Marine Biology (2022) 169: 112
https://doi.org/10.1007/s00227-022-04099-8

ORIGINAL PAPER

Ocean acidification but not nutrient enrichment reduces grazing and alters diet preference in *Littorina littorea*

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Received: 13 January 2022 / Accepted: 1 August 2022 / Published online: 15 August 2022

Abstract

Ocean acidification and eutrophication have direct, positive effects on the growth of many marine macroalgae, potentially resulting in macroalgal blooms and shifts in ecosystem structure and function. Enhanced growth of macroalgae, however, may be controlled by the presence of grazers. While grazing under ocean acidification and eutrophication conditions has variable responses, there is evidence of these factors indirectly increasing consumption. We tested whether a common marine herbivorous snail, *Littorina littorea*, would increase consumption rates of macroalgae (*Ulva* and *Fucus*) under ocean acidification (increased pCO_2) and/or eutrophication conditions, via feeding trials on live and reconstituted algal thalli. We found that increased pCO_2 resulted in reduced grazing rates on live thalli, with snails feeding almost exclusively on *Ulva*. However, eutrophication did not impact consumption rates of live tissues. In addition, similarity in consumption of reconstituted *Ulva* and *Fucus* tissues across all treatments indicated that physical characteristics of algal tissues, rather than tissue chemistry, may drive dietary shifts in a changing climate. In this system, decreased consumption, coupled with increased growth of macroalgae, may ultimately enhance algal growth and spread.

Keywords Acidification · Nutrients · Grazing · Consumption · Macroalgae

Introduction

Atmospheric carbon dioxide (CO_2) delivered into the ocean has driven the process of ocean acidification, resulting in decreased seawater pH and reduced carbonate ion availability (Sabine 2004; Doney et al. 2009; Feely et al. 2009). Ocean acidification has proven detrimental to many marine organisms, particularly calcifying species, which may experience decreased calcification rates, depressed metabolism, and hypercapnia (Anthony et al. 2011; Diaz-Pulido et al. 2011; Young et al. 2019; Young and Gobler 2020). Conversely, many marine primary producers, such as seagrasses, macroalgae, and phytoplankton, may benefit from increased carbon dioxide and bicarbonate associated with acidification (Koch et al. 2013; Grear et al. 2017; Bach et al. 2017). Many species of fleshy macroalgae exhibit increased growth and photosynthetic rates when exposed to higher pCO_2 levels (Kübler et al. 1999; Xu and Gao 2012; Olischläger and Wiencke 2013). In addition to physiological changes, carbon enrichment (via acidification) has also been shown to alter the community composition of primary producers (Ober et al. 2016; Grear et al. 2017). Nutrient loading (eutrophication) in coastal systems creates a similar enrichment effect, altering communities and enhancing the growth of opportunistic macroalgal species at the expense of slow-growing, foundational species (Berger et al. 2004).

The direct effects of ocean acidification and nutrient loading on macroalgal growth may, however, be counteracted by enhanced grazing rates (Connell et al. 2013; Falkenberg et al. 2014). Herbivores have the ability to control growth and expansion of macroalgae and epiphytes (Hughes et al. 2003), and their presence and species diversity have been shown to quell increased algal growth under future climate conditions (Falkenberg et al. 2014; Baggini et al.

Responsible Editor: Fabio Bulleri.

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2015; Ghedini et al. 2015). While nutrient loading stimulates algal growth, increased grazing by invertebrates can keep algal biomass in check (Nielsen 2003; Whalen et al. 2013; McSkimming et al. 2015). Ocean acidification may enhance grazing via altered carbon to nitrogen ratios (C:N) where C:N increases (Hemmi and Jormalainen 2002; Russell and Connell 2007; Falkenberg et al. 2014; Duarte et al. 2015) and results in greater levels of individual consumption (Falkenberg et al. 2014). Due to the species-specific nature of macroalgal response to climate change, tissue quality and consumption are not always affected (Borell et al. 2013; Gutow et al. 2014; Poore et al. 2016). In certain scenarios, climate change may impose direct, negative effects on grazers, reducing their capacity for grazing (Melatunan et al. 2011; Stumpp et al. 2011; Albright et al. 2012; Russell et al. 2013).

The signal of ocean acidification is relatively clear in open ocean habitats, but harder to distinguish in near shore and coastal habitats (Hofmann et al. 2011). The carbonate chemistry within near shore and coastal habitats is influenced by upwelling, eutrophication, and freshwater inputs, among others, making coastal acidification a different process than ocean acidification (Feely et al. 2010; Cai et al. 2011; Wallace et al. 2014). Coastal habitats dominated by macroalgae also exhibit natural, daily pH variability driven by metabolism in primary producers (Krause-Jensen et al. 2015; Hirsh et al. 2020). These factors have led to excessive levels of CO_2, on par with, or exceeding, those predicted for open ocean habitats by the year 2100 (Sabine 2004; Carstensen and Duarte 2019). Thus, in certain scenarios, coastal organisms may be pre-adapted to thriving in a variety of pCO_2 levels.

While many studies have investigated species' responses to acidification or nutrient loading, few studies have looked at their interaction on macroalgal growth (Russell et al. 2009; Falkenberg et al. 2014; Campbell and Fourqurean 2014), and fewer studies have investigated this impact on herbivore consumption (but see Falkenberg et al. 2014). Here, we investigate the effects of ocean acidification and eutrophication on algal consumption and diet preference of a common coastal grazer. For this study, we focused on the green alga *Ulva lactuca* (Linneaus) and the brown alga *Fucus vesiculosus* (Linneaus) (referred to hereby as *Ulva* and *Fucus*) in the northwest Atlantic. *Ulva* is fast-growing, opportunistic, and can readily colonize, whereas *Fucus* is long-lived and slow growing. These species have divergent responses to ocean acidification, nutrients, and their interaction, with increased growth rates of *Ulva* and decreased or null growth rates in *Fucus* (Olischläger et al. 2013; Gutow et al. 2014). Additionally, nutrient loading (but not pCO_2) enhanced tissue quality of both *Ulva* and *Fucus* as a result of lowered tissue C:N ratios (Ober and Thornber 2017).

Under ambient environmental conditions, *Fucus*, despite being competitively disadvantaged, dominates space as *Ulva* is the preferred food source for many grazers, including the abundant gastropod *L. littorea* (Linneaus) (Lubchenco 1978, 1983; Watson and Norton 1985; Bracken et al. 2014). While *Ulva* is preferred by *L. littorea* (hereafter, *Littorina*), these snails will readily consume *Fucus*, and have even exhibited enhanced growth with *Fucus* diets (Peckol and Putnam 2017). *Littorina* can manipulate algal communities and competitive interactions by preferential grazing and clearing space within the intertidal and shallow subtidal (Lubchenco 1983). However, *Littorina* exhibits reduced growth and reduced respiration rates when exposed to ocean acidification conditions (Bibby et al. 2007; Melatunan et al. 2011; Landes and Zimmer 2012), which may ultimately impact their grazing ability.

Using a series of feeding experiments, we investigated the interactive effects of ocean acidification and eutrophication on the grazing rates of a common snail (*Littorina*) when feeding on *Ulva* and *Fucus*. Experiments used either live algal thalli or reconstituted algae to test the role of physical characteristics in grazing preference. We tested the hypotheses that under these novel environmental conditions: (1) grazing organisms would control algal growth by increasing their rate of consumption (Falkenberg et al. 2014), and (2) altered algal tissue quality under high nutrients would drive grazing preferences from mostly *Ulva* to a mixed algal diet. Quantifying these changes in consumption by an abundant grazer will help determine future grazing pressures as well as the potential for modified interactions between primary producers and consumers.

Materials and methods

Snail grazing (live algal thalli)

To test the impacts of ocean acidification and eutrophication on snail grazing, we conducted a series of experiments at a flow-through seawater facility at the US Environmental Protection Agency Atlantic Coastal Environmental Sciences Division in Narragansett, RI USA. *Ulva*, *Fucus*, and *Littorina* were collected from the shallow subtidal zone at the University of Rhode Island's Narragansett Bay Campus (41°29′26″N, − 71°25′11″4 W) in August 2015. Non-reproductive tips of *Fucus* (~ 3–5 cm in length) were cut from adult thalli (as performed in Gutow et al. 2014). *Fucus* tips and *Ulva* thalli were cleaned of any epiphytes, and transferred into separate 20L glass aquaria with flow-through seawater and aeration. Individuals were acclimated to lab conditions (ambient pCO_2 and nutrient levels, artificial lighting; 448 ± 20 ppm, 6.87 ± 0.03 µM, and 128.7 + 2.7 µmol

photons m^{-2} s^{-2} with a light/dark rhythm of 14:10 h (L:D), respectively) for 5 days prior to the start of each experiment.

After 5 days of acclimation, algae and snails were exposed to one of four environmental treatments, based on the factorial combination of two pCO_2 levels (ambient ~ 400 µatm pCO_2, pH 8.10, and high ~ 1200 µatm pCO_2, pH 7.65; Moss et al. 2010) and two levels of nutrient loading (ambient ~ 5 µM dissolved inorganic nitrogen, DIN, and high ~ 200 µM DIN). The high CO_2 treatment is the representative concentration pathway 8.5 (RCP8.5) projections for the year 2100. DIN in Narragansett Bay runs along a north south gradient, where water has an annual mean of 70 µM DIN in the north and annual mean of 4–10 µM DIN in the south, while certain parts of the bay can exceed 180 µM DIN on occasion (Krumholz 2012). There were four 40L headwater tanks which were fed directly by filtered, tempered sea water (set at a constant 18 °C). In the headwater tanks, pure CO_2 gas or ambient air (depending on the treatment) was bubbled in via helium spargers at a constant rate set by an Aalborg Mass Flow Controller GFC (Aalborg Instruments and Controllers, INC) (Ober and Thornber 2017). Mixing of gas and water was aided via a Hydor Circulation Fan. Treated water was pumped from the headwater tank via an Eheim 1200 submersible pump to a manifold, delivering treated water to seven experimental aquaria (thereafter divided by nutrient treatment). Aquaria received water at a rate of 130 ± 5 mL/min, using a flow-through design to mimic the natural variability of coastal pH that, on a daily basis, fluctuated up to 0.2–0.4 units. Although header tanks were utilized for CO_2 treatments, we randomly assigned aquaria from different header tanks to receive the nutrient treatment to minimize pseudoreplication. Ultimately, this resulted in seven aquaria for each treatment, but were fed from one of two header tanks (Supplemental Fig. 1).

Nutrient levels were altered by use of slow-release agar blocks placed in each experimental aquarium (Teichberg et al. 2008). Nitrate (in the form of KNO_3 at 2 M concentration) and ammonium (in the form of NH_4CL at 2 M concentration) were mixed with 3% agar, seawater, and phosphate (in the form of KH_2PO_4 at 1 M concentration to meet the Redfield ratio; Tate 1990) to create the desired nutrient concentrations representing eutrophication events (~ 200 µM DIN for the 20L aquaria) (Teichberg et al. 2008). For ambient nutrient aquaria, blocks containing just agar and seawater were used to simulate the physical addition of the block. Individual blocks contained ~ 6.25 mL of initial mixture (which was poured into a petri dish, chilled to harden, and then divided into eights). All agar blocks were placed in mesh bags and hung from the side of each aquarium allowing nutrients to slowly dissolve out of the blocks, mixing with the water in in each tank. Individual blocks took about 10 days to completely dissolve (Ober, personal observations).

Organisms were exposed to environmental treatments for 1 week prior to the start of consumption experiments. Based on evidence from prior experiments (Ober and Thornber 2017), this amount of time was sufficient for algal tissues to reflect changes in tissue C and N concentrations. *Littorina* were not fed during this acclimation period (Imrie et al. 1990).

Prior to feeding trials, algae were removed, blotted dry, and spun 20 × in a salad spinner to remove excess water (Thornber et al. 2008). Initial algal wet mass of each individual was recorded. The average ratio of starting biomass was 2:1, *Fucus* to *Ulva*, with initial wet mass measuring 1.5 and 0.75 g, respectively. This ratio provided a more equal balance of surface area between the two species.

Of the seven replicate tanks for each environmental treatment, three or four were designated as consumer tanks (three *Littorina* in each, with a piece of *Ulva* and *Fucus*), with the remaining three or four designated as non-consumer controls (tanks with *Ulva* and *Fucus*, but no *Littorina*) (Supplemental Fig. 1). Grazing experiments were run for 1 week and tanks were supplemented with the same artificial light (Sylvania Full Spectrum) described above. Tanks were scrubbed and cleaned daily and any epiphytes growing on the algae were removed. After one week, algae were removed, blotted to remove excess moisture, spun, and assessed for final mass.

Two trials were run for this experiment, with new individuals collected and acclimated for the second trial. In this trial, consumer tanks and non-consumer control tanks were switched, resulting in seven replicates per consumer treatment per environmental and per grazer treatment (Supplemental Fig. 1). Header tanks feeding the experimental aquaria were also swapped in effort to reduce pseudoreplication. There was no significant difference in consumption between trials ($F = 0.82$, $p = 0.37$; Supplemental Table 1); therefore, we pooled our data. Total consumption, based on the total algal biomass consumed by snails (both *Ulva* and *Fucus*), was calculated as $(S_i \times C_f \times C_i^{-1})$-$S_f$, where S_i and S_f were the initial and final mass of the algae exposed to consumption and C_i and C_f were the initial and final mass of the non-consumer control algae (Stachowicz and Hay 1999; Jones and Thornber 2010). Consumption data were then standardized to a grazing rate (mg algae consumed per snail per day). These calculations were repeated for *Ulva* and *Fucus* consumption separately. Similar sized *Littorina* were collected and used in these experiments to avoid size acting as a confounding variable. Mean shell height of snails measured 1.84 (+ 0.18) cm.

Snail grazing (reconstituted food)

To test the mechanisms behind potential shifts in grazing, we ran a series of consumption experiments with reconstituted food. Using reconstituted food, we were able to

remove any physical characteristics of the algal tissue but retain the chemical composition of tissue (i.e., nutritional quality and secondary compounds). In October 2015, *Ulva*, *Fucus*, and *Littorina* were collected from the shallow subtidal zone at the University of Rhode Island's Narragansett Bay Campus beach. Mean shell height for *Littorina* measured 2.08 (± 0.16) cm. Using the same experimental design and set-up as the live thalli consumption experiments, algae and snails were acclimated at the same conditions as the previous experiment (ambient pCO_2 and nutrient levels, artificial lighting; 455 ± 23 ppm, 6.97 ± 0.02 µM, and 128.7 + 2.7 µmol photons m^{-2} s^{-2} with a light/dark rhythm of 14:10 h (L:D), respectively). Algae and snails were then acclimated to experimental conditions for one week. Post-treatment acclimation, *Ulva* and *Fucus* were removed and immediately frozen at − 80C for 24 h. Algae were freeze-dried for 48 h before being ground separately using a Wiley Mill (mesh size 40). Powdered algae of both species was mixed with agar and seawater to reconstitute (Thornber et al. 2006). The reconstituted food was spread over window screen onto Whatman paper (Guidone et al. 2012). We cut 40 mm X 15 mm strips containing ~ 225 squares of reconstituted food. Strips were photographed and the initial number of reconstituted food squares were counted using ImageJ (Schneider et al. 2012). Strips of both reconstituted *Ulva* and *Fucus* were then placed in experimental aquaria along with three snails. The experiment ran for a maximum of three days; replicates were stopped prior to the snails consuming 100% of the food available (squares present). In a few cases, *Littorina* consumed 100% of food squares prior to removal; these replicates were removed from data analyses. Reconstituted food strips were then removed from aquaria and photographed. The final number of squares were counted via ImageJ (Guidone et al. 2012). As in live thalli grazing experiments, reconstituted food consumption experiments were run with both consumer tanks and non-consumer control tanks, to quantify any potential loss of food to treatment conditions. This experiment was run twice to obtain seven replicates per consumer treatment per environmental treatment. We observed no significant differences in consumption between trials and therefore pooled our data ($F = 0.25$, $p = 0.63$; Supplemental Table 1).

There was no loss of reconstituted foods squares in non-consumer control tanks; therefore, we determined reconstituted food consumption for each species by calculating percent change between initial squares count and final square count.

Carbonate chemistry and nutrient concentration analysis

Methods for measuring and calculating carbonate chemistry were taken from Ober and Thornber (2017). Seawater samples were bottled and preserved using mercuric chloride ($HgCl_2$) over the course of each experiment to measure dissolved inorganic carbon (DIC) and total alkalinity (TA), following the Best Practices Guide (Dickson et al. 2007). Two seawater samples were taken from each environmental treatment at the start of experimentation (Day 1) and again twice more (Days 3 and 6) while the experiments were running. Temperature and salinity were measured directly whenever samples were taken for carbonate chemistry. For trials using reconstituted food, seawater samples were taken once daily for carbonate chemistry analysis. All seawater samples were collected midday. DIC was measured using a Shimadzu TOC-V total organic carbon analyzer. TA was determined for each sample using a Metrohm 877 Titrino Plus titrator. In determining DIC and TA, samples were standardized against Dickson seawater standards

Table 1 Carbonate chemistry and nutrient parameters; data averaged across grazing experiments ($N = 24$ per treatment)

Parameter	Ambient pCO_2		High pCO_2	
	Ambient nutrients	High nutrients	Ambient nutrients	High nutrients
$pH_{(total)}$	7.94 + 0.02	7.96 + 0.02	7.58 + 0.02	7.59 + 0.02
pCO_2 (µatm)	476.2 + 24	461.7 + 23	1225.1 + 45	1199.2 + 40
CO_2 (µmol/kgSW)	16.85 + 0.90	16.1 + 0.80	42.39 + 2.0	41.29 + 1.40
HCO_3^- (µmol/kgSW)	1785.2 + 24	1769.77 + 24	1958.8 + 18	1972.9 + 15
CO_3^{2-} (µmol/kgSW)	124.65 + 5.00	126.65 + 4.00	59.2 + 2.40	61.39 + 2.20
DIC (µmol/kgSW)	1926.7 + 25	1912.5 + 24	2060.4 + 20	2075.83 + 16
TA (µmol/kgSW)	2095.3 + 27	2085.2 + 24	2105.8 + 21	2125.9 + 18
Temp. (°C)	18.44 + 0.16	18.1 + 0.08	18.3 + 0.09	18.49 + 0.15
Salinity (ppt)	31.1 + 0.10	31.1 + 0.10	31.2 + 0.10	31.08 + 0.09
DIN (µM)	6.92 + 0.78	202.4 + 6.90	6.96 + 0.50	196.6 + 11.00

DIC and TA were measured via water samples collected during each experiment. Temperature and salinity were measured directly. Seacarb (R software; Gattuso et al. 2021) was used to calculate $pH_{(total)}$, pCO_2, CO_2, HCO_3^-, and CO_3^{2-}. Dissolved inorganic nitrogen (DIN) was measured from water samples that were taken during experimentation ($N = 8$ per treatment). All values represent means + 1 standard error

CRM Batch 151. All parameters of carbonate chemistry were calculated using the seacarb package (R software; Gattuso et al. 2021) (Table 1). Natural variation of seawater pH was observed using WTW Profiline 3110 pH meter with SenTix 21 glass electrodes recording high frequency pH measurements in each of the four treatments (Supplemental Fig. 1).

Nutrient levels were optimized prior to the start of each experiment, and additional samples were taken from each treatment midway through each experiment. Here, 60 mL of seawater was filtered and samples were frozen at − 20 °C for preservation. Samples were later analyzed for DIN concentration at the URI Marine Science Research Facility, a RI NSF EPSCoR Core Facility.

Statistical methods

Grazing rates (mg of algal tissue per snail per day) were compared across environmental treatments using two-way, fixed factor analysis of variance (ANOVA) with pCO_2 and nutrient levels as categorical, fixed factors. Individual aquaria from trials were treated as replicates. Assumptions of normality and equal variance were tested using Shapiro-Wilks and Levene's tests (R software), respectively, prior to running the ANOVA. To determine diet preference, mean grazing rates on *Ulva* and mean grazing rates on *Fucus* were compared across environmental treatments using a factorial MANOVA to account for non-independence of algal consumption (Roa 1992). As thalli of both species were present for grazers, any consumption (or non-consumption) of one species is likely dependent on the consumption (or non-consumption) of the other. The MANOVA used combined grazing rates of *Ulva* and *Fucus* separately as response variables. Protected ANOVAs, where species specific grazing rates were tested separately, were run post-hoc to determine which algal species contributed to statistical significance. Mean total consumption of reconstituted *Ulva* and *Fucus* (proportion of food squares per species consumed) were arcsine transformed and analyzed using a factorial MANOVA. If the MANOVA produced a significant environmental effect, protected ANOVAs were run to determine differences in grazing on reconstituted food. Assumptions of normality and equal variance were tested using Shapiro-Wilks and Levene's tests (R software), respectively prior to running the MANOVA. All statistics were performed using JMP v. 11 (www.jmp.com) and R software ("car" and "ggplot2" packages; R Development Core Team 2022, R-project.org).

Results

Seawater parameters

Our manipulation of both pCO_2 and nutrients proved effective, as we were able to obtain desired environmental levels (Table 1). Natural variation in pH throughout the course of experimentation was measured and logged by sensors and is presented in the supplemental materials (Supplemental Fig. 2). By adding nutrients to our aquaria, we effectively increased concentrations of DIN above ambient levels (Table 1).

Grazing (live algal thalli)

Under conditions of high pCO_2, grazing by *Littorina* was significantly reduced (Table 2). Mean grazing rates by *Littorina* were reduced by more than half under high pCO_2 compared to ambient pCO_2 (53.5 and 113.3 mg snail^{-1} day^{-1}, respectively; Supplemental Fig. 3; Table 2). Grazing rates were not affected, however, by nutrient level (86.5 mg snail^{-1} day^{-1} for high nutrients and 80.3 mg snail^{-1} day^{-1} for ambient nutrients), with a non-significant interaction (Table 2).

Our MANOVA highlighted differences in grazing by algal species (Table 3). We found a significant effect of pCO_2 on *Ulva* vs *Fucus* grazing (Table 3). While there was no significant effect of environment on snail grazing of *Ulva* (Fig. 1; Table 3), grazing of *Fucus* was significantly decreased (Table 3) and almost nonexistent under conditions of acidification, as rates over the course of experimentation ranged from 53.6 mg snail^{-1} day^{-1} under ambient pCO_2 to 8.0 mg snail^{-1} day^{-1} under high pCO_2 (Fig. 1; Table 3). Snail grazing of *Fucus* was not impacted by nutrient level or the interaction of pCO_2 and nutrients (Table 3).

Grazing (reconstituted food)

Total grazing of reconstituted food by *Littorina* was unaffected by pCO_2, nutrients, and their interaction (Table 4). Here, total consumed proportions of reconstituted food ranged between 0.54 and 0.70 (Supplemental Fig. 4). *Littorina* consumed similar proportions of both reconstituted *Ulva* and *Fucus* across all environmental treatments. *Ulva* consumption ranged between 0.44 and 0.70 while *Fucus* consumption ranged between 0.58 and 0.73 (Fig. 2).

Table 2 Summary of the two-way ANOVA showing the effects of ocean acidification (pCO_2), nutrient addition (Nutrients), and their interaction (pCO_2 X Nutrients) on the feeding rates of *Littorina* on macroalgae (mg snail^{-1} day^{-1}) by *Littorina*

Model source	df	SS	*F*	*p*
pCO_2	1	25,039	24.2	< 0.0001*
Nutrients	1	265	0.25	0.62
pCO_2 X Nutrients	1	133	0.13	0.72
Error	24	24,877		

*Represent significant *p*-values ($\alpha < 0.05$)

Table 3 Summary of the factorial MANOVA and protected ANOVA showing the effects of ocean acidification (pCO_2), nutrient addition (Nutrients), and their interaction (pCO_2 X Nutrients) on the grazing rates (mg snail^{-1} day^{-1}) of *Ulva* and *Fucus* by *Littorina*

MANOVA Source of variation	Wilks' λ	df	*F*	*p*
pCO_2	0.54	2, 23	9.61	< 0.0001*
Nutrients	0.99	2, 23	0.05	0.95
pCO_2 X nutrients	0.99	2, 23	0.04	0.96

ANOVA Response variable	Source of variation	df	SS	*F*	*p*
Ulva consumed	pCO_2	1	1348	1.95	0.18
	Nutrients	1	24	0.03	0.86
	pCO_2 X nutrients	1	44	0.06	0.80
	Error	24	16,577		
Fucus consumed	pCO_2	1	14,530	33.5	< 0.0001*
	Nutrients	1	161	0.37	0.55
	pCO_2 X nutrients	1	9	0.02	0.88
	Error	24	10,406		

*Represent significant *p*-values ($\alpha < 0.05$)

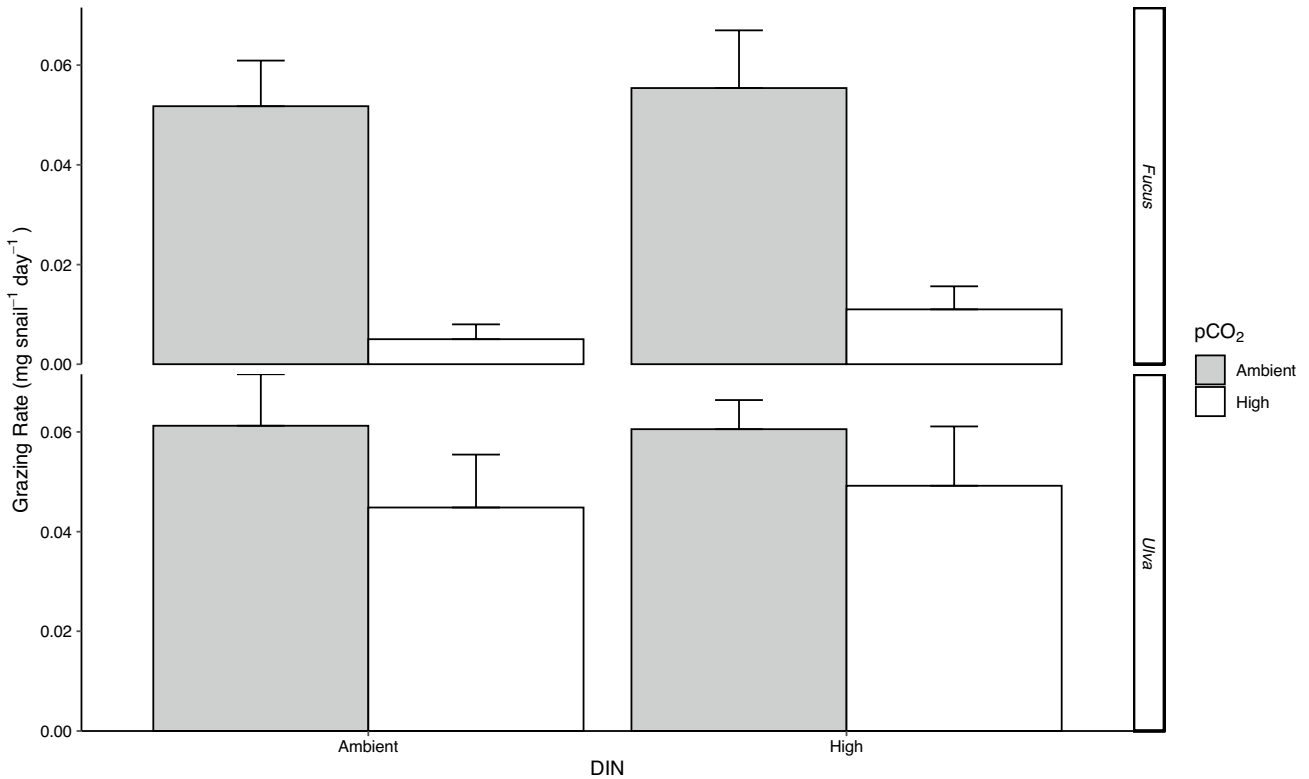

Fig. 1 Mean consumption of *Ulva* and *Fucus* (mg ± 1 SE) by environmental treatment. No significant differences were observed in the consumption of *Ulva* by environment. Consumption rates on *Fucus* were significantly reduced under high pCO2 ($p < 0.0001$; Table 3)

Table 4 Summary of the factorial MANOVA showing the effects of ocean acidification (pCO_2), nutrient addition (Nutrients), and their interaction (pCO_2 X Nutrients) on the consumption (mg) of reconstituted *Ulva* and *Fucus* by *Littorina*

MANOVA Source of variation	Wilks' λ	df	*F*	*p*
pCO_2	0.95	2, 16	0.42	0.66
Nutrients	0.97	2, 16	0.22	0.81
pCO_2 X nutrients	0.98	2, 16	0.18	0.84

Discussion

Few studies have investigated the interactive effects of ocean acidification and nutrients on coastal communities, despite these factors aiding increased growth and spread of many macroalgal species (Russell et al. 2009; Falkenberg et al. 2014; Campbell and Fourqurean 2014). In particular, little is known about how the impacts of grazers may shift due to changing climate conditions. Falkenberg et al. (2014) found that *Austrocochlea* snails can control the excess growth of opportunistic turf algae under high CO_2 and high nutrients. Our findings indicate that *Littorina* exposed to high levels of pCO_2 exhibit reduced macroalgal consumption and shift to a diet mostly consisting of *Ulva*. However, high pCO_2 treatments in Falkenberg et al. (2014) were around 580 ppm, whereas our high pCO_2 treatment was nearly double that (~ 1200 ppm), this is likely a significant factor that dictated differences in results. Unlike Falkenberg et al. (2014), we did not observe enhanced grazing with elevated nutrient levels, despite previous evidence of enhanced tissue quality (Ober and Thornber 2017). When feeding on reconstituted algae, high pCO_2 did not lead to significant decreases in feeding rates and *Littorina* did not exhibit the same shift in algal preference. These findings may highlight the importance of physical characteristics of algal tissue in grazer preference, over chemical and nutritional tissue differences.

Negative impacts to grazing marine organisms from exposure to high pCO_2 have been observed across many species and systems. High pCO_2 (> 970 ppm) has been shown to decrease *Littorina* consumption of biofilms and *Fucus* (Russell et al. 2013; Kinnby et al. 2021). Young et al. (2019) observed decreased consumption of *Ulva* by another marine snail, *Lacuna vincta*, when exposed to high levels of acidification (> 800 atm). Decreases in snail grazing rates can be linked to the direct effects of acidification on physiology. *Littorina* exposed to high pCO_2 exhibit decreased respiration rates and metabolism (Leung et al. 2015). Young et al.

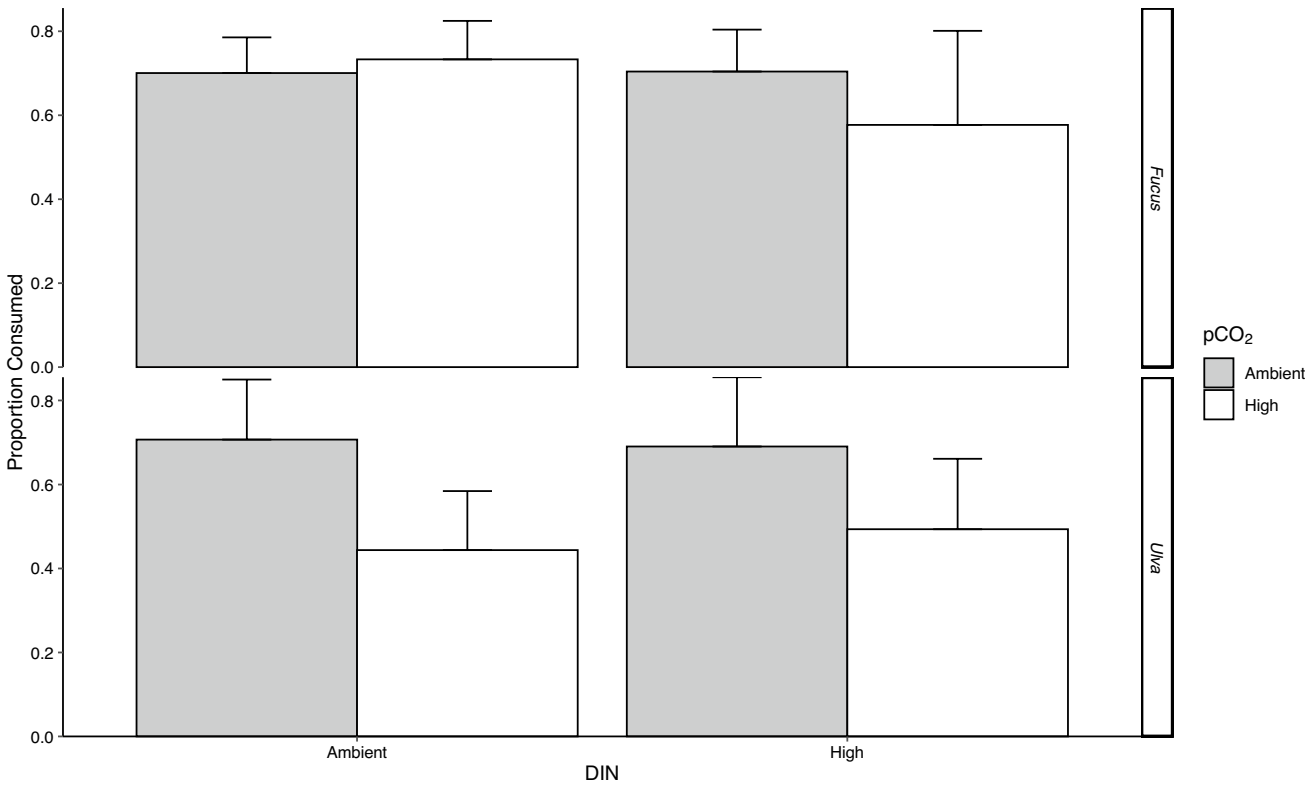

Fig. 2 Mean proportion consumed of reconstituted *Ulva* and *Fucus* by *Littorina*, for each environmental treatment. Data are means ± 1 SE. No significant impact of environment on consumption was found for either species

(2019) linked a decrease in the respiration rate of *L. vinta* to decreased consumption of *Ulva*, and highlighted decreased kelp grazing by *L. vincta* while also decreasing snail survival rates (Young et al. 2021). Elevated pCO_2 has been shown to induce acidosis, disrupting metabolism and shifting energy away somatic growth (Pörtner et al. 1998). Gastropods shells are also vulnerable to elevated pCO_2 as there is evidence of reduced shell growth rates and reduced repair rates (Shirayama and Thornton 2005), weakened, slow growing shells impact organism survival. Pteropods were found to divert energy from metabolism and growth to address shell dissolution associated with high pCO_2 (Manno et al. 2012). Altering shell thickness, a defense for *Littorina,* is depressed with exposure to low pH (Bibby et al. 2007). Other grazing gastropods exhibit behavioral changes in response to elevated pCO_2, where many species are unable to detect predator cues (Jellison et al. 2016; Jellison and Gaylord 2019) and may expose themselves to increased predation risk.

While our results highlight potential physiological changes in *Littorina*, it is important to note that our experiment quantified short term, acute impacts of elevated pCO_2. Numerous studies have shown the differences in short term and long term responses to high pCO_2. Acclimation and adaptation to high pCO_2 has been shown in corals, coralline algae, and sea urchins, among others (Form and Riebesell 2012; Ragazzola et al. 2013; Suckling et al. 2015). Given a longer acclimation, *Littorina* metabolism and grazing may recover. However, in coastal systems, exposure to high pCO_2 is common and this study provides insight on the implications of short term, acute exposure.

When exposed to high nutrients, C:N ratios in both *Ulva* and *Fucus* decrease (Ober and Thornber 2017), making them of higher nutritional value to consumers. Our study offered *Ulva* and *Fucus* grown under high nutrients, but no evidence of increased consumption was observed. We did not directly measure C:N in this experiment and therefore cannot state whether our study organisms had lower atomic ratios. Others have found, however, that decreased C:N can increase grazer consumption of macroalgae. Falkenberg et al. (2014) found that turf algae grown under elevated pCO_2 and nutrients had higher tissue quality (via decreased C:N) and were consumed at an increased rate by gastropods. Similarly, Hemmi and Jormalainen (2002) found that elevated nutrients increased the quality of *Fucus vesiculosus* and promoted enhanced growth rates and consumption by isopods, and Poore et al. (2012) observed increased feeding rates by amphipods feeding on *Sargassum spp*. as a result of exposure to high CO_2. By contrast, Duarte et al. (2015) found CO_2-induced decreases in organic content (the concentration of carbon within algal tissue) and proteins in the brown alga *Durvillaea antarctica,* but the loss in quality was correlated with compensatory feeding by amphipods. Decreased C:N does not always enhance consumption; Gutow et al. (2014) found evidence of decreased C:N in *Fucus vesiculosus* but no change in consumption by isopods.

Our study assessed feeding on both live algal thalli and reconstituted algal tissue, however, these studies were run in August and October, respectively. Importantly, season has been shown to impact the C:N ratios within macroalgae. Yates and Peckol (1993) observed a decrease in C:N in *Fucus* moving from summer months to cooler months, meaning *Fucus* would become more valuable to consumers. It is possible that *Fucus* collected for the trials utilizing reconstituted algae had a more favorable C:N which resulted in more balanced consumption across algal species. However, *Ulva* shows a similar pattern by season, where C:N ratios decreased from summer to fall. Jansen et al. (2022) highlight a decline in C:N by roughly 50% in *Ulva* tissues from August to October. As such, C:N was likely different between live thalli and reconstituted algal trials. Since both *Fucus* and *Ulva* would have exhibited the same chemical change, our interpretation of our results doesn't change.

Dietary preferences of many marine grazers are highly correlated with both tissue quality and tissue toughness (Cruz-Rivera and Hay 2000; Watson and Norton 2009; Molis et al. 2015). Marine grazers, including *Littorina*, exhibit a preference for higher quality food (Watson and Norton 1985) and early successional, ephemeral species (Lubchenco 1978). *Littorina* consume both *Ulva* and *Fucus*, with a preference for *Ulva* over *Fucus*, but also preferentially feed on algal epiphytes and microalgae (Watson and Norton 1985; Russell et al. 2013; Bracken et al. 2014). It is possible that the reconstituted food utilized in this experiment closely resembles the size and shape of epiphytes and microalgae and thus was consumed without specific preference. When comparing the results of the live thalli trials with those from the reconstituted food trials, dietary preference was only evident during live thalli trials. Our results suggest that under high pCO_2, *Ulva* was selected over *Fucus* as a result of the physical characteristics of the algal tissue, with *Fucus* having tougher tissue (Watson and Norton 2009). In general, *Littorina* appear to preferentially choose easy to access food (whether microalgae or *Ulva*). When stressed with high pCO_2, changes in respiration and metabolism may drive this preference even more. Tissue toughness and strength is evident in healthy thalli, however, *Fucus* exposed to increased pCO_2 for 30 days may experience a loss in tissue strength and toughness (Kinnby et al. 2021). This response, however, likely did not influence our results as our study only exposed *Fucus* to elevated pCO_2 for 5 days prior to the start of feeding trials. It is possible, that in the process of creating reconstituted food, the use of agar may have altered C:N, thus affecting our ability to use compare the results of this trial with the live thalli trial.

Increases in pCO_2 have also been tied to changes in secondary metabolites (including grazing defense

compounds) in many algal species as most secondary metabolites are carbon-based (Borell et al. 2013; Kinnby et al. 2021). Here, macroalgae exposed to elevated pCO_2 may increase allelopathic compounds that aid defense against grazers and competitors. Del Monaco et al. (2017) highlighted increased allelopathy under high pCO_2 in some macroalgae, resulting in enhanced tissue loss of neighboring corals. It is possible that thalli used in our high pCO_2 trials were better defended than those in low pCO_2 trials. Overall, these secondary compounds likely would have been present in both live and reconstituted algal tissues. Given the differences in results between these live thalli and reconstituted trials, it does not appear that allelopathy played a significant role in either experiment, but this was not quantified as part of this study. However, with the temporal difference between the two trials, it is possible that levels of secondary compounds differed in the specimens used.

Despite a lack of preference for *Fucus*, our study remains ecologically relevant as *Littorina* can appear in such high densities along the coastline of the northwest Atlantic (greater than 200 individuals m^{-2}) that even minimal consumption plays a large role in structuring the algal communities (Perez et al. 2009; Poore et al. 2012). While our study showed changes in herbivore preference (or choice) under acidification conditions, aspects of algal use or selection may also be important. The amount of time *Littorina* spends on individual algal species under different environmental scenarios could provide further insights as to how these two algal species are used by snails in a changing climate.

Ocean acidification and nutrient loading are predicted to enhance the growth and spread of ephemeral and turf algae at the expense of foundational species like corals, seagrasses, and perennial macroalgae (i.e., fucoids), as well as reduce overall community diversity (Worm and Lotze 2006; Connell and Russell 2010; Diaz-Pulido et al. 2011; Hale et al. 2011; Koch et al. 2013). Increasing evidence points to the indirect effects of climate change on herbivores to exert top-down control on excessive algal growth, promoting community resilience (Russell and Connell 2005). Enhanced growth of bloom forming species, like *Ulva*, may be balanced by increased grazing by common herbivores. While our results point to evidence of physiological impairments to a common grazer, community resilience will depend on a diversity of herbivores (Baggini et al. 2015). While certain species might not have an ability to increase consumption under high pCO_2, other herbivores in this ecosystem may be able to compensate. As such, our understanding of ecosystem response to climate change will be dictated by the species involved and the diversity of the community.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-022-04099-8.

Acknowledgements The manuscript was submitted with EPA tracking number ORD-017577. We thank the US EPA Coastal Environmental Sciences Division for support and aide in experimental set up and design, and A. Pimenta for laboratory assistance. Additionally, we thank two anonymous reviewers for their feedback on this manuscript.

Author contributions All authors contributed to the development and design of the study. Data collection was performed by GTO, data analyses were performed by GTO with help from CST and JSG. The original draft of the manuscript was written by GTO with reviewing and editing provided by CST and JSG. Additional resources provided by JSG. All authors have read and approved the manuscript in its current form.

Funding This research has been supported by a grant from the U.S. Environmental Protection Agency's Science to Achieve Results (STAR) program (awarded to GTO). This material is based upon work supported in part by the National Science Foundation EPSCoR Cooperative Agreement #EPS-1004057 and OIA-1655221.

Data availability Data on grazing of live algal thalli and reconstituted food for all statistical analyses and figures, as well as logged pH data, are available in the figshare repository https://doi.org/10.6084/m9.figshare.18326366.v1.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable national and/or institutional guidelines for sampling, care, and experimental use of organisms for the study were followed.

References

Albright R, Bland C, Gillette P, Serafy JE, Langdon C, Capo TR (2012) Juvenile growth of the tropical sea urchin *Lytechinus variegatus* exposed to near-future ocean acidification scenarios. J Exp Mar Biol Ecol 426–427:12–17. https://doi.org/10.1016/j.jembe.2012.05.017

Anthony KRN, Maynard JA, Diaz-Pulido G, Mumby PJ, Marshall PA, Cao L, Hoegh-Guldberg O (2011) Ocean acidification and warming will lower coral reef resilience. Glob Change Biol 17:1798–1808. https://doi.org/10.1111/j.1365-2486.2010.02364.x

Bach LT, Alvarez-Fernandez S, Hornick T, Stuhr A, Riebesell U (2017) Simulated ocean acidification reveals winners and losers in coastal phytoplankton. PLoS ONE 12:e0188198. https://doi.org/10.1371/journal.pone.0188198

Baggini C, Issaris Y, Salomidi M, Hall-Spencer J (2015) Herbivore diversity improves benthic community resilience to ocean acidification. J Exp Mar Biol Ecol 469:98–104. https://doi.org/10.1016/j.jembe.2015.04.019

Berger R, Bergström L, Granéli E, Kautsky L (2004) How does eutrophication affect different life stages of *Fucus vesiculosus* in the Baltic Sea?–a conceptual model. Hydrobiologia 514:243–248

Bibby R, Cleall-Harding P, Rundle S, Widdicombe S, Spicer J (2007) Ocean acidification disrupts induced defences in the intertidal gastropod *Littorina littorea*. Biol Let 3:699–701. https://doi.org/10.1098/rsbl.2007.0457

Borell EM, Steinke M, Fine M (2013) Direct and indirect effects of high pCO_2 on algal grazing by coral reef herbivores from the Gulf

of Aqaba (Red Sea). Coral Reefs 32:937–947. https://doi.org/10.1007/s00338-013-1066-5
Bracken MES, Dolecal RE, Long JD (2014) Community context mediates the top-down vs. bottom-up effects of grazers on rocky shores. Ecology 95:1458–1463. https://doi.org/10.1890/13-2094.1
Cai W-J, Hu X, Huang W-J, Murrell MC, Lehrter JC, Lohrenz SE, Chou W-C, Zhai W, Hollibaugh JT, Wang Y, Zhao P, Guo X, Gundersen K, Dai M, Gong G-C (2011) Acidification of subsurface coastal waters enhanced by eutrophication. Nat Geosci 4:766–770. https://doi.org/10.1038/ngeo1297
Campbell JE, Fourqurean JW (2014) Ocean acidification outweighs nutrient effects in structuring seagrass epiphyte communities. J Ecol 102:730–737. https://doi.org/10.1111/1365-2745.12233
Carstensen J, Duarte CM (2019) Drivers of pH variability in coastal ecosystems. Environ Sci Technol 53:4020–4029. https://doi.org/10.1021/acs.est.8b03655
Connell SD, Russell BD (2010) The direct effects of increasing CO_2 and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. Proc R Soc B: Biol Sci 277(1686):1409–1415
Connell SD, Kroeker KJ, Fabricius KE, Kline DI, Russell BD (2013) The other ocean acidification problem: CO_2 as a resource among competitors for ecosystem dominance. Philos Trans Royal Soc b: Biol Sci 368:20120442
Cruz-Rivera E, Hay ME (2000) Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. Ecology 81:201–219
Del Monaco C, Hay ME, Gartrell P, Mumby PJ, Diaz-Pulido G (2017) Effects of ocean acidification on the potency of macroalgal allelopathy to a common coral. Sci Rep 7:41053
Diaz-Pulido G, Gouezo M, Tilbrook B, Dove S, Anthony K (2011) High CO_2 enhances the competitive strength of seaweeds over corals. Ecol Lett 14:156–162
Dickson AG, Sabine CL, Christian JR (2007) Guide to best practices for ocean CO_2 measurements. PICES Special Publication 3
Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO_2 problem. Ann Rev Mar Sci 1:169–192. https://doi.org/10.1146/annurev.marine.010908.163834
Duarte C, López J, Benítez S, Manríquez PH, Navarro JM, Bonta CC, Torres R, Quijón P (2015) Ocean acidification induces changes in algal palatability and herbivore feeding behavior and performance. Oecologia 180:453–462. https://doi.org/10.1007/s00442-015-3459-3
Falkenberg LJ, Connell SD, Russell BD (2014) Herbivory mediates the expansion of an algal habitat under nutrient and CO2 enrichment. Mar Ecol Prog Ser 497:87–92
Feely RA, Doney SC, Cooley SR (2009) Ocean acidification: present conditions and future changes in a high-CO_2 world. Oceanography 22:36–47
Feely RA, Alin SR, Newton J, Sabine CL, Warner M, Devol A, Krembs C, Maloy C (2010) The combined effects of ocean acidification, mixing, and respiration on pH and carbonate saturation in an urbanized estuary. Estuar Coast Shelf Sci 88:442–449. https://doi.org/10.1016/j.ecss.2010.05.004
Form AU, Riebesell U (2012) Acclimation to ocean acidification during long-term CO_2 exposure in the cold-water coral *Lophelia pertusa*. Glob Change Biol 18:843–853. https://doi.org/10.1111/j.1365-2486.2011.02583.x
Gattuso JP, Epitalon JM, Lavigne H, Orr J (2021) seacarb: Seawater Carbonate Chemistry. R package version 3.3.0. https://CRAN.R-project.org/package=seacarb. Accessed Aug 2021
Ghedini G, Russell BD, Connell SD (2015) Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances. Ecol Lett 18:182–187
Grear JS, Rynearson TA, Montalbano AL, Govenar B, Menden-Deuer S (2017) pCO_2 effects on species composition and growth of an estuarine phytoplankton community. Estuar Coast Shelf Sci 190:40–49. https://doi.org/10.1016/j.ecss.2017.03.016
Guidone M, Thornber CS, Vincent E (2012) Snail grazing facilitates growth of two morphologically similar bloom-forming *Ulva* species through different mechanisms. J Ecol 100:1105–1112. https://doi.org/10.1111/j.1365-2745.2012.02002.x
Gutow L, Rahman MM, Bartl K, Saborowski R, Bartsch I, Wiencke C (2014) Ocean acidification affects growth but not nutritional quality of the seaweed *Fucus vesiculosus* (Phaeophyceae, Fucales). J Exp Mar Biol Ecol 453:84–90
Hale R, Calosi P, McNeill L, Mieszkowska N, Widdicombe S (2011) Predicted levels of future ocean acidification and temperature rise could alter community structure and biodiversity in marine benthic communities. Oikos 120:661–674. https://doi.org/10.1111/j.1600-0706.2010.19469.x
Hemmi A, Jormalainen V (2002) Nutrient enhancement increases performance of a marine herbivore via quality of its food alga. Ecology 83:1052–1064. https://doi.org/10.1890/0012-9658(2002)083[1052:NEIPOA]2.0.CO;2
Hirsh HK, Nickols KJ, Takeshita Y, Traiger SB, Mucciarone DA, Monismith S, Dunbar RB (2020) Drivers of biogeochemical variability in a central California kelp forest: implications for local amelioration of ocean acidification. J Geophys Res: Oceans. https://doi.org/10.1029/2020JC016320
Hofmann GE, Smith JE, Johnson KS, Send U, Levin LA, Micheli F, Paytan A, Price NN, Peterson B, Takeshita Y, Matson PG, Crook ED, Kroeker KJ, Gambi MC, Rivest EB, Frieder CA, Yu PC, Martz TR (2011) High-frequency dynamics of ocean pH: a multi-ecosystem comparison. PLoS ONE 6:e28983. https://doi.org/10.1371/journal.pone.0028983
Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J et al (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933
Imrie DW, McCrohan CR, Hawkins SJ (1990) Feeding behaviour in *Littorina littorea*: a study of the effects of ingestive conditioning and previous dietary history on food preference and rates of consumption. Hydrobiologia 193:191–198. https://doi.org/10.1007/BF00028076
Jansen HM, Bernard MS, Nederlof MAJ, van der Meer IM, van der Werf A (2022) Seasonal variation in productivity, chemical composition and nutrient uptake of *Ulva spp*. (Chlorophyta) strains. J Appl Phycol 34:1649–1660. https://doi.org/10.1007/s10811-022-02708-z
Jellison BM, Gaylord B (2019) Shifts in seawater chemistry disrupt trophic links within a simple shoreline food web. Oecologia 190:955–967. https://doi.org/10.1007/s00442-019-04459-0
Jellison BM, Ninokawa AT, Hill TM, Sanford E, Gaylord B (2016) Ocean acidification alters the response of intertidal snails to a key sea star predator. Proc Royal Soc b: Biol Sci 283:20160890. https://doi.org/10.1098/rspb.2016.0890
Jones E, Thornber CS (2010) Effects of habitat-modifying invasive macroalgae on epiphytic algal communities. Mar Ecol Prog Ser 400:87–100. https://doi.org/10.3354/meps08391
Kinnby A, White JCB, Toth GB, Pavia H (2021) Ocean acidification decreases grazing pressure but alters morphological structure in a dominant coastal seaweed. PLoS ONE 16:e0245017. https://doi.org/10.1371/journal.pone.0245017
Koch M, Bowes G, Ross C, Zhang X-H (2013) Climate change and ocean acidification effects on seagrasses and marine macroalgae. Glob Change Biol 19:103–132. https://doi.org/10.1111/j.1365-2486.2012.02791.x
Krause-Jensen D, Duarte CM, Hendriks IE, Meire L, Blicher ME, Marbà N, Sejr MK (2015) Macroalgae contribute to nested mosaics of pH variability in a subarctic fjord. Biogeosciences 12:4895–4911. https://doi.org/10.5194/bg-12-4895-2015

Krumholz JS (2012) Spatial and temporal patterns in nutrient standing stock and mass-balance in response to load reductions in a temperate estuary. Ph.D. Dissertation in Oceanography, University of Rhode Island, Kingston, RI

Kübler JE, Johnston AM, Raven JA (1999) The effects of reduced and elevated CO_2 and O_2 on the seaweed *Lomentaria articulata*. Plant, Cell Environ 22:1303–1310. https://doi.org/10.1046/j.1365-3040.1999.00492.x

Landes A, Zimmer M (2012) Acidification and warming affect both a calcifying predator and prey, but not their interaction. Mar Ecol Prog Ser 450:1–10. https://doi.org/10.3354/meps09666

Leung JYS, Russell BD, Connell SD, Ng JCY, Lo MMY (2015) Acid dulls the senses: impaired locomotion and foraging performance in a marine mollusc. Anim Behav 106:223–229. https://doi.org/10.1016/j.anbehav.2015.06.004

Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am Nat 112:23–39

Lubchenco J (1983) *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64:1116–1123. https://doi.org/10.2307/1937822

Manno C, Morata N, Primicerio R (2012) *Limacina retroversa's* response to combined effects of ocean acidification and sea water freshening. Estuar Coast Shelf Sci 113:163–171. https://doi.org/10.1016/j.ecss.2012.07.019

McSkimming C, Tanner JE, Russell BD, Connell SD (2015) Compensation of nutrient pollution by herbivores in seagrass meadows. J Exp Mar Biol Ecol 471:112–118. https://doi.org/10.1016/j.jembe.2015.05.018

Melatunan S, Calosi P, Rundle SD, Moody AJ, Widdicombe S (2011) Exposure to elevated temperature and pCO_2 reduces respiration rate and energy status in the periwinkle *Littorina littorea*. Physiol Biochem Zool 84:583–594

Molis M, Scrosati RA, El-Belely EF, Lesniowski TJ, Wahl M (2015) Wave-induced changes in seaweed toughness entail plastic modifications in snail traits maintaining consumption efficacy. J Ecol 103:851–859. https://doi.org/10.1111/1365-2745.12386

Moss RH, Edmonds JA, Hibbard KA, Manning MR, Rose SK et al (2010) The next generation of scenarios for climate change research and assessment. Nature 463:747–756

Nielsen KJ (2003) Nutrient loading and consumers: agents of change in open-coast macrophyte assemblages. Proc Natl Acad Sci 100:7660–7665. https://doi.org/10.1073/pnas.0932534100

Ober GT, Thornber CS (2017) Divergent responses in growth and nutritional quality of coastal macroalgae to the combination of increased pCO_2 and nutrients. Mar Environ Res 131:69–79. https://doi.org/10.1016/j.marenvres.2017.09.003

Ober GT, Diaz-Pulido G, Thornber C (2016) Ocean acidification influences the biomass and diversity of reef-associated turf algal communities. Mar Biol 163:204. https://doi.org/10.1007/s00227-016-2978-8

Olischläger M, Wiencke C (2013) Ocean acidification alleviates low-temperature effects on growth and photosynthesis of the red alga *Neosiphonia harveyi* (Rhodophyta). J Exp Bot 64:5587–5597. https://doi.org/10.1093/jxb/ert329

Olischläger M, Bartsch I, Gutow L, Wiencke C (2013) Effects of ocean acidification on growth and physiology of *Ulva lactuca* (Chlorophyta) in a rockpool-scenario. Phycol Res 61:180–190

Peckol P, Putnam AB (2017) Differential toxic effects of *Ulva lactuca* (Chlorophyta) on the herbivorous gastropods, *Littorina littorea* and *L. obtusata* (Mollusca). J Phycol 53:361–367. https://doi.org/10.1111/jpy.12507

Perez KO, Carlson RL, Shulman MJ, Ellis JC (2009) Why are intertidal snails rare in the subtidal? Predation, growth and the vertical distribution of *Littorina littorea* (L.) in the Gulf of Maine. J Exp Mar Biol Ecol 369:79–86. https://doi.org/10.1016/j.jembe.2008.09.019

Poore AGB, Campbell AH, Coleman RA, Edgar GJ, Jormalainen V, Reynolds PL, Sotka EE, Stachowicz JJ, Taylor RB, Vanderklift MA, Emmett Duffy J (2012) Global patterns in the impact of marine herbivores on benthic primary producers. Ecol Lett 15:912–922. https://doi.org/10.1111/j.1461-0248.2012.01804.x

Poore AGB, Graham SE, Byrne M, Dworjanyn SA (2016) Effects of ocean warming and lowered pH on algal growth and palatability to a grazing gastropod. Mar Biol 163:1–11. https://doi.org/10.1007/s00227-016-2878-y

Pörtner HO, Reipschläger A, Heisler N (1998) Acid-base regulation, metabolism and energetics in *Sipunculus nudus* as a function of ambient carbon dioxide level. J Exp Biol 201:43–55. https://doi.org/10.1242/jeb.201.1.43

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. Accessed Jan 2022

Ragazzola F, Foster LC, Form AU, Büscher J, Hansteen TH, Fietzke J (2013) Phenotypic plasticity of coralline algae in a high CO_2 world. Ecol Evol 3:3436–3446. https://doi.org/10.1002/ece3.723

Roa R (1992) Design and analysis of multiple-choice feeding-preference experiments. Oecologia 89:509–515. https://doi.org/10.1007/BF00317157

Russell B, Connell S (2005) A novel interaction between nutrients and grazers alters relative dominance of marine habitats. Mar Ecol-Prog Ser 289:5–11

Russell BD, Connell SD (2007) Response of grazers to sudden nutrient pulses in oligotrophic versus eutrophic conditions. Mar Ecol Prog Ser 349:73–80. https://doi.org/10.3354/meps07097

Russell BD, Thompson J-AI, Falkenberg LJ, Connell SD (2009) Synergistic effects of climate change and local stressors: CO_2 and nutrient-driven change in subtidal rocky habitats. Glob Change Biol 15:2153–2162

Russell BD, Connell SD, Findlay HS, Tait K, Widdicombe S, Mieszkowska N (2013) Ocean acidification and rising temperatures may increase biofilm primary productivity but decrease grazer consumption. Philos Trans R Soc B 368:20120438. https://doi.org/10.1098/rstb.2012.0438

Sabine CL (2004) The oceanic sink for anthropogenic CO_2. Science 305:367–371. https://doi.org/10.1126/science.1097403

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH image to imagej: 25 years of image analysis. Nat Methods 9:671–675

Shirayama Y, Thornton H (2005) Effect of increased atmospheric CO_2 on shallow water marine benthos. J Geophys Res: Oceans. https://doi.org/10.1029/2004JC002618

Stachowicz JJ, Hay ME (1999) Mutualism and coral persistence: the role of herbivore resistance to algal chemical defense. Ecology 80:2085–2101. https://doi.org/10.1890/0012-9658(1999)080[2085:MACPTR]2.0.CO;2

Stumpp M, Wren J, Melzner F, Thorndyke MC, Dupont ST (2011) CO_2 induced seawater acidification impacts sea urchin larval development I: elevated metabolic rates decrease scope for growth and induce developmental delay. Comp Biochem Physiol a: Mol Integr Physiol 160:331–340. https://doi.org/10.1016/j.cbpa.2011.06.022

Suckling CC, Clark MS, Richard J, Morley SA, Thorne MAS, Harper EM, Peck LS (2015) Adult acclimation to combined temperature and pH stressors significantly enhances reproductive outcomes compared to short-term exposures. J Anim Ecol 84:773–784. https://doi.org/10.1111/1365-2656.12316

Tate CM (1990) Patterns and controls of nitrogen in tallgrass prairie streams. Ecology 71:2007–2018. https://doi.org/10.2307/1937609

Teichberg M, Fox SE, Aguila C, Olsen YS, Valiela I (2008) Macroalgal responses to experimental nutrient enrichment in shallow coastal waters: growth, internal nutrient pools, and isotopic signatures.

Mar Ecol Prog Ser 368:117–126. https://doi.org/10.3354/meps07564

Thornber C, Stachowicz JJ, Gaines S (2006) Tissue type matters: selective herbivory on different life history stages of an isomorphic alga. Ecology 87:2255–2263. https://doi.org/10.1890/0012-9658(2006)87[2255:TTMSHO]2.0.CO;2

Thornber CS, DiMilla P, Nixon SW, McKinney RA (2008) Natural and anthropogenic nitrogen uptake by bloom-forming macroalgae. Mar Pollut Bull 56:261–269

Wallace RB, Baumann H, Grear JS, Aller RC, Gobler CJ (2014) Coastal ocean acidification: the other eutrophication problem. Estuar Coast Shelf Sci 148:1–13. https://doi.org/10.1016/j.ecss.2014.05.027

Watson DC, Norton TA (1985) Dietary preferences of the common periwinkle, *Littorina littorea* (L.). J Exp Mar Biol Ecol 88:193–211. https://doi.org/10.1016/0022-0981(85)90230-8

Watson DC, Norton TA (2009) The physical characteristics of seaweed thalli as deterrents to Littorine grazers. Bot Mar 28:383–388. https://doi.org/10.1515/botm.1985.28.9.383

Whalen MA, Duffy JE, Grace JB (2013) Temporal shifts in top-down vs. bottom-up control of epiphytic algae in a seagrass ecosystem. Ecology 94:510–520. https://doi.org/10.1890/12-0156.1

Worm B, Lotze HK (2006) Effects of eutrophication, grazing, and algal blooms on rocky shores. Limnol Oceanogr 51:569–579. https://doi.org/10.4319/lo.2006.51.1_part_2.0569

Xu J, Gao K (2012) Future CO_2-induced ocean acidification mediates the physiological performance of a green tide alga. Plant Physiol 160:1762–1769. https://doi.org/10.1104/pp.112.206961

Yates JL, Peckol P (1993) Effects of nutrient availability and herbivory on polyphenolics in the seaweed *Fucus versiculosus*. Ecology 74:1757–1766. https://doi.org/10.2307/1939934

Young CS, Gobler CJ (2020) Hypoxia and acidification, individually and in combination, disrupt herbivory and reduce survivorship of the gastropod Lacuna Vincta. Front Marine Sci 7:785. https://doi.org/10.3389/fmars.2020.547276

Young CS, Lowell A, Peterson B, Gobler CJ (2019) Ocean acidification and food limitation combine to suppress herbivory by the gastropod *Lacuna vincta*. Mar Ecol Prog Ser 627:83–94. https://doi.org/10.3354/meps13087

Young CS, Doall MH, Gobler CJ (2021) Dual benefit of ocean acidification for the laminarialean kelp *Saccharina latissima*: enhanced growth and reduced herbivory. Mar Ecol Prog Ser 664:87–102. https://doi.org/10.3354/meps13659