, for ambient conditions, and 7.36 and 1860 µatm, respectively, for elevated pCO_2 conditions. These values were within the range found seasonally in some estuarine environments (Baumann and Smith 2017; Baumann et al. 2015; Wallace et al. 2014; Wallace and Gobler 2015).

Assessing the effects of elevated pCO2 and nutrient levels on Dasysiphonia and Porphyra

Dasysiphonia and *Porphyra* were collected from a shallow-water (depths of 1–2 m) area in Great South Bay, New York, USA (Fig. 1; 40.73° N, −73.05° W) during low tide. All macroalgae collected were found growing subtidally. 20-L carboys were used to collect water from the collection sites. Large, well-pigmented, robust fronds of *Dasysiphonia* and *Porphyra* were collected, placed in coolers of seawater from the collection site, and transported to the Stony Brook Southampton Marine Science Center within 30 min of collection. Identification of macroalgae was based on morphology, microscopy, and known biogeography.

Dasysiphonia is a common, but non-native species of red macroalgae along the North American east coast including around Long Island (Newton et al. 2013; Ramsay-Newton et al. 2017; Schneider 2010). *Porphyra* is a common species of rhodophyte in estuaries across Long Island (Pedersen et al. 2008; Stewart Van Patten and Yarish 2009; Tang et al. 2015). While *Dasysiphonia* is present most of the year in NY coastal waters, *Porphyra* is present seasonally during warmer months. Hence, experiments for *Dasysiphonia* were performed February through November, whereas *Porphyra* experiment were performed May through November. Pieces approximately 5 cm in length were cut from larger thalli, rinsed in filtered (0.2 µm) seawater and placed in a salad spinner to remove debris and epiphytes. They were then extensively rinsed with filtered seawater before being spun again to further remove any debris, epiphytes, and excess seawater (Young and Gobler 2016). Additional samples of were cut, cleaned, rinsed, and spun as described, and frozen for later analyses (*see below*). From the 5-cm pieces of thalli, a sub-sample was removed and weighed on a Scientech ZSA-120 digital microbalance ($\pm$ 0.0001 g) to obtain initial wet weights which were typically $\sim$ 1 g. All samples were kept in 100-mL filtered seawater after cleaning and weighing to prevent desiccation prior to introduction to experiments.

Experiments began with the introduction of macroalgae and nutrients into vessels that had been bubbling at the desired pCO_2 levels for several days as described above. Vessels were monitored daily for one week during the experiment as described above. Periodic light measurements were made using a LI-COR LI-1500 light sensor logger and HOBO pendant temperature and light data loggers. At the conclusion of experiments, final pH and temperature measurements were made and a final DIC sample from each bottle was analyzed as described above. Macroalgae samples were removed from their respective vessels and rinsed, spun, re-rinsed, re-spun, and weighed as described above. After being weighed, samples were placed into small freezer bags for further analysis. Weight-based growth rates for all species were determined using the relative growth rate formula (growth d^{-1}) = (ln W_{final}–ln $W_{initial}$)/(Δt), where W_{final} and $W_{initial}$ are the final and initial weights in grams and Δt is the duration of the experiment in days. Normality and equal variance of growth rates were
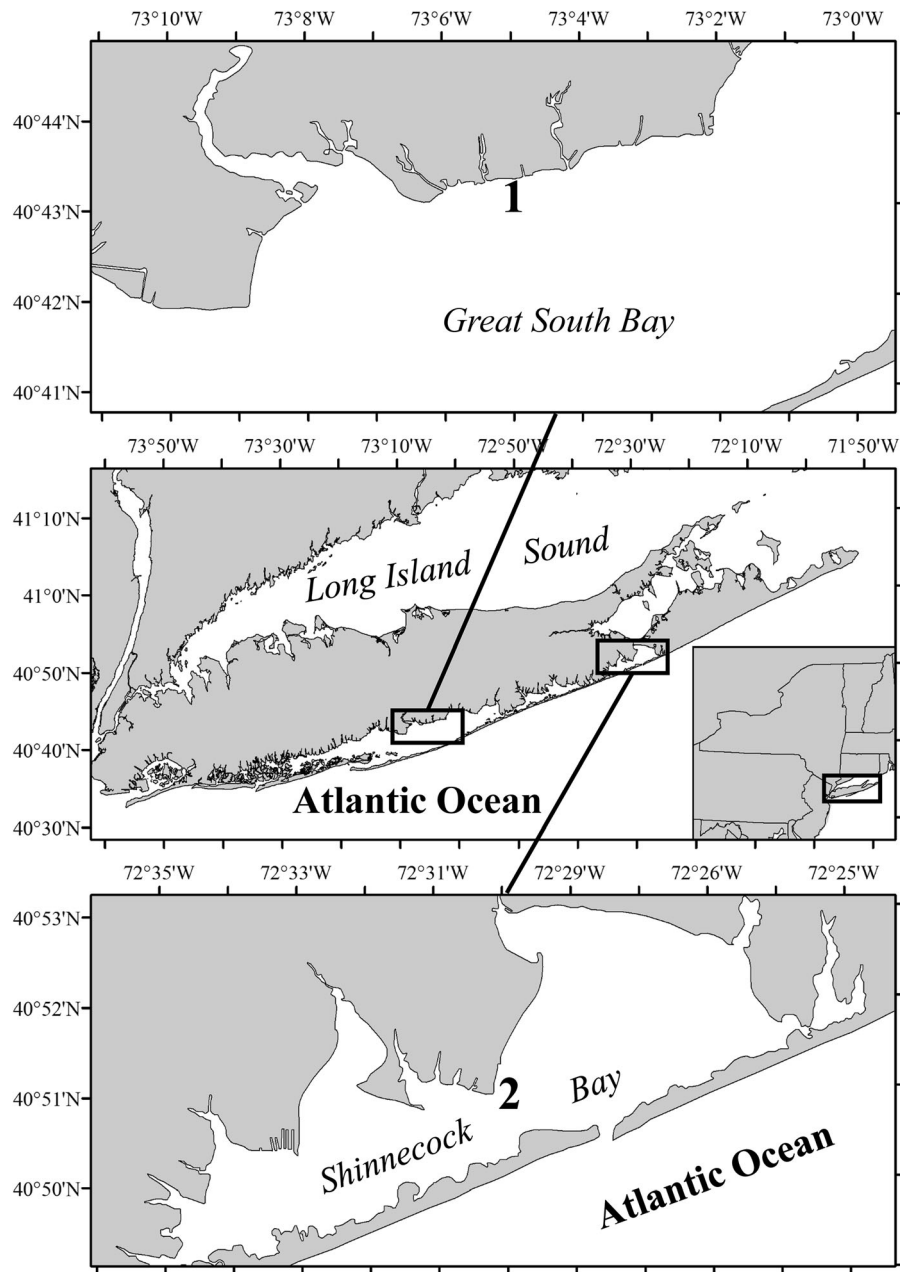
Fig. 1 Maps of Great South Bay and Shinnecock Bay, NY, USA. Numbers represent shallow-water regions where collections of 1) *Dasysiphonia japonica* and *Porphyra purpurea* for March 2018 through February 2019 experiments, and 2) *Dasysiphonia japonica* and *Agardhiella subulata* for the October 2019 experiment. All maps were generated using ArcMap (Version 10.6) (Esri)

assessed via the use of Shapiro–Wilk and Leven tests; assumptions of equal variance and normality were met for all data. Differences in the growth rates of *Dasysiphonia* or *Porphyra* under ambient and elevated pCO_2 and nutrients were assessed via two-way

ANOVAs performed using SigmaPlot 11.0 for which the main treatment effects were pCO_2 (ambient or elevated) and nutrients (ambient or elevated). For comparison of growth rates between *Dasysiphonia*

and *Porphyra*, Tukey Honest Difference (Tukey HSD) tests using R 3.4.0 within 1.0.143 were performed.

Assessing the effects of elevated pCO_2 and nutrients, and competition

A final laboratory experiment was performed to assess the effects of competition and elevated pCO_2 and nutrients on the growth of *Dasysiphonia* and *Agardhiella*. Identification of macroalgae was based on morphology, microscopy, and known biogeography. *Dasysiphonia* and *Agardhiella* were collected during low tide from a shallow-water (depths of 1–2 m) area in Shinnecock Bay, New York, USA (Fig. 1; 40.85° N, −72.50° W) and prepared in the same manner described above. All macroalgae collected were found growing subtidally. The experiment was performed in 1-L polycarbonate vessels in an environmental control chamber as described above. Containers were randomly assigned, in quadruplicate, to one of six treatments: two controls with ambient pCO_2 ($\sim$ 400 µatm) and ambient nutrients (1 µM nitrate, 0.5 µM phosphate) that received either *Agardhiella* or *Dasysiphonia*, a treatment with ambient pCO_2 and nutrients that received *Agardhiella* and *Dasysiphonia*, and three treatments with elevated pCO_2 ($\sim$ 1,800 µatm) with daily nutrient additions (20 µM nitrate, 1.2 µM phosphate) that received either *Agardhiella* only, *Dasysiphonia* only, or *Agardhiella* and *Dasysiphonia*, resulting in 24 experimental units. This level of nutrient addition (20 µM N added daily over six days = 120 µM) is slightly more than twice what was used in the single species experiment (50 µM) to accommodate for the biomass of macroalgae that was twice the level of the single alga experiments (1 v 2 g). Nutrient concentrations were consistent with those observed in waterbodies around Long Island, New York (NY), and with Redfield stoichiometry (Gobler et al. 2006; Wallace and Gobler 2015). As described above, (1) experiments began with the introduction of macroalgae and nutrients into experimental vessels that had been bubbling at the desired pCO_2 levels for several days as described above. Vessels were monitored daily for one week during the experiment; (2) final pH and temperature measurements were made and a final DIC sample from each vessel was analyzed; (3) macroalgae samples were removed from their respective vessels and rinsed, spun, re-rinsed, re-spun, weighed, and placed into small freezer bags for further

analysis; (4) Weight-based growth rates for all species were determined using the relative growth rate formula and differences among growth rates were statistically evaluated.

Pre- and post-experimental analyses

For carbon (C), nitrogen (N), $\delta^{15}N$, and $\delta^{13}C$ analyses, frozen samples of *Dasysiphonia* from March 2018 through February 2019 experiments were dried at 60 °C for 48 h and then homogenized into a fine powder using a mortar and pestle. Tissue C, N, $\delta^{15}N$, and $\delta^{13}C$ were analyzed using an elemental analyzer interfaced to a Europa 20–20 isotope ratio mass spectrometer at the UC Davis Stable Isotope Facility. For comparison to *Dasysiphonia*, samples of *Fucus vesiculosus*, *Gracilaria tikvahiae*, *Porphyra purpurea*, *Saccharina latissima*, and *Ulva rigida* were collected from Shinnecock Bay, where *Dasysiphonia* co-occurs during the same period in which the macroalga was collected, and prepared for analysis of $\delta^{13}C$ as described above. These species are common and native to Long Island (Stewart Van Patten and Yarish 2009; Wallace and Gobler 2015). Differences in tissue content of *Dasysiphonia* among treatments were statistically evaluated as described above. For all experiments involving *Dasysiphonia*, concentrations of nitrate (NO_3^-), phosphate (PO_4^{3-}), and ammonium (NH_4^+) within experimental vessels, 20 mL of seawater was removed from each vessel and filtered by passing the seawater through pre-combusted (4 h at 450 °C) glass fiber filters (GF/F, 0.7-µm pore size) at the beginning and at the end of the experiments. The filtrate was frozen in 20 mL acid-washed scintillation vials for future analysis. A QuikChem 8500 (Lachat Instruments) flow injection analysis system was used to analyze the filtrate colormetrically to measure NO_3^-, PO_4^{3-}, and NH_3 (Parsons 2013). Initial, ambient concentrations of NO_3^-, PO_4^{3-}, and NH_3 were 2.65, 0.95, and 0.35 µM, respectively, and final concentrations of NO_3^-, PO_4^{3-}, and NH_3 were 0.66, 1.18, and 0.60 µM, respectively, with no significant differences in concentrations between ambient or elevated pCO_2 or nutrient treatments.

Field surveys of Dasysiphonia

During October and November 2019, field surveys for *Dasysiphonia* were conducted along the south shore of

Long Island, NY (Fig. 1). A total of 32 land-accessible sites were sampled in Great South Bay, Moriches Bay, Narrow Bay, Quantuck Bay, Shinnecock Bay, and Peconic Bay, NY. Identification of macroalgae was based on morphology and microscopy. The morphology and pigmentation of macroalgal fronds used in this study were fully consistent with prior descriptions of the macroalgae in the region (Newton et al. 2013; Ramsay-Newton et al. 2017; Schneider 2010). Upon arrival at each site, a 100-m transect was performed parallel to the shore. When *Dasysiphonia* was found, large, well-pigmented fronds were collected, placed in 50-mL centrifuge tubes in a cooler, and transported to the laboratory where they were examined microscopically and subsequently frozen for further analysis. The samples were dried at 60 °C for 48 h and then homogenized into a fine powder using a mortar and pestle. Tissue δ^{13}C and δ^{15}N was analyzed at the UC Davis Stable Isotope Facility as described above.
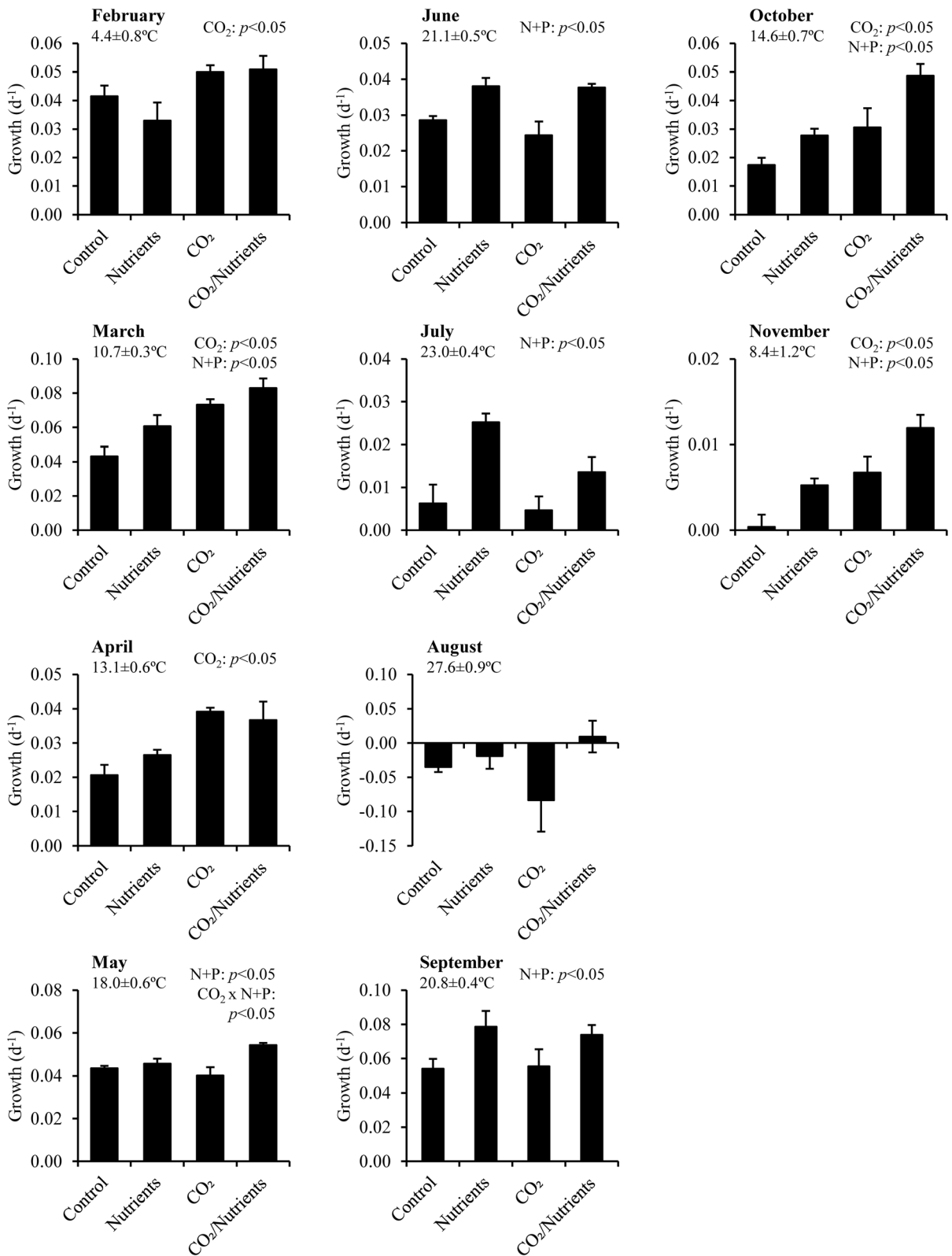
Results

Response of Dasysiphonia to elevated nutrients and/or pCO₂

Growth rates of *Dasysiphonia* were responsive to pCO$_2$ levels during experiments performed in winter, spring and fall (February, March, April, October, and November), where a higher level of pCO$_2$ significantly increased growth relative to ambient pCO$_2$ treatments regardless of nutrient concentrations (Two-way ANOVA; $p < 0.05$; Fig. 2; Supplementary Table S2). For those experiments, growth rates of *Dasysiphonia* were $\sim 60\%$ higher when it was exposed to elevated pCO$_2$ compared to ambient conditions (Fig. 2). Across all experiments, growth rates of *Dasysiphonia* were 26% higher under elevated pCO$_2$ treatments compared to ambient treatments (Fig. 2). During late spring and summer experiments, growth was not significantly affected by elevated pCO$_2$ as a single factor (Two-way ANOVA; $p > 0.05$; Fig. 2; Supplementary Table S2). Furthermore, for seven of ten experiments, growth rates of *Dasysiphonia* were significantly higher when exposed to elevated nutrient concentrations, regardless of pCO$_2$ level (Two-way ANOVA; $p < 0.05$; Fig. 2; Supplementary Table S2) with the exceptions being during April, August, and February (Two-way ANOVA;

$p > 0.05$; Fig. 2; Supplementary Table S2). When exposed to elevated nutrient levels, *Dasysiphonia* growth rates were 40% and $\sim 25\%$ higher in ambient and elevated pCO$_2$ treatments, respectively (Fig. 2). There were no significant interactions between levels of pCO$_2$ and nutrients during experiments (Two-way ANOVA; $p > 0.05$; Fig. 2; Supplementary Table S2), except for the May experiment when neither pCO$_2$ nor nutrients alone altered growth rates but the combination of elevated pCO$_2$ and nutrient levels synergistically increased the growth of *Dasysiphonia* by 30% relative to the control (Two-way ANOVA; $p < 0.05$; Fig. 2; Supplementary Table S2). The August experiment, when water temperatures were ~ 28 °C, was unique in that *Dasysiphonia* had negative growth rates across all treatments and was not significantly affected by elevated pCO$_2$ or nutrient levels (Two-way ANOVA; $p > 0.05$; Fig. 2; Supplementary Table S2).

The δ^{13}C content of *Dasysiphonia* was significantly lower when exposed to elevated pCO$_2$ ($-43.4‰$) compared to control conditions (-31.7‰; Two-way ANOVA; $p < 0.05$; Fig. 3; Supplementary Table S3). In contrast, there was no difference in δ^{13}C content when *Dasysiphonia* was exposed to elevated nutrients for any experiment (Two-way ANOVA; $p > 0.05$; Fig. 3; Supplementary Table S3). The tissue C content of *Dasysiphonia* was not significantly altered by elevated pCO$_2$ or nutrient conditions across all experiments (Two-way ANOVA; $p > 0.05$; Fig. 4; Supplementary Table S4). Tissue N content was not significantly changed by pCO$_2$ (Two-way ANOVA; $p > 0.05$; Fig. 5; Supplementary Table S5) but was significantly higher under elevated nutrient conditions ($p < 0.05$) in experiments performed from April through September (Fig. 5). For April through September experiments, average tissue N content of *Dasysiphonia* under elevated nutrients was 12% and $\sim 16\%$ higher under ambient and elevated pCO$_2$, respectively (Fig. 5). Furthermore, C:N ratios of *Dasysiphonia* were significantly lower when exposed to elevated nutrients for April through July and November to February experiments (Two-way ANOVA; $p < 0.05$; Fig. 6; Supplementary Table S5). The average tissue C:N ratio of *Dasysiphonia* was 10% and $\sim 18\%$ lower under elevated nutrient levels in ambient and elevated pCO$_2$ treatments, respectively (Fig. 6). Tissue C:N ratios were unaffected by elevated pCO$_2$ levels (Two-way ANOVA; $p > 0.05$; Fig. 6; Supplementary Table S6) except for the May

Figure showing monthly growth rates (d⁻¹) for Control, Nutrients, CO₂, and CO₂/Nutrients treatments:

February 4.4±0.8°C — CO$_2$: $p<0.05$

June 21.1±0.5°C — N+P: $p<0.05$

October 14.6±0.7°C — CO$_2$: $p<0.05$; N+P: $p<0.05$

March 10.7±0.3°C — CO$_2$: $p<0.05$; N+P: $p<0.05$

July 23.0±0.4°C — N+P: $p<0.05$

November 8.4±1.2°C — CO$_2$: $p<0.05$; N+P: $p<0.05$

April 13.1±0.6°C — CO$_2$: $p<0.05$

August 27.6±0.9°C

May 18.0±0.6°C — N+P: $p<0.05$; CO$_2$ x N+P: $p<0.05$

September 20.8±0.4°C — N+P: $p<0.05$

Fig. 2 Growth rates of *Dasysiphonia japonica* exposed to ambient and elevated pCO$_2$ with and without nutrient additions for March 2018 through February 2019 experiments. Columns represent means ± standard error. Temperatures represent means ± standard deviation for all treatments. Two-way ANOVA performed with significant differences ($p < 0.05$) in main treatment effects, (CO$_2$ and Nutrients, abbreviated as N + P), appearing at the top right of each panel

and July experiments when tissue C:N ratios were significantly higher under elevated pCO$_2$ (Two-way ANOVA; $p < 0.05$; Fig. 6; Supplementary Table S6).

Response of Porphyra to elevated nutrients and/or pCO$_2$ and comparison to Dasysiphonia

Porphyra growth rates was rarely or never responsive to pCO$_2$ levels and nutrient additions, respectively (Two-way ANOVA; $p > 0.05$; Fig. 7; Supplementary Table S7). Of the seven experiments performed, *Porphyra* only grew faster in response to elevated pCO$_2$ during the July and August experiments (Two-way ANOVA; $p < 0.05$ for both; Fig. 7; Supplementary Table S7).

When comparing the growth of *Dasysiphonia* to *Porphyra*, there were several significant differences among treatments and seasons. For spring experiments, *Dasysiphonia* growth was 13-fold and significantly higher than that of *Porphyra* in all treatments, regardless of pCO$_2$ or nutrient level (Tukey HSD; $p < 0.05$ for all; Supplementary Table S8). During the summer experiments, *Dasysiphonia* growth was 40% higher than that of *Porphyra* and significantly higher in ambient pCO$_2$ treatments and treatments that received nutrient additions as well as when all treatments were combined (Tukey HSD; $p < 0.05$ for all; Supplementary Table S8). For the fall experiments, *Dasysiphonia* growth rates were significantly higher than *Porphyra* in the ambient pCO$_2$ treatment that received nutrient additions (Tukey HSD; $p < 0.05$; Supplementary Table S8) whereas *Porphyra* growth was significantly higher than that of *Dasysiphonia* in ambient pCO$_2$ treatments that did not receive nutrient additions, (Tukey HSD; $p < 0.05$ for all; Supplementary Table S8). Overall, during the fall, *Porphyra* growth was ∼ 70% higher than that of *Dasysiphonia* (Figs. 2 and 7).

Competition of Agardhiella and Dasysiphonia under ambient and elevated nutrients and/or pCO$_2$

There were differing growth responses for *Agardhiella* and *Dasysiphonia* exposed to combined elevated pCO$_2$ and nutrients. *Agardhiella* growth rates were not significantly altered by elevated pCO$_2$ and nutrient levels or by competition with *Dasysiphonia* (Two-way ANOVA; $p > 0.05$; Fig. 8; Supplementary Table S9). In contrast, *Dasysiphonia* growth rates were ∼ 120% higher under elevated pCO$_2$ and nutrients (Two-way ANOVA; $p < 0.05$; Fig. 8; Supplementary Table S9) but were unaffected by competition with *Agardhiella* (Two-way ANOVA; $p > 0.05$; Supplementary Table S9). While growth rates of *Dasysiphonia* and *Agardhiella* were similar under ambient levels of nutrients and pCO$_2$, the growth rates of *Dasysiphonia* were three times greater than *Agardhiella* under elevated levels of nutrients and pCO$_2$ (Two-way ANOVA; $p < 0.05$; Fig. 8; Supplementary Table S9).

Field surveys of Dasysiphonia across the south shore of Long Island

The field surveys of the southern shore of Long Island revealed that *Dasysiphonia* was widespread across the area. The macroalga was present at 24 of 32 sites (Fig. 9; Supplementary Table S10) including all 15 sites in Great South Bay, two sites in Narrow Bay, and two sites in western Moriches Bay. It was absent from eastern Moriches Bay, Quantuck Bay, and western Shinnecock Bay but was present at all four sites across eastern Shinnecock Bay and the single site in the southern section of Great Peconic Bay (Fig. 9; Supplementary Table S10). In Great South Bay, *Dasysiphonia* δ^{15}N signatures varied by site, with no noticeable trends across the bay. Signatures of δ^{15}N in Great South Bay ranged from 6.4 to 11.7‰ (sites 1–15; Fig. 10; Supplementary Table S10). In Narrow Bay, the average δ^{15}N signature for *Dasysiphonia* was ∼ 10‰, while the Mastic Beach and Center Moriches sites in Moriches Bay (sites 18 and 19, respectively) were 10.6 and 7.5‰, respectively (Fig. 10; Supplementary Table S10). The sole site in Peconic Bay (site 27) had a δ^{15}N signature of 8.6‰. For eastern Shinnecock Bay, *Dasysiphonia* in the northern sites (Ponquogue Bridge and Shinnecock Hills, sites 28 and 29, respectively) had δ^{15}N values of ∼ 10‰ while macroalgae from the southern sites
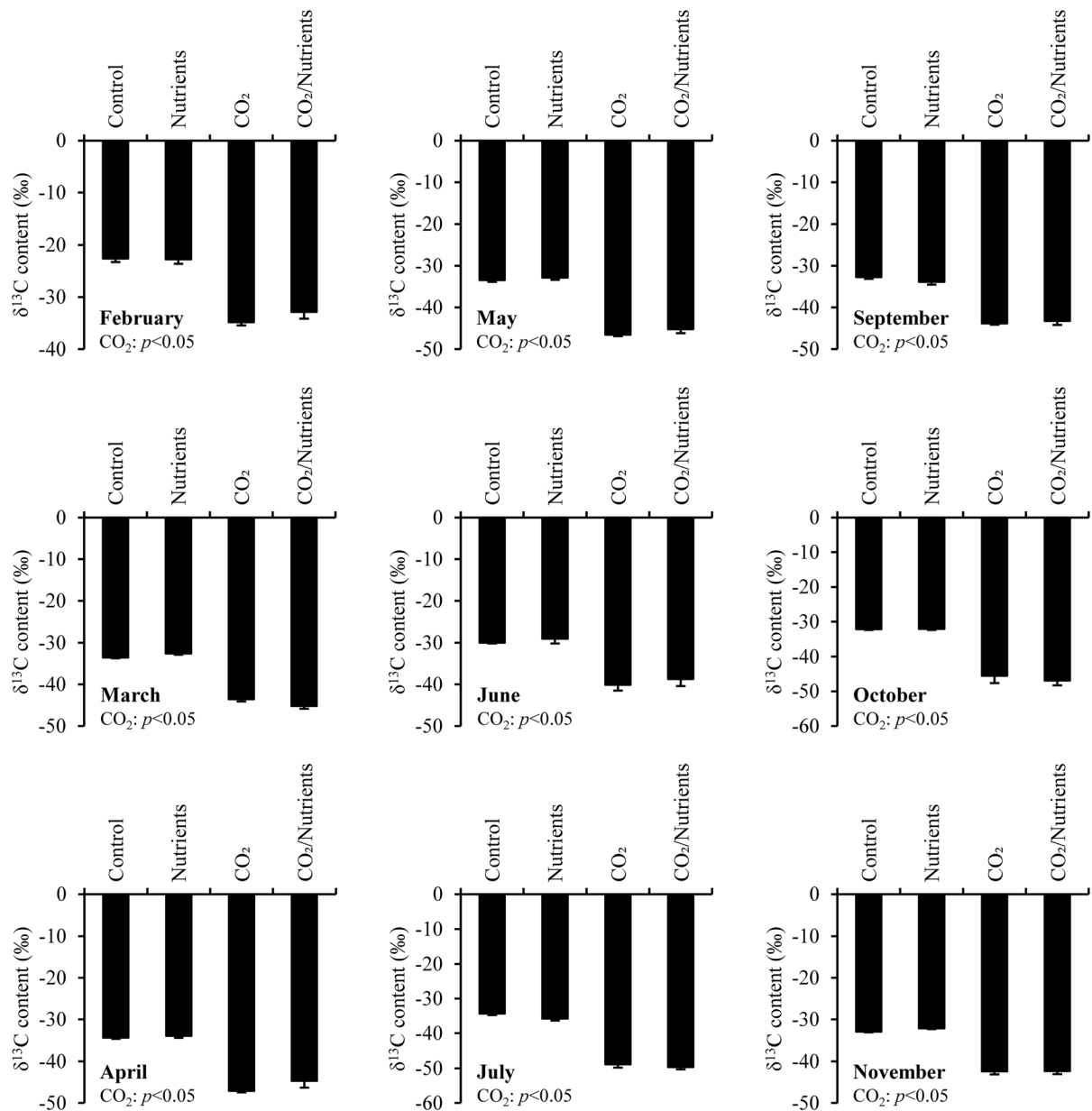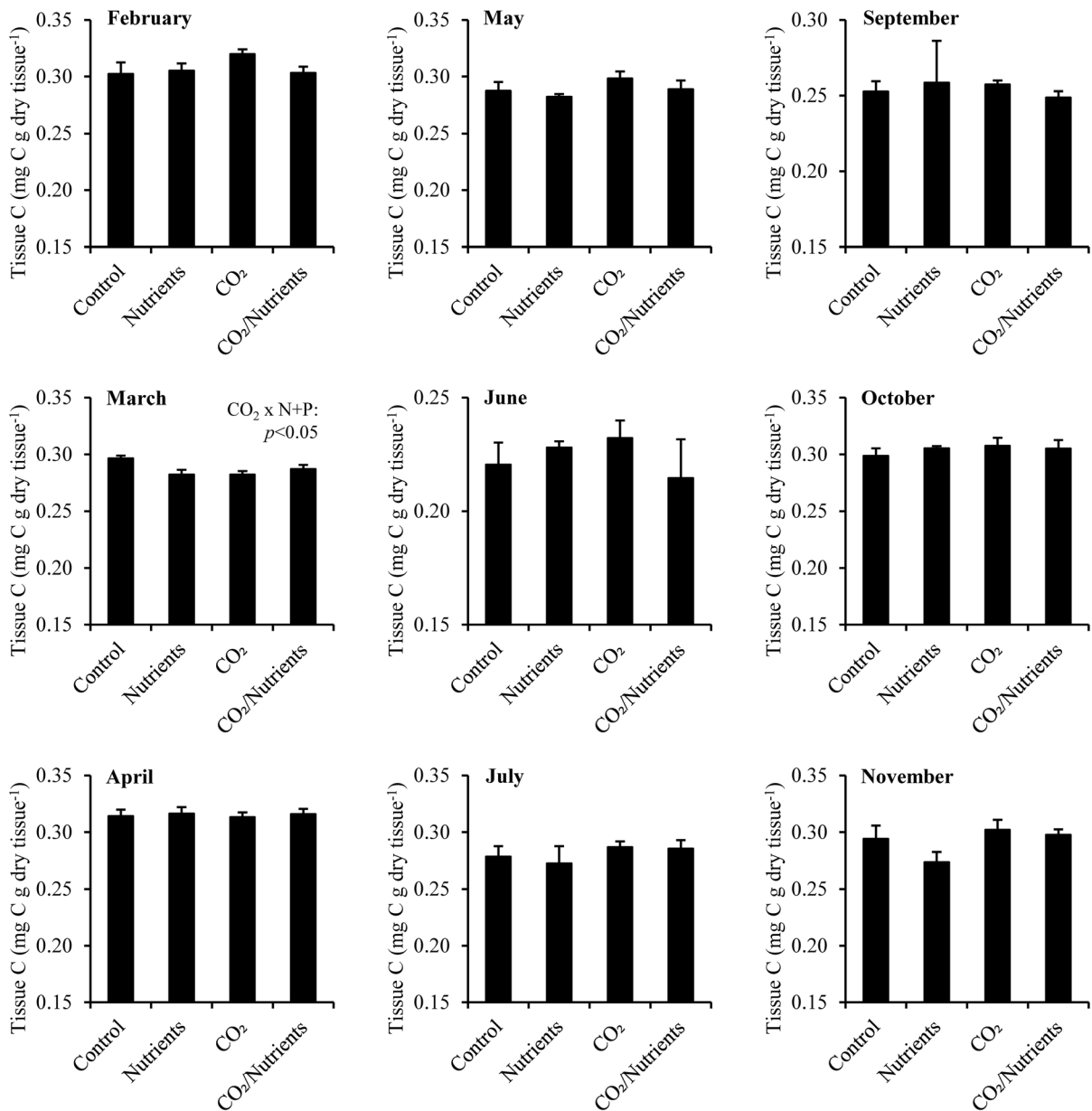
Fig. 3 Tissue $\delta^{13}C$ content of *Dasysiphonia japonica* exposed to ambient and elevated pCO_2 levels with and without nutrient additions for March 2018 through February 2019 experiments. Columns represent means ± standard deviation. Two-way ANOVA performed with significant differences ($p < 0.05$) in main treatment effects, (CO_2 and Nutrients, abbreviated as N + P), appearing at the top right of each panel

(Shinnecock Inlet, sites 30 and 31) had $\delta^{15}N$ values of $\sim 8‰$ (Fig. 10; Supplementary Table S10). The overall minimum, maximum, and average $\delta^{15}N$ content of *Dasysiphonia* was 6.4, 11.7, and 9.1‰, respectively (Fig. 10; Supplementary Table S10).

Discussion

Given that the growth of *Dasysiphonia* generally increased when exposed to elevated pCO_2 and nutrient levels in contrast to indigenous macroalgae, this study provides insight regarding the factors driving invasions of this macroalga. During this study, elevated
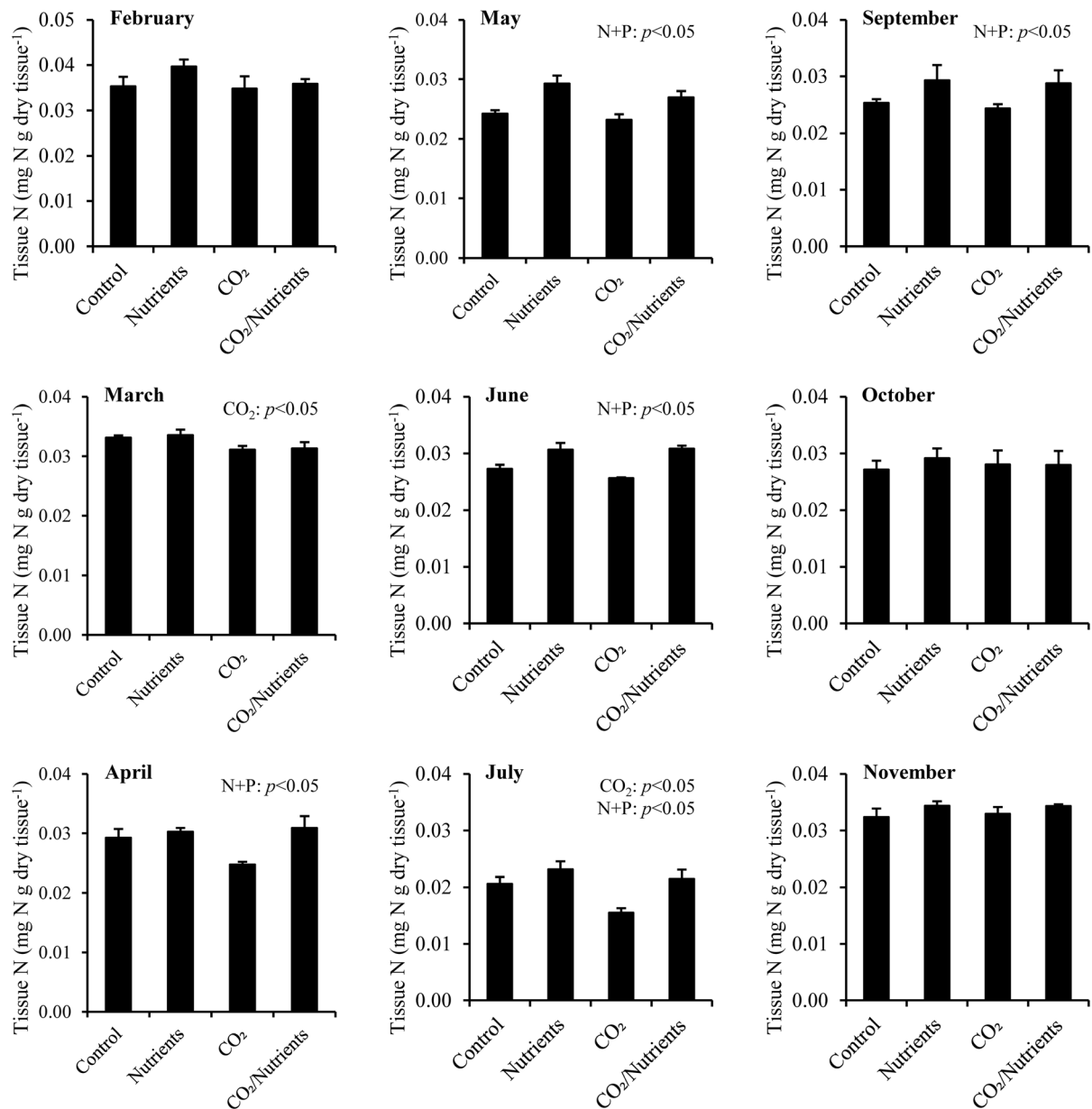
Fig. 4 Tissue carbon content of *Dasysiphonia japonica* exposed to ambient and elevated $p CO_2$ levels with and without nutrient additions for March 2018 through February 2019 experiments. Columns represent means ± standard deviation.

Two-way ANOVA performed with significant differences ($p < 0.05$) in main treatment effects, (CO_2 and Nutrients, abbreviated as N + P), appearing at the top right of each panel

$p CO_2$ was found to significantly enhance the growth rates of the invasive red macroalga *Dasysiphonia* during experiments performed when water temperatures were at or below 15 °C. In contrast, elevated nutrient concentrations significantly increased growth rates during experiments across a wider range of temperatures (4–23 °C). Tissue N and C:N content

were significantly increased and decreased, respectively, when *Dasysiphonia* was exposed to elevated nutrient concentrations. The growth rates of *Dasysiphonia* were generally greater than those of two other indigenous macroalgae, especially when levels of nutrients and $p CO_2$ were elevated. The $\delta^{13}C$ and $\delta^{15}N$
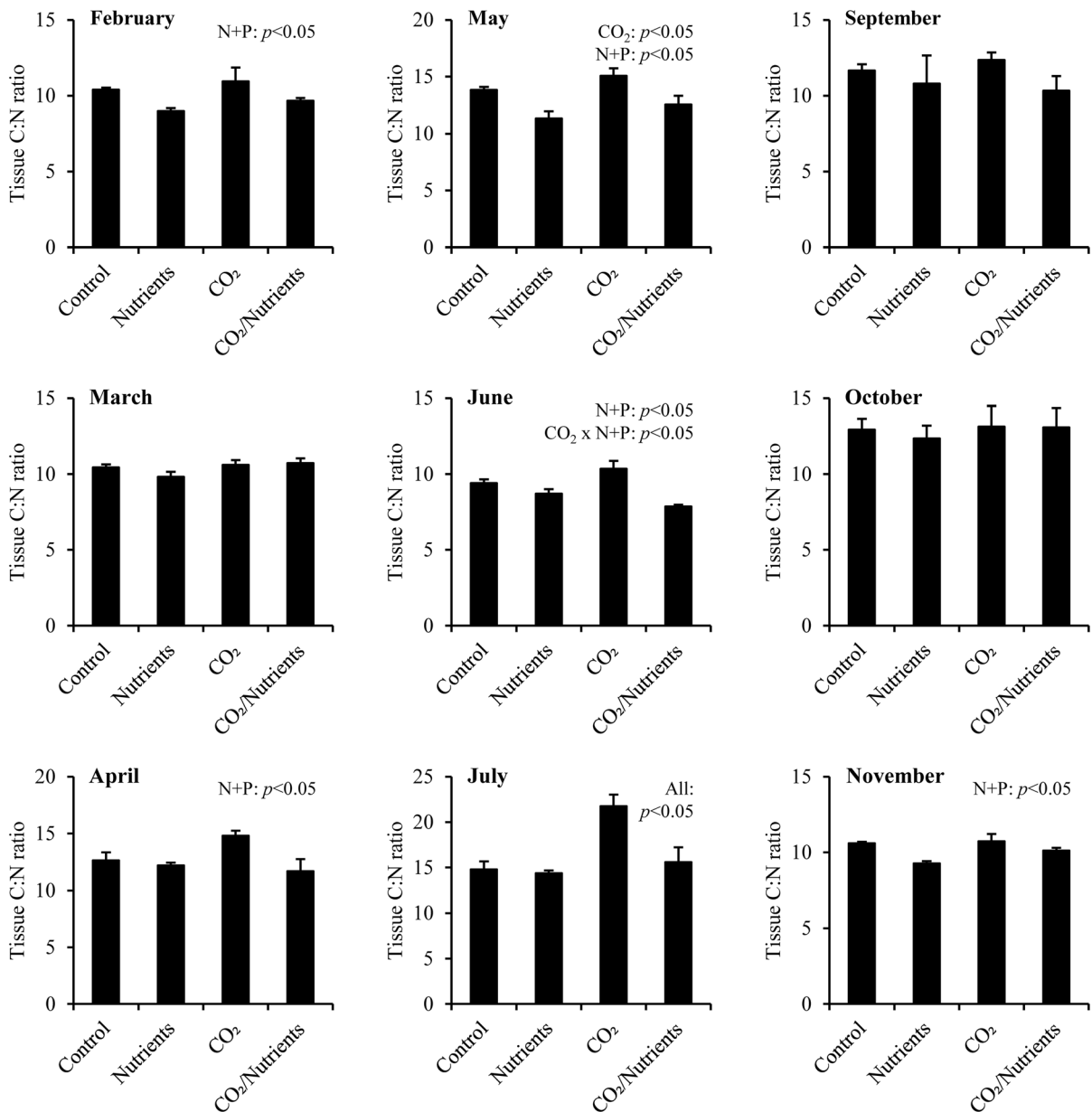
Fig. 5 Tissue nitrogen content of *Dasysiphonia japonica* exposed to ambient and elevated pCO_2 levels with and without nutrient additions for March 2018 through February 2019 experiments. Columns represent means ± standard deviation.

Two-way ANOVA performed with significant differences ($p < 0.05$) in main treatment effects, (CO_2 and Nutrients, abbreviated as N + P), appearing at the top right of each panel

of this macroalga indicated that it relied on CO_2 and wastewater-derived N for in situ growth.

The response of macroalgae to pCO_2 levels may depend on their mode of C acquisition as well as the extent to which inorganic carbon uptake of the organism is substrate-saturated at current pCO_2 levels (Badger 2003; Koch et al. 2013). When exposed to

elevated pCO_2, macroalgae may downregulate their carbon concentrating mechanisms (CCMs) that convert HCO_3^- to CO_2, allowing more energy to be available for processes such as vegetative growth (Björk et al. 1993; Cornwall et al. 2012; Koch et al. 2013). Values of $\delta^{13}C$ are often used to assess the types of inorganic carbon used by macroalgae for

Fig. 6 Tissue C:N ratios of *Dasysiphonia japonica* exposed to ambient and elevated pCO_2 levels with and without nutrient additions for March 2018 through February 2019 experi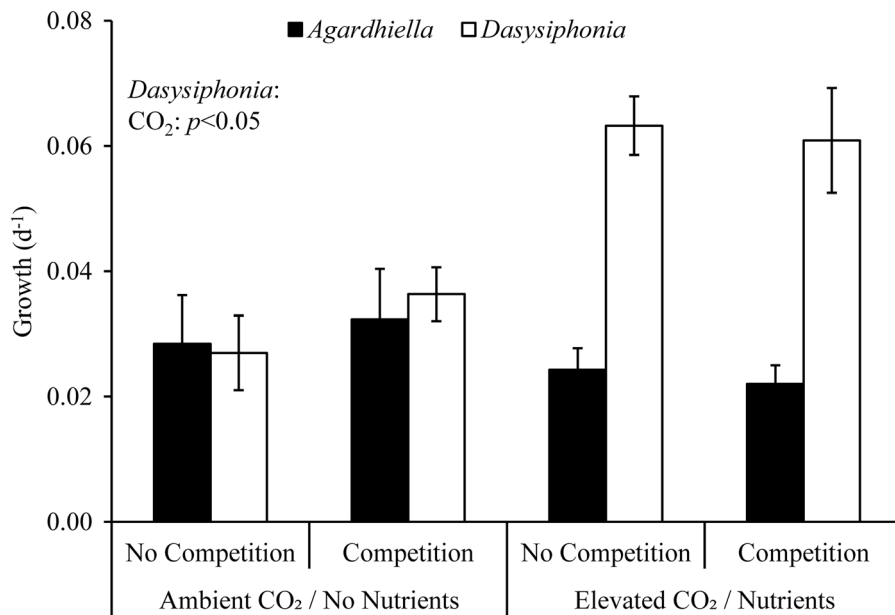ments. Columns represent means ± standard deviation. Two-way ANOVA performed with significant differences ($p < 0.05$) in main treatment effects, (CO_2 and Nutrients, abbreviated as N + P), appearing at the top right of each panel

photosynthesis, with a $\delta^{13}C$ signature of -10‰ being indictive of HCO_3^- use and signatures of -30‰ or lower characteristic of diffusive uptake of CO_2 (Bricelj et al. 2001; Hepburn et al. 2011; Maberly et al. 1992; Raven et al. 2002). In the present study, *Dasysiphonia* had significantly lower $\delta^{13}C$ signatures when exposed to experimentally elevated pCO_2,

evidencing uptake of the $\delta^{13}C$-enriched experimental CO_2 source (Young and Gobler 2016). Furthermore, under ambient conditions, the $\delta^{13}C$ signatures of *Dasysiphonia* were consistently at -30‰ or lower, a finding consistent with prior studies of this macroalga (Kang et al. 2008; Leclerc et al. 2013) and indicating that *Dasysiphonia* predominately uses CO_2 for

Fig. 7 Growth rates of
Porphyra purpurea exposed
to ambient and elevated
$p\mathrm{CO_2}$ with and without
nutrient additions for May
through November 2018
experiments. Columns
represent means ± standard
deviation. Temperatures
represent means ± standard
deviation for all treatments.
Two-way ANOVA
performed with significant
differences ($p < 0.05$) in
main treatment effects, ($\mathrm{CO_2}$
and Nutrients, abbreviated
as N + P), appearing at the
top right of each panel
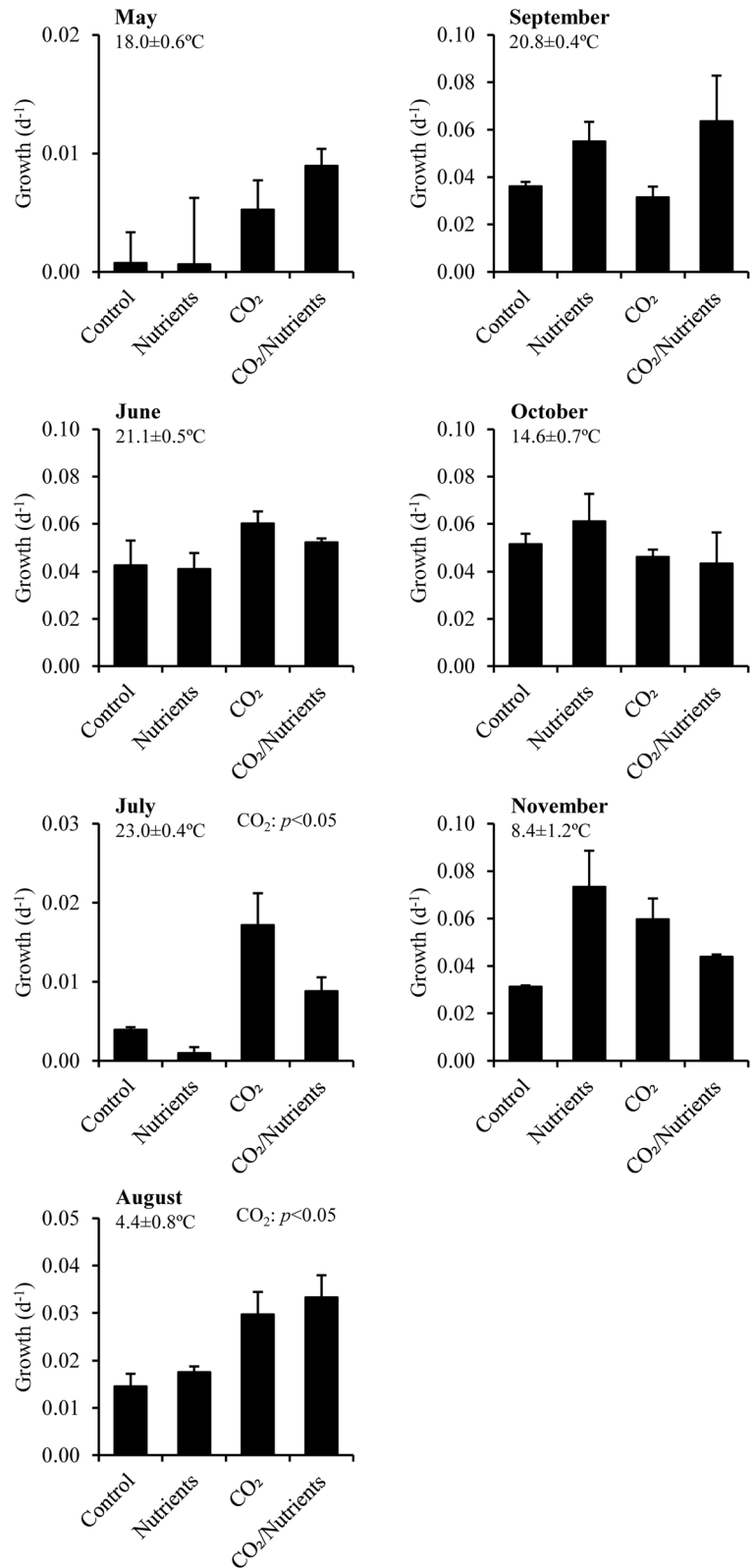
Fig. 8 Growth rates of *Agardhiella subulata* and *Dasysiphonia japonica* exposed to ambient and elevated CO_2 and nutrient conditions, with and without competition from the other macroalga for the October 2019 experiment. Columns represent means ± standard deviation. Two-way ANOVA performed with significant differences ($p < 0.05$) in main treatment effects, (CO_2 and Nutrients, abbreviated as N + P), for each species appearing at the top left of the panel
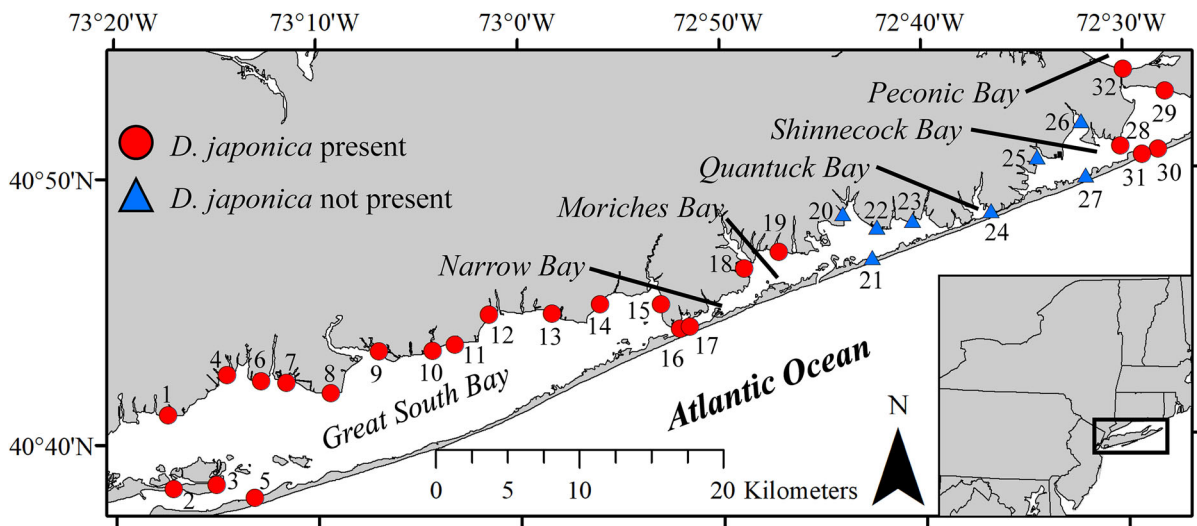
Fig. 9 *Dasysiphonia japonica* field surveys conducted during October and November 2019. Site numbers correlate with the locations, bays, and coordinates in Supplementary Table S10

photosynthesis (Bricelj et al. 2001; Hepburn et al. 2011; Maberly et al. 1992; Raven et al. 2002). Rhodophytes are known to have a high affinity for CO_2 and RuBisCO that minimizes CO_2 loss from photorespiration despite not using HCO_3^- or having a

CCM (Badger et al. 1998; Johnson et al. 1992; Koch et al. 2013). While not all rhodophytes may benefit from increased pCO_2, (Britton et al. 2019; Koch et al. 2013), the results of the present study demonstrate that *Dasysiphonia* is likely not substrate-saturated at
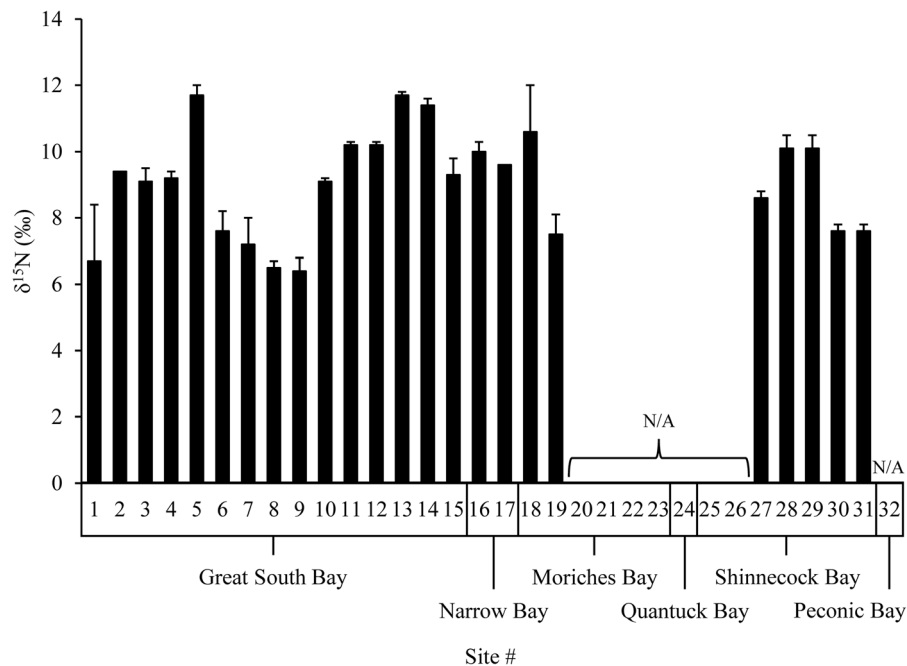
Fig. 10 Tissue $\delta^{15}N$ content of *Dasysiphonia japonica* collected during field surveys conducted during October and November 2019. Site numbers correlate with locations, bays, and coordinates in Supplementary Table S10. 'N/A' denotes sites where *Dasysiphonia japonica* was not collected during the field surveys

ambient pCO$_2$ levels ($\sim$ 400 µatm) given the seasonally increased growth rates in response to elevated pCO$_2$.

Dasysiphonia differs from many other macroalgal species that comprise the assemblages in the waters around New York, including *Fucus vesiculosus*, *Gracilaria tikvahiae*, *Porphyra purpurea*, *Saccharina latissima*, and *Ulva rigida*, which have $\delta^{13}C$ signatures ranging from -12 to -18% (Young and Gobler 2016, 2017; Young et al. 2018; Fig. 11). This finding suggests that among all of these co-occurring macroalgae, *Dasysiphonia* is the most reliant on CO$_2$ as a carbon source (Bricelj et al. 2001; Hepburn et al. 2011; Maberly et al. 1992; Raven et al. 2002) and may, therefore, be the most likely to benefit from higher pCO$_2$ in coastal waters. In addition to the rapid rise in atmospheric pCO$_2$ during the past half century (Meehl et al. 2007), it has become well recognized that eutrophication-enhanced organic-matter loading to coastal waters also causes seasonally elevated pCO$_2$ (Cai et al. 2011; Melzner et al. 2013; Wallace et al. 2014). It seems plausible that high pCO$_2$ levels seasonally present today in the coastal waters may be favoring the proliferation of *Dasysiphonia* over

other macroalgae that are substrate-saturated at present pCO$_2$ levels or are unable to utilize CO$_2$ for photosynthesis under acidified conditions (Cornwall et al. 2012; Koch et al. 2013).

Elevated nutrient concentrations significantly increased and decreased tissue N and C:N content, respectively, of *Dasysiphonia*, indicating that while both N and P were added during experiments, N was a critical element. Beyond these changes in N content relative to the control treatment, the absolute N content of *Dasysiphonia* usually increased to ≥ 0.03 g N per g tissue following nutrient additions, a level known to represent N saturation (Lyngby et al. 1999; Wallace and Gobler 2015). These trends align with growth rates in most experiments of the present study, where *Dasysiphonia* responded positively to elevated nutrient levels during most experiments. *Dasysiphonia* has been shown to have a high nitrate uptake efficiency consistent with rapid growth compared to native macroalgal species (Low et al. 2015). In the present study, while the presence of *Dasysiphonia* did not significantly affect the growth rates of a common native rhodophyte (*Agardhiella*) in ambient or elevated pCO$_2$ and nutrient conditions, the former
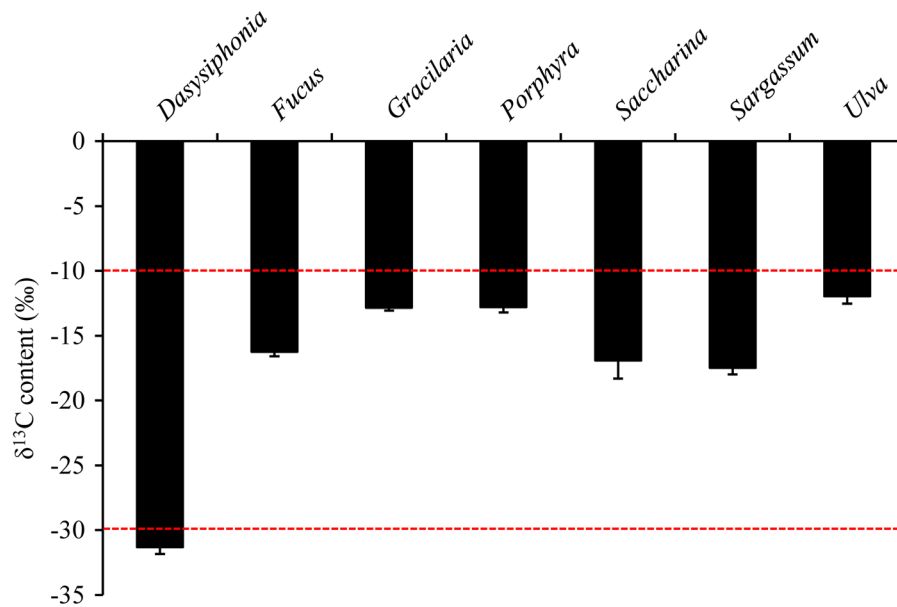
Fig. 11 The $\delta^{13}C$ content of various species of macroalgae (*Dasysiphonia japonica*, *Fucus vesiculosus*, *Gracilaria tik-vahiae*, *Porphyra purpurea*, *Saccharina latissima*, and *Ulva rigida*) under ambient pCO$_2$ levels without nutrient additions. Columns represent means ± standard deviation. Red dashed lines represent divisions in macroalgae that solely rely on HCO$_3^-$ (0 to −10‰), can use both HCO$_3^-$ and CO$_2$ (−10 to −30‰), or solely rely on CO$_2$ (−30‰ or less) for photosynthesis (Maberly et al. 1992; Bricelj et al. 2001; Raven et al. 2002; Hepburn et al. 2011)

outgrew the latter by nearly two-fold when high levels of nutrients and pCO$_2$ were present. Similarly, the growth rates of *Dasysiphonia* exceeded those of *Porphyra* during most seasons when nutrients and pCO$_2$ levels were high. The filamentous morphology of *Dasysiphonia* affords it a surface-area-to-volume ratio greater than bladed and branching macroalgae and allows for a higher nutrient uptake capacity (Low et al. 2015; Rosenberg and Ramus 1984). These traits may allow *Dasysiphonia* to undergo rapid growth in eutrophic settings (Valiela et al. 1997; Wallace and Gobler 2015). Eutrophication can promote coastal ocean acidification due to the accumulation of respiratory CO$_2$ due to microbial degradation of excessive organic matter, resulting in seasonal pCO$_2$ levels (> 1000 µatm) not predicted to occur in open ocean regions for more than a century (Wallace et al. 2014). As such, eutrophication may promote seasonally-elevated pCO$_2$ levels that may yield nutrient- and CO$_2$-mediated enhanced growth of *Dasysiphonia*, a scenario that would make eutrophied estuaries more susceptible to invasion by the macroalga. Furthermore, given that climate change is expected to increase incidences of eutrophication in many estuaries due to increased precipitation-driven N loading

(Sinha et al. 2017), these systems may become more susceptible to invasion by macroalgae such *Dasysiphonia*.

Seasonal response to nutrients and CO$_2$

The response of *Dasysiphonia* varied seasonally with CO$_2$ responses being limited to cool water conditions, and nutrient effects present during warmer periods of the year with these changing responses being reflective of seasonal cycles in nutrients and acidification. For example, continuous measurements of pH in Great South Bay during this study, the collection site for *Dasysiphonia*, revealed pH values decreased from > 8.1 during early April to < 7.9 from May through September, and values > 8 during the fall (Fig. 12a). Given that values of pH and pCO$_2$ are inversely related in oceans (Caldeira and Berner 1999; Marsh 2008; Martz et al. 2010) and Long Island estuaries (Baumann et al. 2015; Gobler and Baumann 2016; Wallace et al. 2014), these patterns in pH suggest in situ pCO$_2$ levels were low during the colder months and higher during the warmer months of the study, a trend consistent with other studies in the region (Baumann et al. 2015; Gobler and Baumann 2016; Wallace et al. 2014). In
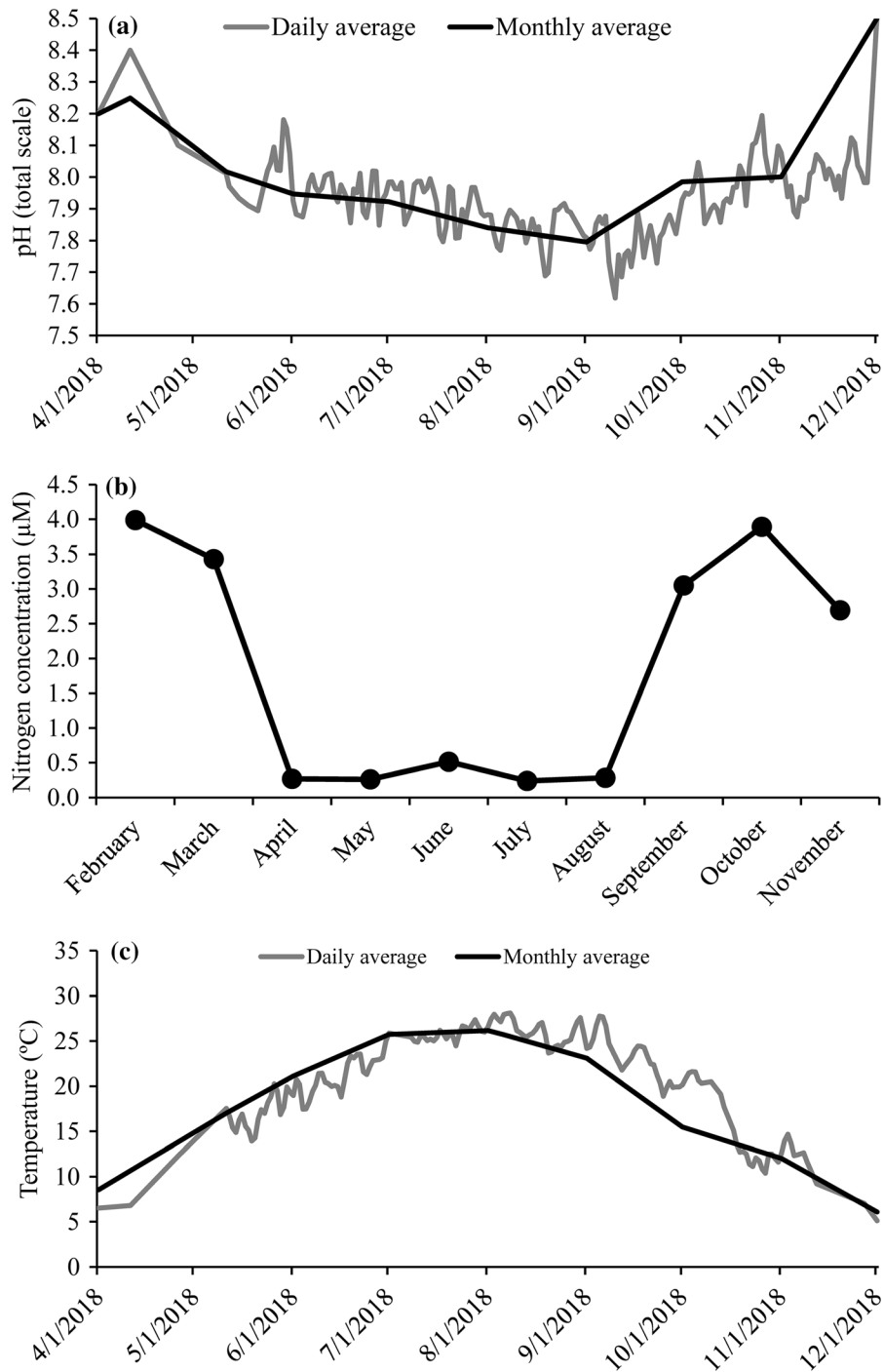
Fig. 12 a Daily and monthly pH values (total scale) obtained from a continuous monitoring buoy in Bellport Bay, NY (40.7533°, -72.9321°), **b** Monthly dissolved inorganic nitrogen (DIN) concentrations (μM) obtained from discrete monitoring at various locations in Great South Bay in 2018 by the Suffolk County Department of Health Services (SCDHS), and **c** Daily and monthly surface water temperatures obtained from the buoy in Bellport Bay

contrast, concentrations of dissolved inorganic nitrogen (DIN) during this study revealed a steady decrease from ~ 4.0 μM in February to ~ 0.3 μM in May, low concentrations (0.4 ± 0.2 μM) throughout the summer before increasing to > 2.7 μM in the fall (SCDHS 2018; Fig. 12b). This trend is consistent with prior coastal studies showing nutrients drawn down by enhanced rates of productivity during warmer months (Carpenter and Dunham 1985; Glibert et al. 2007; Woodwell et al. 1979). Collectively, these seasonal patterns in nitrogenous nutrients and pH/CO_2 align well with the experimental outcomes of this study. During the colder months (< 15 °C; February, March, April, October, and November), pH levels were higher and pCO_2 levels were likely lower, and CO_2 was likely a limiting resource for the growth of the obligate CO_2-user, *Dasysiphonia*. During the warmer months, when pCO_2 levels were higher but DIN concentrations levels were low, growth of *Dasysiphonia* was limited by N but not pCO_2 levels. The only experiment that revealed co-limitation of nutrients and CO_2 was during the transition month of May, when nutrients and CO_2 combined to synergistically enhance the growth of *Dasysiphonia*. Lastly, the $\delta^{15}N$ content of macroalgae is < 3‰ when utilizing N from fertilizer or atmospheric deposition, and > 3‰ when utilizing N from wastewater (Kang et al. 2015; Kendall and McDonnell 2012; Lapointe et al. 2004). Based on samples collected during field surveys of the present study, the $\delta^{15}N$ content of *Dasysiphonia* across Long Island was up to ~ 12‰ and averaged ~ 9‰, indicating that wastewater was the primary source of N for the macroalga, an outcome consistent with the finding that wastewater supplies $\sim 70\%$ of the N to Long Island estuaries (Kinney and Valiela 2011). Given that N is often a limiting resource for macroalgae in estuaries (Valiela et al. 1997) and given the significantly higher growth rates of *Dasysiphonia* in the majority of experiments following N enrichment, it seems likely that while pCO_2 levels can limit *Dasysiphonia* growth, N may be the more important resource.

During this study, *Dasysiphonia* populations were observed in Great South Bay throughout the year, during which the macroalga was exposed to temperatures ranging from 0 °C to 28 °C (Fig. 12c). *Dasysiphonia* is an invasive species, in part, due to its ability to tolerate a wide temperature range (0 °C to 30 °C), although reduced growth and cellular damage can occur at temperatures exceeding 28 °C (Bjærke and

Rueness 2004; Husa et al. 2004). This upper temperature limit is consistent with the present study, where negative growth rates occurred during the August experiment, when temperatures were ~ 28 °C. This is also consistent with continuous measurements of temperature in Great South Bay, with the highest daily temperatures (27–28 °C) occurring throughout August and the beginning of September (Fig. 12c). While Bjærke and Rueness (2004) found that the optimal temperature for growth of *Dasysiphonia* (as *Heterosiphonia japonica*) was 19–24 °C, in this study growth rates were similar across a wide range of seasonal experiments (4–24 °C), suggesting that the optimal temperature range for growth may be wider than previously thought. This difference may be, in part, because the current study sampled macroalgae from the field over a complete annual cycle, allowing for natural acclimation at the population or clonal level to in situ temperatures. Regardless, as water temperatures increase this century and some northern estuaries more regularly enter the 19–24 °C range, they may become vulnerable to invasion by *Dasysiphonia*. The upper temperature limit of *Dasysiphonia* in the present study and others (Bjærke and Rueness 2004) suggests that the timing of future invasions in areas south of Long Island may be limited to some, but not all, months of the year. Isotherms in the North Atlantic Ocean are expected to shift as much as 600 km northwards by the end of the twenty-first century (Hansen et al. 2006), with annual mean water temperatures increasing by 4 °C on rocky shores in the North Atlantic (Müller et al. 2009). This increase in temperature is expected to cause poleward shifts in pelagic and benthic communities, including macroalgal assemblages (Jueterbock et al. 2013; Southward et al. 1995; Wernberg et al. 2011). Considering the enhanced growth of *Dasysiphonia* under elevated pCO_2 and nutrient levels (current study), the thermal tolerance of *Dasysiphonia* (Bjærke and Rueness 2004; Husa et al. 2004), and the higher levels of pCO_2 at higher latitudes across North America (Gledhill et al. 2015), eutrophic estuaries of the northeast US and eastern Canada may be the most vulnerable to future invasion by *Dasysiphonia*. Given the ability of this macroalgae to persist at lower levels during the warmest month, invasions to the south of its southern-most site in the North Atlantic (Long Island, NY; this study) may also be possible.

*Past, present, and future invasions
of Dasysiphonia*

Dasysiphonia is native to East Asian waters, where it occurs sporadically throughout the year and generally comprises a small fraction of macroalgal communities (Kang et al. 2008; Kim et al. 2008). Since the 1980s, the macroalga has spread throughout the eastern Atlantic Ocean (Moore and Harries 2009; Sagerman et al. 2015; Sjøtun et al. 2008; Supplementary Fig. S1), the US East Coast, (Idlebrook 2012) and Canada (Savoie and Saunders 2013). Schneider (2010) documented the macroalga's presence in the waters around Rhode Island in 2007 but did not find the macroalga in the waters around Long Island. However, Newton et al. (2013) reported the presence of the macroalga in Long Island Sound in 2012 (Supplementary Fig. S1). As evident by the present study, the macroalga has continued its western North Atlantic invasion of more than two dozen sites across the south shore of Long Island since its first appearance in Long Island Sound, representing the southernmost observations of *Dasysiphonia* in North America.

Non-indigenous macroalgae can outcompete native species for space and with respect to growth and nutrient acquisition (Hayes and Barry 2008; Low et al. 2015; Theoharides and Dukes 2007). High levels of biomass of *Dasysiphonia* have been shown to exceed that of native species by an order of magnitude (Sagerman et al. 2014) and can lower native macroalgal species richness, evenness, and diversity (Low et al. 2015; Sagerman et al. 2014). In the present study, spring, and summer growth rates of *Dasysiphonia* exceeded those of *Porphyra* by as much as 13-fold and $\sim$ 25%, respectively. Additionally, *Dasysiphonia* outgrew *Agardhiella* by $\sim$ 70% under high nutrient and high pCO_2 conditions. We note, however, that this experiment assessed interspecific competition but did not establish a control with double the levels of each seaweed individually to assess intraspecific competition (Underwood 1986). Ramsay-Newton et al. (2017) found that, following invasion of *Dasysiphonia* in Nahant, MA in 2011, there was a significant decline in macroalgal species richness. Introduced macroalgae such as *Dasysiphonia* can form dense mats that limit light availability and inhibit the recruitment and establishment of other macroalgae species, such as kelp (Ambrose and Nelson 1982; Britton-Simmons 2004). *Dasysiphonia* can occupy up

to 80% available substrate and can grow epiphytically on other macroalgae (Moore and Harries 2009; Newton et al. 2013; Supplementary Fig. S2). The literature regarding management of *Dasysiphonia* is currently limited, but it appears that the most effective means of limiting invasions by the macroalga, and others, is prevention of introduction through means such as transoceanic shipping, aquaculture and aquarium trade, fishing/boating activities, and the opening of canals (Doelle et al. 2007; Mathieson et al. 2008; Mineur et al. 2014; Petrocelli et al. 2013; Sant et al. 1996; Vranken et al. 2018). Given the results of this study, it would seem efforts to reduce N loading to coastal waters may also reduce metabolic CO_2 production, and may slow or reverse invasions of *Dasysiphonia*, thereby mitigating the negative effects of this macroalga on marine ecosystems. Reductions in N inputs to coastal ecosystems have been shown to reduce the frequency and intensity of harmful algal blooms (Heisler et al. 2008) caused by microalgae (Gobler et al. 2005; Nuzzi and Waters 2004), as well as macroalgae (Harlin 1995).

There are numerous ecosystem implications associated with the ability of nutrient loading and ocean acidification to promote invasions of *Dasysiphonia*. In the North Atlantic Ocean, the replacement of kelp beds with invasive species, such as *Dasysiphonia*, may alter the ecosystem services provided by kelp, such as a refuge from predation (Watanabe 1984). The ability of macroalgae to serve as refuge from predation can partly depend on the complexity of the macroalga's thallus. The thalli of *Dasysiphonia* are complex and filamentous (O'Brien et al. 2018), which, in higher densities, can form a biogenically complex habitat capable of hosting some meso-invertebrates due to smaller interstitial volume and area compared to macroalgae with branched or blade morphology (Dijkstra et al. 2017; Holmlund et al. 1990; Veiga et al. 2014; Ware et al. 2019; Warfe et al. 2008). Dijkstra et al. (2017) found that invasive filamentous red macroalgae, such as *Dasysiphonia*, supported two to three times more meso-invertebrate individuals and species that form the base of food webs, which may benefit higher trophic levels. However, several studies have found that while cunner prefer to refuge in the tall, simple blades provided by kelp (*Saccharina latissima*), they will use turf macroalgae (i.e. *Dasysiphonia*) if kelp becomes scarce, although this is not preferred, as turf macroalgae do not provide as much

protection from predation as kelp (Dijkstra et al. 2019; O'Brien et al. 2018). While *Dasysiphonia* may provide a suitable habitat for some organisms, its value as a food source could alter herbivore assemblages. Some herbivores avoid grazing on the invasive species (Low et al. 2015) and Sagerman et al. (2015) reported that *Dasysiphonia* (as *Heterosiphonia japonica*) is not a preferred food source for several common invertebrates, an outcome that may allow for continued proliferation of the macroalga. Given *Dasysiphonia* can grow epiphytically on other macroalgae (Moore and Harries 2009; Supplementary Fig. S2) and seagrass (García-Redondo et al. 2019), the further invasion, proliferation, and overgrowth of this macroalga in response to acidification and eutrophication could disrupt seaweed assemblages and/or seagrass beds due to decreased light availability (Valiela et al. 1997) and/or direct competition for nutrients (Duarte 1995; Young and Gobler 2017; Young et al. 2018). Macroalgal overgrowth can also smother benthic habitats and promote diel hypoxia/anoxia (Liu et al. 2009; Valiela and Cole 2002; Valiela et al. 1997). Lastly, the overgrowth of *Dasysiphonia* may be problematic for shellfisheries, as it can overgrow oysters (Haydar and Wolff 2011). A study by Glenn et al. (2020) found that within the Great Bay Estuary in New Hampshire, USA, 81% of all biomass on oyster farm gear consisted of non-native macroalgae, including *Dasysiphonia*, which may provide additional substrate for the macroalga to propagate.

In conclusion, the invasive red macroalga *Dasysiphonia* experienced enhanced growth compared to other red macroalgae when exposed to elevated pCO_2 and nutrient levels. Based on the $\delta^{13}C$ signatures of *Dasysiphonia*, the macroalga appears to predominately use CO_2 as a source of carbon for photosynthesis, which may give it a competitive advantage over other macroalgae in high CO_2 ecosystems. Its $\delta^{15}N$ signatures suggest its growth is being promoted by excessive wastewater-derived N loading. *Dasysiphonia* has spread across estuaries of the northwestern and northeastern Atlantic Oceans since the 1980s. Given predicted trends in N loading, acidification, and warming of coastal ecosystems in the coming decades (Doney et al. 2009; Sinha et al. 2017), it may continue to spread into eutrophied estuaries further north and south due to its ability to rapidly grow under elevated pCO_2 and nutrient conditions and its wide thermal tolerance.

Author's contribution CJG and CSY conceived and designed the experiments. CSY performed the experiments and sample analyses. CSY and CJG analyzed the data. CJG contributed reagents, materials, and analysis tools. CSY and CJG wrote the paper.

Compliance with ethical standards

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