Vol. 664: 87–102, 2021
https://doi.org/10.3354/meps13659

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 15

Dual benefit of ocean acidification for the laminarialean kelp *Saccharina latissima*: enhanced growth and reduced herbivory

Craig S. Young, Michael H. Doall, Christopher J. Gobler*

School of Marine and Atmospheric Sciences, Stony Brook University, Southampton, NY 11968, USA

ABSTRACT: The laminarialean kelp *Saccharina latissima* is a common macroalga along rocky shorelines that is also frequently used in aquaculture. This study examined how ocean acidification may alter the growth of *S. latissima* as well as grazing on *S. latissima* by the gastropod *Lacuna vincta*. Under elevated nutrients, *S. latissima* experienced significantly enhanced growth at pCO_2 levels ≥1200 µatm compared to ambient pCO_2 (~400 µatm). Elevated pCO_2 (≥830 µatm) also significantly reduced herbivory of *L. vincta* grazing on *S. latissima* relative to ambient pCO_2. There was no difference in grazing of *S. latissima* previously grown under elevated or ambient pCO_2, suggesting lowered herbivory was due to harm to the gastropods rather than alteration of the biochemical composition of the kelp. Decreased herbivory was specifically elicited when *L. vincta* were exposed to elevated pCO_2 in the absence of food for ≥18 h prior to grazing, with reduced grazing persisting 72 h. Elevated growth of *S. latissima* and reduced grazing by *L. vincta* at 1200 µatm pCO_2 combined to increase net growth rates of *S. latissima* more than 4-fold relative to ambient pCO_2. *L. vincta* consumed 70% of daily production by *S. latissima* under ambient pCO_2 but only 38 and 9% at 800 and 1200 µatm, respectively. Collectively, decreased grazing by *L. vincta* coupled with enhanced growth of *S. latissima* under elevated pCO_2 demonstrates that increased CO_2 associated with climate change and/or coastal processes will dually benefit commercially and ecologically important kelps by both promoting growth and reducing grazing pressure.

KEY WORDS: Ocean acidification · Kelp · Gastropods · Grazing

1. INTRODUCTION

Ocean acidification is changing marine ecosystems. As anthropogenic CO_2 accumulates in the atmosphere and surface oceans, levels of pH, CO_3^{2-}, and the saturation states of calcium carbonate are declining (Doney et al. 2009, Feely et al. 2009). In addition, many coastal ecosystems can experience partial pressure of CO_2 (pCO_2) levels not projected to occur in open ocean systems until the year 2100 (>1000 µatm) due to a multitude of processes, including upwelling (Feely et al. 2008), riverine discharge (Vargas et al. 2016), macrophyte respiration (Wahl et al. 2018), and eutrophication-enhanced microbial respiration (Wallace et al. 2014). These changes in ocean chemistry stand to reorganize the function of coastal ecosystems, as acidification can be inhibitory to some marine animals (Poloczanska et al. 2016), especially calcifiers (Talmage & Gobler 2010, Young et al. 2019), but may benefit other ocean organisms (Koch et al. 2013, Young & Gobler 2016).

Saccharina latissima (also known as sugar kelp) is a bladed, cold-water brown macroalga that is widely distributed across the North Atlantic, Pacific, and Arctic Oceans (Brinkhuis et al. 1983, Sivertsen & Bjørge 2015). *S. latissima* can form dense, highly productive and biologically diverse beds that provide numerous ecosystem services, including nursery

*Corresponding author: christopher.gobler@stonybrook.edu

Publisher: Inter-Research · www.int-res.com

habitat, refuge from predators, coastal defense, carbon and nitrogen sequestration, and food sources for other organisms (Norderhaug et al. 2005, Chung et al. 2013, Smale et al. 2013). More recently, the commercial importance and aquaculture of *S. latissima* and other species of kelp has grown (Marinho et al. 2015). Excessive grazing, however, can significantly lower kelp abundance and ecosystem function (Scheibling et al. 1999, Norderhaug & Christie 2009). Moreover, global distributions of *S. latissima* are declining due to increasing temperatures (Filbee-Dexter et al. 2016), eutrophication (Moy & Christie 2012), and overfishing of the predators of kelp grazers (Steneck et al. 2002). However, recent evidence suggests that elevated pCO_2 associated with ocean acidification could benefit some species of kelp, potentially counteracting the processes contributing to their decline (Hepburn et al. 2011).

Beyond climate change, eutrophication may also act to negatively impact kelp communities. In some temperate regions, excessive nutrient loading can initiate a succession whereby kelp forests become overgrown by turf algae (Eriksson et al. 2002, Connell et al. 2008) and this succession may be accelerated by acidification (Connell & Russell 2010). Still, kelp can also exist in ecosystems where turf algae are rare, and kelp can be purposely grown in more eutrophic locales for aquaculture purposes (Kim et al. 2015, Jiang et al. 2020). While climate change and eutrophication are strong environmental drivers in coastal ecosystems, the manner in which nutrients and acidification act, and potentially interact, to directly alter kelp growth is not fully clear.

The northern *Lacuna* snail *Lacuna vincta* (Gastropoda) is a common grazer in coastal North Atlantic and North Pacific ecosystems (Chavanich & Harris 2002, Janiak & Whitlatch 2012) and is a well-known grazer of macroscopic kelp sporophytes (Brady-Campbell et al. 1984, Johnson & Mann 1986). Grazing by large populations of *L. vincta* can cause extensive damage to kelp blades in kelp beds (Chenelot & Konar 2007, Krumhansl & Scheibling 2011), consuming up to 10% of the surface area of *S. latissima* (Molis et al. 2010, Krumhansl & Scheibling 2011). The resulting damage done by the grazer on the kelp blade, meristem, and stipe can significantly lower the tensile strength of the kelp, making it more susceptible to breakage (Chenelot & Konar 2007, Molis et al. 2010). High grazing intensity by *L. vincta* on the reproductive sorus tissue of *S. latissima* may exacerbate recruitment limitation and further hinder the recovery of degraded kelp beds (O'Brien & Scheibling 2016). Compared to other macroalgae native to the northern Atlantic Ocean, laminarialean kelps are preferred by *L. vincta* due to overall lower phlorotanins (anti-grazing defense) and relatively high palatability (Wakefield & Murray 1998). While ocean acidification can disrupt the grazing by *L. vincta* on some macroalgae (Young et al. 2019), the manner in which *L. vincta* herbivory on kelps might be altered by this process is unknown.

The overarching objective of this study was to assess how coastal acidification may affect Northwest Atlantic populations of *S. latissima*. Experiments quantified the growth rates as well as elemental and isotopic content of *S. latissima* under treatment levels of pCO_2 with and without nutrients. Experiments were also performed to quantify herbivory rates of *L. vincta* on *S. latissima* under normal and elevated levels of pCO_2. Given that prior research has determined that the effects of acidification on grazing by *L. vincta* are dose-dependent with regard to both pCO_2 levels and exposure duration (Young et al. 2019), experiments exploring differing levels of pCO_2 and differing durations of exposure were performed. Given that the effects of acidification on invertebrates can depend on food supply (Melzner et al. 2011, Thomsen et al. 2013, Pansch et al. 2014), exposures to acidification were made following periods of ad libitum and restricted feeding. Finally, the net growth rates (growth minus grazing) of *S. latissima* were determined under treatment pCO_2 conditions, providing a novel examination of the net effects of ocean acidification on a keystone macrophyte. While studies exploring how ocean acidification affects herbivory have been limited, to our knowledge this is the first study to assess how ocean acidification concurrently alters growth and grazing for a macrophyte.

2. MATERIALS AND METHODS

2.1. Collection and preparation of *Lacuna vincta* and *Saccharina latissima*

Lacuna vincta used for this study were collected by hand during low tide from Shinnecock Bay, NY, USA (40.85° N, 72.50° W), part of New York's South Shore Estuary Reserve (NYSSER) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m664p087_supp.pdf). *L. vincta* are an abundant macroalgae grazer in estuaries of the northeastern USA (Chavanich & Harris 2002, Janiak & Whitlatch 2012) and were identified based on morphology. *Saccharina latissima* used in the study was cultured from blades collected from

Long Island Sound, spawned on line, and grown along horizontal longlines at a commercial oyster farm (i.e. Great Gun Shellfish) in Moriches Bay, NY (40.78° N, 72.78° W), a lagoon contiguous with Shinnecock Bay to the east. Large, well-pigmented blades of *S. latissima* were selected from samples collected by hand at low tide (Fig. S1). *S. latissima* were cut from their holdfasts as close to the longlines as possible. Following collection, *S. latissima* and *L. vincta* were immediately placed in seawater-filled containers and transported to the Stony Brook Southampton Marine Science Center of Stony Brook University within 30 min of collection. Upon arrival to the facility, *L. vincta* were placed in a 20 l polycarbonate vessel filled with filtered (0.2 µm) seawater taken from the collection site. The vessel was supplied with air and recently collected *S. latissima* as a food source until experiments were initiated (Duffy et al. 2014). *S. latissima* used in experiments were placed in a large, round ~2000 l tank filled with flowing, 1 µm filtered seawater from Shinnecock Bay.

For experiments performed to quantify algal growth rates in response to elevated pCO_2 and/or nutrients, individual *S. latissima* rectangular sporophytes were prepared by cutting the stipe 2.5 cm below the blade–stipe interface and cutting the blade 5 cm above the blade–stipe interface. This was done to standardize initial kelp blade tissue type and size (Boderskov et al. 2016). *S. latissima* samples were weighed on a Scientech ZSA 120 digital microbalance (±0.0001 g) to obtain initial fresh weight in grams. For experiments performed to quantify grazing rates on *S. latissima*, rectangular sections (2 × 4 cm, length × width) of the algae were cut from large blades with care taken to ensure uniformity of size, shape, and tissue type. Sections from the upper blades of *S. latissima* were used due to *L. vincta*'s preference for this section of the organism over the lower blade, meristem, or stipe (Molis et al. 2010). All samples were spun in a salad spinner to remove debris and epiphytes, extensively rinsed with filtered (0.2 µm) seawater before being spun again to further remove any remaining debris, epiphytes, and excess seawater (Young & Gobler 2016), and weighed as described above.

2.2. Preparation of experiments

Two experiments were performed to assess the effects of pCO_2 and nutrients on the growth rates of *S. latissima* and 5 experiments were performed to assess the effects of elevated pCO_2 on the herbivory rates of *L. vincta* on *S. latissima*. Each experiment was performed in 1 l polycarbonate vessels that were acid-washed (10% HCl) and liberally rinsed with deionized water. All experimental containers were placed in an environmental control chamber set to a temperature (~10–18°C), light intensity (~250 µmol photons m^{-2} s^{-1}), and duration (12 h light:12 h dark cycle) that matched ambient conditions at the collection site to allow for optimal conditions for *L. vincta* and *S. latissima*. As temperatures rose through the spring, so did the temperatures used for experiments to minimize thermal shock to the kelp and snails. All containers were filled with filtered seawater, randomly placed within the environmental control chamber, and randomly assigned in quadruplicate to each treatment, which varied based on the experiment performed. For grazing experiments (see below), 2 additional containers were filled with filtered seawater and assigned, without *L. vincta*, to assess *S. latissima* residual growth (i.e. additional growth the *S. latissima* samples experienced during the grazing period). During those experiments, the lights of the environmental control chamber were turned off 24 h prior to the introduction of *Lacuna* in order to minimize residual *S. latissima* growth (Nelson et al. 2008, Young et al. 2019). For each grazing experiments, 8 *L. vincta* (~3 mm) were added to each separate container, mimicking densities found on macroalgae at the collection site (0.5–1 grazer cm^{-2}) and reported in the literature (Chenelot & Konar 2007, Dubois & Iken 2012, Young et al. 2019).

Dissolved gases were delivered into each experimental container via air diffusers (Pentair) connected to 1 ml polystyrene serological pipettes inserted into the bottom of each vessel and connected via Tygon tubing to an air source. The containers that were subjected to treatment CO_2 conditions utilized multitube gas proportioner systems (Cole Parmer® Flowmeter) to mix ambient air with 5% CO_2 (Talmage & Gobler 2010). The containers subjected to ambient conditions utilized single tube proportioner systems to introduce only ambient air into the containers. The gases were mixed through gang valves and were delivered at a flow rate of 2500 ± 5 ml min^{-1} to experimental containers through serological pipettes inserted through plexiglass covers on the containers. The bubbling rates in the containers turned over the volume >1000 times d^{-1}, and bubbling was initiated at least 2–3 d prior to the initiation of experiments to allow CO_2 levels and carbonate chemistry to reach a state of equilibrium. A Honeywell DuraFET III ion-sensitive field effect transistor-based (ISFET) solid-state pH sensor (±0.01 pH unit, total scale) was used to measure pH

within containers each day of the experiments. Dissolved inorganic carbon (DIC) within experimental vessels was measured directly from water samples that were collected at the beginning and end of experiments and preserved using a saturated mercuric chloride ($HgCl_2$) solution and stored at ~4°C until they were analyzed on a VINDTA 3D (Versatile Instrument for the Determination of Total inorganic carbon) delivery system coupled within a UIC Inc. coulometer (model CM5017O). During the coulometric analyses, all inorganic carbon species were converted to CO_2 gas by the addition of excess hydrogen to the sample, and the evolved CO_2 gas was subsequently carried into the titration cell of the coulometer. The gas then reacted quantitatively with an ethanolamine-based reagent to generate hydrogen ions, which are titrated with coulometrically generated OH^-, and CO_2 was measured by integrating the total change required to titrate the hydrogen ions (Johnson et al. 1993). The pCO_2 concentrations (Table 1) were calculated from measured levels of DIC, pH, temperature, salinity, and the first and second dissociation constants of carbon acid in seawater (Millero 2010) using the program CO2SYS (http://cdiac.ess-dive.lbl.gov/ftp/co2sys/). Certified reference material (CRM) provided by Dr. Andrew Dickson (University of California, San Diego, Scripps Institution of Oceanography; Batch 180 = 2021.87 µmol DIC kg^{-1} seawater) was used as a quality assurance measure, and analyses only proceeded when recovery of the CRM was 99.8–100%. Final DIC concentration of the CRM was 2019.85 µmol DIC kg^{-1} seawater.

2.3. Assessing the effects of elevated nutrients and pCO_2 on *S. latissima*

To quantify the effects of elevated pCO_2 and/or nutrients on the growth of *S. latissima*, 2 experiments were performed. In the first experiment (designated as 'Co-effects of pCO_2 and nutrients'; Table 2), the goal was to assess how high and low pCO_2 and nutrients altered the growth rates of *S. latissima*. Estuaries are dynamic environments where levels of nutrients and pCO_2 vary in time and space (Wallace et al. 2014, R. B. Wallace et al. unpubl. data). Given prior studies (Olischläger et al. 2012, Zhang et al. 2020), we hypothesized that elevated pCO_2 would increase *S. latissima* growth, but that ele-

Table 1. Mean (±SD) pH (total scale), temperature (°C), salinity (g kg^{-1}), pCO_2 (µatm), total dissolved inorganic carbon (DIC; µmol kg^{-1} seawater [SW]), total alkalinity (TA; µmol kg^{-1} SW), and HCO_3^- (µmol kg^{-1} SW), and the saturation states of aragonite and calcite (Ω_{arag} and Ω_{calc}, respectively) for all experiments

Experiment	pCO_2 level	pH	Temp.	Salinity	pCO_2	Total DIC	TA	HCO_3^-	Ω_{arag}	Ω_{calc}
Co-effectsof pCO_2 and nutrients	Ambient	7.98 ± 0.04	14.9 ± 0.7	28.4 ± 0.4	377 ± 11	1710 ± 66	1857 ± 74	1591 ± 59	1.65 ± 0.11	2.61 ± 0.17
	Elevated	7.31 ± 0.03	15.1 ± 0.5	28.4 ± 0.4	2053 ± 132	1877 ± 12	1836 ± 15	1775 ± 12	0.38 ± 0.02	0.60 ± 0.04
pCO_2 dose response	Ambient	7.89 ± 0.01	20.3 ± 0.4	28.7 ± 0.9	479 ± 9	1961 ± 5	2084 ± 3	1844 ± 6	1.48 ± 0.02	2.34 ± 0.03
	Low	7.69 ± 0.02	20.3 ± 0.4	28.0 ± 0.4	802 ± 2	2057 ± 41	2122 ± 45	1957 ± 38	1.01 ± 0.04	1.60 ± 0.06
	Medium	7.50 ± 0.04	20.2 ± 0.4	27.8 ± 0.1	1232 ± 6	2061 ± 7	2073 ± 6	1965 ± 7	0.66 ± 0.00	1.05 ± 0.01
	High	7.27 ± 0.05	20.2 ± 0.4	30.3 ± 1.5	2338 ± 3	2118 ± 3	2051 ± 3	1994 ± 3	0.35 ± 0.00	0.56 ± 0.00
Effects of high and low pCO_2 on herbivory	Ambient	7.90 ± 0.03	14.4 ± 1.0	29.0 ± 0.0	425 ± 11	1729 ± 16	1866 ± 14	1614 ± 16	1.57 ± 0.01	2.47 ± 0.02
	Elevated	7.30 ± 0.04	14.4 ± 0.9	29.0 ± 0.0	1884 ± 191	1958 ± 51	1933 ± 65	1857 ± 53	0.47 ± 0.07	0.75 ± 0.12
Direct vs. indirect effects of elevated pCO_2 on herbivory	Ambient	7.95 ± 0.05	15.5 ± 1.7	29.3 ± 0.4	453 ± 9	1831 ± 64	1985 ± 68	1702 ± 59	1.80 ± 0.08	2.82 ± 0.12
	Elevated	7.41 ± 0.05	15.5 ± 1.7	29.3 ± 0.4	1808 ± 28	1921 ± 3	1908 ± 6	1824 ± 3	0.52 ± 0.01	0.82 ± 0.02
Co-effects of elevatedpCO_2 and food restriction on herbivory	Ambient	8.00 ± 0.04	16.0 ± 0.7	30.0 ± 0.3	459 ± 25	1939 ± 71	2086 ± 70	1811 ± 68	1.72 ± 0.03	2.72 ± 0.05
	Elevated	7.28 ± 0.03	15.8 ± 0.7	29.9 ± 0.1	2035 ± 33	1856 ± 0	1814 ± 2	1753 ± 1	0.37 ± 0.01	0.58 ± 0.01
Effective minimum exposure duration	Ambient	7.87 ± 0.05	19.7 ± 0.3	29.1 ± 0.1	453 ± 8	1906 ± 2	2084 ± 6	1759 ± 0	2.10 ± 0.04	3.28 ± 0.06
	Elevated	7.24 ± 0.03	19.3 ± 0.3	29.9 ± 0.1	2843 ± 5	1934 ± 4	1874 ± 4	1816 ± 4	0.36 ± 0.00	0.56 ± 0.00
Effective minimum dose	Ambient	7.92 ± 0.01	20.3 ± 0.1	27.8 ± 0.2	451 ± 6	1701 ± 3	1848 ± 5	1579 ± 2	1.73 ± 0.02	2.70 ± 0.04
	Low	7.70 ± 0.02	20.4 ± 0.1	27.7 ± 0.0	830 ± 1	1745 ± 2	1814 ± 2	1653 ± 2	1.03 ± 0.01	1.61 ± 0.00
	Medium	7.46 ± 0.03	20.4 ± 0.1	27.4 ± 0.3	1418 ± 74	1807 ± 9	1820 ± 5	1719 ± 8	0.65 ± 0.02	1.02 ± 0.04
	High	7.21 ± 0.05	20.4 ± 0.1	28.8 ± 1.0	2453 ± 79	2044 ± 42	2007 ± 41	1933 ± 39	0.48 ± 0.01	0.75 ± 0.01

Table 2. List of experiments with their respective incubation or starvation and grazing periods, and conditions

Experiment	Incubation period (d)		Figure no.	Experimental conditions
Co-effects of pCO_2 and nutrients	7		1	*Saccharina latissima* incubated under ambient or elevated pCO_2 with and without nutrient additions
pCO_2 dose response	14		2	*S. latissima* incubated under treatment pCO_2 levels with elevated nutrients
	Starvation period (h)	Grazing period (h)		
Effects of high and low pCO_2 on herbivory	24	48	4	*Lacuna vincta* starved and grazed under ambient or elevated pCO_2 on *S. latissima* that was grown at ambient pCO_2 levels
Direct vs. indirect effects of elevated pCO_2 on herbivory	24	96	5	*L. vincta* starved under ambient or elevated pCO_2; half of snails from each group grazed under ambient and elevated pCO_2 on *S. latissima* that was pre-incubated for ~1 wk under ambient or elevated pCO_2
Co-effects of elevated pCO_2 and food restriction on herbivory	24	24	6	*L. vincta* starved or fed under ambient or elevated pCO_2 for 24 h and then grazed on *S. latissima* that was grown at ambient pCO_2 levels
Effective minimum exposure duration	24	24	7	*L. vincta* starved under elevated pCO_2 for 0, 6, 12, 18, or 24 h before grazing on *S. latissima* that was grown at ambient pCO_2 levels
Effective minimum dose	24	24	8	*L. vincta* starved and grazed on *S. latissima* under a range of pCO_2 levels. *S. latissima* was grown at ambient pCO_2 levels prior to the experiment

vated nutrients might be inhibitory (Connell et al. 2008). *S. latissima* was placed in 1 of 4 treatments established in quadruplicate (for this and all experiments): a control with ambient pCO_2 levels (350–450 µatm) and no nutrient additions, a treatment with ambient pCO_2 and nutrient additions (50 µM nitrate, 3 µM phosphate), a treatment with elevated pCO_2 levels (~1800–2100 µatm) and no nutrient additions, and a treatment with elevated pCO_2 and nutrient additions. For this experiment, *S. latissima* samples were incubated under these conditions for 7 d. The elevated nutrients and pCO_2 concentrations were higher than levels present at the collection site (0–10 µM nitrate, 0–1 µM phosphate, 400–800 µM pCO_2), but consistent with concentrations present in some US East Coast estuaries, including those in the nearby New York region during winter and spring (Gobler et al. 2006, Wallace et al. 2014). For example, total dissolved nitrogen concentrations exceeding 50 µM have been reported in Quantuck Bay (Gobler et al. 2011), the estuary contiguous with and 10 km from the *S. latissima* collection site, and pCO_2 levels in the range of 1000–3000 µatm have recently been reported for Shinnecock Bay and the Peconic Estuary (Wallace et al. unpubl. data), systems contiguous with the *S. latissima* collection site. Given the ability of future ocean acidification to synergistically depress pH values when coupled with eutrophication-driven acidification (Sunda & Cai 2012), we expect future climate change scenarios to increase regional pCO_2 concentrations to levels higher than presently observed.

For the second experiment ('pCO_2 dose response'; Table 2), the goal was to identify the minimum level of pCO_2 needed to yield enhanced growth rates considering the levels currently present in regional estuaries (Wallace et al. 2014, Wallace et al. unpubl. data) and levels that may be present in the coming centuries due to climate change (IPCC 2014). We hypothesized that, like other carbon-limited autotrophs (Raven et al. 2020), growth rates would increase linearly with increasing levels of pCO_2. *S. latissima* samples were placed in 1 of 4 treatments: a control with ambient pCO_2 (350–450 µatm), a treatment with 750–850 µatm pCO_2, a treatment with 1200–1500 µatm pCO_2, and a treatment with 1800–2100 µatm pCO_2. While the higher pCO_2 levels used in this and the prior experiment exceed 21st century climate change projections, they capture the range of levels observed in coastal ecosystems influenced by eutrophication (Wallace et

al. 2014), upwelling (Feely et al. 2008), macrophyte respiration (Wahl et al. 2018), or riverine discharge (Vargas et al. 2016). Each treatment was supplied with nutrients (50 µM nitrate, 3 µM phosphate), and *S. latissima* samples were incubated for ~2 wk. At the end of the incubation periods for this and the first experiment, samples were removed from their respective treatments, weighed as described above, and final length and width measurements were made. Weight-based growth rates were determined by the following formula:

$$\text{mg d}^{-1} = \frac{(W_{\text{final}} + W_{\text{initial}}) \times 1000}{\Delta t} \quad (1)$$

where W_{final} and W_{initial} are the final and initial fresh weights, in grams, and Δt is the duration of the experiment in days.

2.4. Herbivory by *L. vincta* on *S. latissima*

Five herbivory experiments were performed, the first of which (designated as 'Effects of high and low pCO_2 on herbivory') gauged the herbivory rates of *L. vincta* feeding on *S. latissima* under ambient (350–400 µatm) and elevated (1800–2100 µatm) pCO_2 levels (Table 2). We hypothesized that *L. vincta* herbivory rates would be lower under higher pCO_2 levels (Young et al. 2019). *L. vincta* were placed in ambient or elevated pCO_2 conditions without *S. latissima* and starved for 24 h and then placed into containers with *S. latissima* (never exposed to elevated pCO_2) under ambient or elevated pCO_2 for 48 h. At the end of the grazing period, *L. vincta* and *S. latissima* were removed from the containers and *S. latissima* samples were weighed as described above. Herbivory rates were calculated by obtaining the difference in the initial and final corrected weights divided by the number of grazers and the elapsed time of the grazing period and multiplied by 1000 to convert weights to mg (mg grazer^{-1} d^{-1}). Final weights were corrected using residual growth of the additional *S. latissima* samples grown without *L. vincta* (see above).

The next experiment ('Direct vs indirect effects of elevated pCO_2 on herbivory'; Table 2) was performed to determine if lowered herbivory rates of *L. vincta* under high pCO_2 were caused by direct effects on *L. vincta* or indirectly by altering the palatability of *S. latissima*. Given prior studies of this snail, we hypothesized that *L. vincta* herbivory rates would be lowered due to direct exposure to high pCO_2 levels and not due to exposure of *S. latissima* to high pCO_2 (Young et al. 2019). *L. vincta* were starved under ambient (350–450 µatm) or elevated (1800–2100 µatm) pCO_2 levels and feed *S. latissima* incubated under either ambient or elevated pCO_2, with the intent of placing one-half of the *L. vincta* from each pCO_2 group in either the pCO_2 level they were starved in or the opposite pCO_2 group. For this experiment, *S. latissima* was incubated for ~1 wk under ambient or elevated pCO_2; on the final day of the incubation period, *L. vincta* were starved in separate vessels under ambient or elevated pCO_2 without *S. latissima* for 24 h. At the end of the 1 wk *S. latissima* incubation period and concurrent 24 h *L. vincta* starvation period, the lights of the environmental chamber were turned off, and *L. vincta* were introduced into the vessels containing *S. latissima* for a total of 4 treatments: a control with ambient pCO_2 containing *L. vincta* starved under ambient pCO_2 and allowed to graze on *S. latissima* incubated under ambient pCO_2, a treatment with elevated pCO_2 containing *L. vincta* starved under ambient pCO_2 and allowed to graze on *S. latissima* incubated under elevated pCO_2, a treatment with ambient pCO_2 containing *L. vincta* starved under elevated pCO_2 and allowed to graze on *S. latissima* incubated under ambient pCO_2, and a treatment with elevated pCO_2 containing *L. vincta* starved under elevated pCO_2 and allowed to graze on *S. latissima* incubated under elevated pCO_2. Once in their respective containers, *L. vincta* were allowed to graze for 96 h, with *S. latissima* samples being replaced every 24 h with the same source of *S. latissima* (high or ambient pCO_2 exposure). At the end of each 24 h grazing period, *S. latissima* samples were removed from the containers and were weighed as described above and herbivory was calculated.

Given that the effects of acidification on invertebrates can depend on food supply (Melzner et al. 2011, Thomsen et al. 2013, Pansch et al. 2014), for the next experiment ('Co-effects of elevated pCO_2 and food restriction on herbivory'; Table 2), herbivory rates of *L. vincta* were quantified on individuals that were either starved or fed under ambient (350–450 µatm) or elevated pCO_2 (1800–2100 µatm) for 24 h. Given prior studies, we hypothesized that *L. vincta* exposure to high pCO_2 during the starvation period would yield lowered herbivory rates while exposure during the grazing period would not (Young et al. 2019). There were 4 treatments: starved under ambient pCO_2, fed at ambient pCO_2, starved under high pCO_2, or fed at high pCO_2. After 24 h, fresh *S. latissima* blade portions were placed in the containers and *L. vincta* were allowed to graze for 24 h. At the end of the grazing periods, *L. vincta* and *S. latissima* were removed from the containers and

S. latissima samples were weighed as described above and herbivory was calculated.

The final experiments were performed to determine how the intensity and duration of CO_2 exposure altered herbivory of *L. vincta* grazing on *S. latissima*. These experiments specifically assessed the effective minimum duration of elevated pCO_2 required to alter herbivory rates ('Effective minimum exposure duration'; Table 2) and the effective minimum concentration of pCO_2 to alter herbivory rates of *L. vincta* ('Effective minimum dose'; Table 2). Given that pCO_2 concentrations can vary diurnally within shallow estuaries (Baumann et al. 2015) and that even short-term exposure to acidification can disrupt herbivory (Young et al. 2019), the 'effective minimum exposure duration' experiment was designed to identify the minimum duration exposure needed to disrupt herbivory in *L. vincta*. We hypothesized that exposure to high pCO_2 for less than 24 h would still lower grazing rates (Young et al. 2019). There were 5 treatments in this experiment: a control with ambient pCO_2 (350–450 µatm) during the 24 h starvation period (no dose), a treatment with elevated pCO_2 (1800–2100 µatm) during the entire 24 h starvation period, and treatments with 6, 12, and 18 h of exposure to elevated pCO_2 during the starvation period with 18, 12, and 6 h, respectively, of ambient pCO_2 exposure prior to exposure to elevated pCO_2. At the end of the starvation period, *L. vincta* were placed in containers with ambient pCO_2 levels, *S. latissima* samples were introduced, and *L. vincta* were allowed to graze for 24 h, after which herbivory rates were calculated. Given that pCO_2 levels can be dynamic in estuaries (Wallace et al. 2014) and that levels of pCO_2 are expected to more than double this century, the 'effective minimum dose' experiment was conducted to assess how levels of pCO_2 found in estuaries today (Wallace et al. 2014) as well as those projected for the future in less impacted regions (IPCC 2014) affect herbivory by *L. vincta.* Given prior studies with *L. vincta*, we hypothesized that moderately elevated (>1500 µatm) concentrations of pCO_2 would significantly lower herbivory rates (Young et al. 2019). This experiment established 4 treatments: a control with ambient pCO_2 (350–450 µatm), a treatment with slightly elevated pCO_2 (750–850 µatm), a treatment with moderately elevated pCO_2 (1200–1500 µatm), and a treatment with high pCO_2 (1800–2100 µatm). During this experiment, *L. vincta* were placed in 1 of the 4 treatments and starved for 24 h. At the end of the starvation period, *S. latissima* samples were introduced, and *L. vincta* were allowed to graze for 24 h at their respective pCO_2 levels. At the end of the grazing period, *L. vincta* and *S. latissima* were removed from the containers and *S. latissima* samples were weighed as described above and herbivory was calculated.

2.5. Post-experimental analyses

For carbon (C) and nitrogen (N) analyses of *S. latissima*, frozen samples were dried at 60°C for 24 h, and then homogenized into a fine powder with a mortar and pestle. Tissue C, 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. The measured $\delta^{13}C$ levels of the CO_2 gas (–80‰) used in experiments and isotopic mixing models (Young & Gobler 2016, 2017) were used to identify the relative use of CO_2 and HCO_3^- by *S. latissima*.

Net algal growth rates were calculated using growth rates and total herbivory rates from the 'pCO_2 dose response' and 'effective minimum dose' experiments, respectively. The herbivory rates for each replicate in each pCO_2 treatment in the 'effective minimum dose' experiment were calculated by subtracting the final *S. latissima* fresh weight from the initial fresh weight. We note that the *S. latissima* in this herbivory experiment were all raised at ambient pCO_2. The mean total herbivory rate for each pCO_2 treatment was subtracted from the *S. latissima* growth rates in the corresponding pCO_2 treatment in the 'pCO_2 dose response' experiment to obtain the net growth rate (growth minus herbivory) for 4 pCO_2 levels.

One-way ANOVAs were performed within SigmaPlot 11.0 to assess significant differences in herbivory rates in the 'pCO_2 dose response', 'effects of high and low pCO_2 on herbivory', 'effective minimum exposure duration', and 'effective minimum dose' experiments (n = 4 treatment^{-1} for each experiment). Two-way ANOVAs were performed with SigmaPlot to assess herbivory rates in the 'co-effects of pCO_2 and nutrients', 'direct vs. indirect effects of elevated pCO_2 on herbivory', and 'co-effects of elevated pCO_2 and food restriction on herbivory' experiments (n = 4 treatment^{-1} for each experiment), where the main treatment effects were pCO_2 and nutrient levels (ambient or elevated for both) for the 'co-effects of pCO_2 and nutrients' experiment, pCO_2 level for the *S. latissima* incubation and *L. vincta* starvation periods (ambient and elevated for both) for the 'direct vs. indirect effects of elevated pCO_2 on herbivory' experiment, and pCO_2 level (ambient or elevated) and starvation (starved or not starved) for the 'co-effects of elevated

pCO_2 and food restriction on herbivory' experiment. Normality and equal variance were tested via the use of Shapiro-Wilk and Leven tests within SigmaPlot 11.0; assumptions of equal variance and normality were met for all data. For all experiments, if significant differences were detected, a Tukey's HSD test using R v.3.4.0 within RStudio v.1.0.143 was performed (R Core Team 2020, RStudio Team 2020).

3. RESULTS

3.1. Effects of elevated pCO_2 and nutrients on *Saccharina latissima* growth rates

In the 'co-effects of pCO_2 and nutrients' experiment, growth rates of *Saccharina latissima* were significantly higher in elevated than in ambient pCO_2 by ~70% (2-way ANOVA and Tukey's HSD, $p < 0.05$; Fig. 1, Tables S1 & S2 in the Supplement). Furthermore, growth rates were significantly higher by ~50% under elevated nutrient conditions relative to treatments that did not receive nutrient additions (2-way ANOVA and Tukey's HSD, $p < 0.05$; Fig. 1, Tables S1 & S2), and there was no interaction between nutrient additions and pCO_2 levels (Fig. 1).

For the 'pCO_2 dose response' experiment, growth rates in the ~1200 and ~2300 µatm pCO_2 treatments were double the ambient (~500 µatm) pCO_2 treatment (1-way ANOVA and Tukey's HSD, $p < 0.05$ for both; Fig. 2, Tables S3 & S4) but were not different from each other. While growth rates were 45% higher in the 800 µatm pCO_2 treatment relative to the ambient treatment, the difference was not statistically different

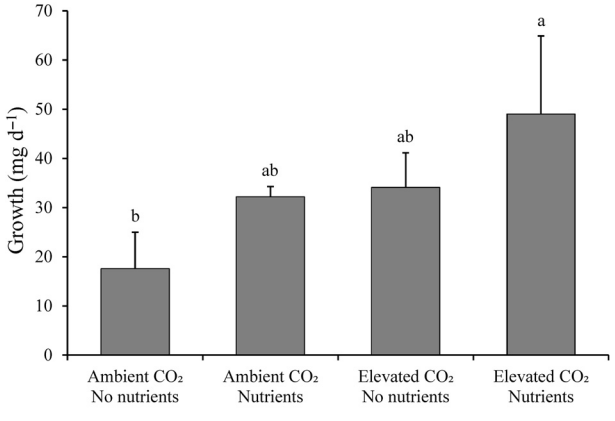

Fig. 1. Mean (SD) growth rates of *Saccharina latissima* under ambient and elevated pCO_2 levels with nutrient additions ('Co-effects of pCO_2 and nutrients'; Table 2). Statistical analyses: 2-way ANOVA and post hoc Tukey's HSD tests (n = 4 for all treatments); significant differences ($p < 0.05$) between treatments are indicated by letters

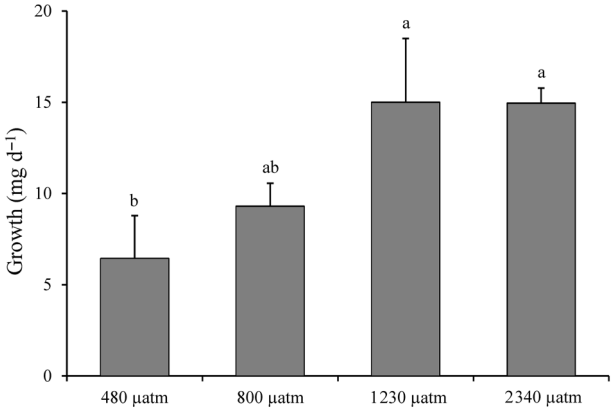

Fig. 2. Mean (SD) growth rates of *Saccharina latissima* grown under treatment pCO_2 levels with nutrient additions ('pCO_2 dose response'; Table 2). Statistical analyses: 2-way ANOVA and post hoc Tukey's HSD tests (n = 4 for all treatments); significant differences ($p < 0.05$) between treatments indicated by letters

(1-way ANOVA and Tukey's HSD, $p > 0.05$; Fig. 2, Tables S3 & S4). Further, there was no difference in growth between the 800, ~1200, and ~2300 µatm pCO_2 treatments (1-way ANOVA and Tukey's HSD, $p > 0.05$ for both; Fig. 2, Tables S3 & S4).

3.2. *S. latissima* tissue analyses

During the 'co-effects of pCO_2 and nutrients' experiment, tissue $\delta^{13}C$ was significantly lower under elevated pCO_2 (–29‰) relative to ambient conditions (–16‰) (2-way ANOVA and Tukey's HSD, $p < 0.05$; Fig. 3, Tables S5 & S6), while nutrients did not significantly alter $\delta^{13}C$ (2-way ANOVA, $p > 0.05$; Fig. 3, Tables S5 & S6). The mixing model performed for this experiment showed the actual $\delta^{13}C$ signatures following exposure to elevated pCO_2 (–27.9‰) to be similar to predicted $\delta^{13}C$ for exclusive uptake of CO_2 (–26.8‰) as opposed to exclusive HCO_3^- uptake (–16.3‰). In the 'pCO_2 dose response' experiment, the ~2300 µatm pCO_2 treatment had significantly lower tissue $\delta^{13}C$ (–22‰) than in the ~500 and ~800 µatm pCO_2 treatments (–18 and –19‰, respectively) (2-way ANOVA and Tukey's HSD, $p < 0.05$ for both; Fig. 3, Tables S5 & S6). While tissue $\delta^{13}C$ in the ~1200 µatm pCO_2 treatment (–21‰) was significantly lower than in the ~500 µatm pCO_2 treatment (2-way ANOVA and Tukey's HSD, $p < 0.05$; Fig. 3, Tables S5 & S6), there was no significant difference in $\delta^{13}C$ between the ~1200 and ~800 µatm pCO_2 treatments (2-way ANOVA and Tukey's HSD; $p > 0.05$; Fig. 3, Tables S5 & S6). There was no significant

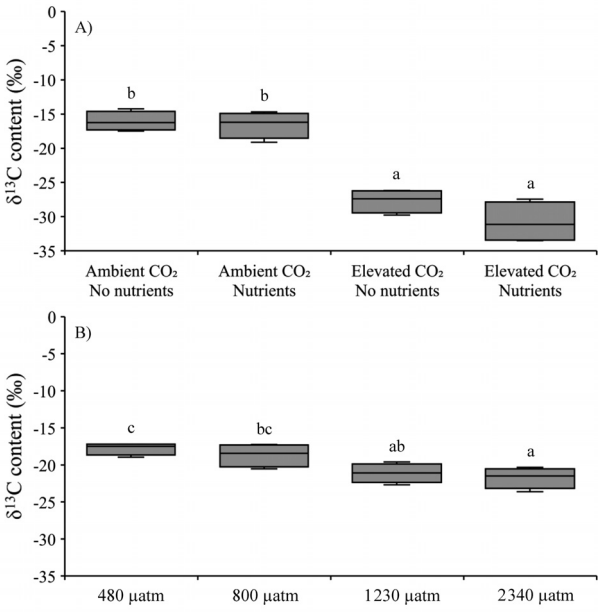

Fig. 3. Mean (±SD) tissue $\delta^{13}C$ content of *Saccharina latissima* grown under treatment pCO_2 levels with nutrient additions for the (A) 'Co-effects of pCO_2 and nutrients' and (B) 'pCO_2 dose response' experiments, respectively (Table 2). Statistical analyses: 2-way ANOVA and post hoc Tukey's HSD tests (n = 4 for all treatments); significant differences ($p < 0.05$) between treatments indicated by letters

difference in $\delta^{13}C$ between the ~500 and ~800 µatm pCO_2 treatments (2-way ANOVA and Tukey's HSD, $p > 0.05$; Fig. 3, Tables S5 & S6). Mixing models performed for the ~800, ~1200, and ~2300 µatm pCO_2 treatments showed the actual $\delta^{13}C$ signatures (–18.7, –21.6, and –22.2‰, respectively) of *S. latissima* shifted from being similar to predicted $\delta^{13}C$ signatures from exclusive HCO_3^- use (–15.8‰ for all) to predicted signatures from exclusive CO_2 use (–28.1, –27.6, and –25.2‰, respectively) as pCO_2 levels increased across treatments. There were no significant differences in tissue C, N, and C:N between any of the pCO_2 treatments (2-way ANOVA and Tukey's HSD, $p > 0.05$ for all; Table 3, Tables S7–S9).

3.3. Herbivory rates of *Lacuna vincta* grazing on *S. latissima*

During the 'effects of high and low pCO_2 on herbivory' experiment, which examined how high and low pCO_2 affected herbivory of *Lacuna vincta* that were fed *S. latissima*, grazing rates in the elevated pCO_2 treatment were significantly reduced by 60% relative to the ambient pCO_2 after 48 h (1-way ANOVA, $p < 0.05$; Fig. 4, Table S10). For the 'direct vs. indirect effects of elevated pCO_2 on herbivory' experiment, *L. vincta* herbivory rates were sensitive to pCO_2 levels during the starvation period, but not the pCO_2 conditions that *S. latissima* were incubated under (Fig. 5). Specifically, for the 24, 48, and 72 h timepoints, herbivory was significantly decreased by ~78, ~86, and ~94% when *Lacuna* were starved under elevated pCO_2 relative to ambient conditions (2-way ANOVA, $p < 0.05$ for all; Fig. 5, Table S11). In contrast, herbivory was not significantly altered by the pCO_2 conditions in which *S. latissima* were grown under throughout the experiment (2-way ANOVA, $p > 0.05$ for all; Fig. 5, Table S11). After 96 h, herbivory rates of *L. vincta* exposed to elevated pCO_2 recovered and were no longer affected by the pCO_2 levels it had been exposed to during the starvation period (2-way ANOVA, $p > 0.05$ for both; Fig. 5, Table S11).

In the 'co-effects of elevated pCO_2 and food restriction on herbivory' experiment, pCO_2 levels and being starved or fed prior to grazing was examined in a 2 × 2 experimental design. While herbivory rates of *L. vincta* on *S. latissima* during this experiment were not significantly affected by whether snails were starved under ambient pCO_2 (2-way ANOVA, $p > 0.05$; Fig. 6, Tables S12 & S13), exposure to elevated pCO_2 during the starvation period significantly depressed herbivory rates of starved snails (2-way ANOVA and Tukey's HSD, $p < 0.05$; Fig. 6, Tables S12 & S13). Within the elevated pCO_2 treatments, *L. vincta* that were starved had herbivory rates that were ~85% lower than individuals that were fed throughout experimentation (Tukey's HSD, $p < 0.05$; Fig. 6, Tables S12 & S13).

During the 'effective minimum exposure duration' experiment, exposure to elevated pCO_2 levels for 6

Table 3. Tissue carbon (mg C mg^{-1} dry tissue), nitrogen (mg N mg^{-1} dry tissue), and the molar carbon:nitrogen (C:N) ratios of *Saccharina latissima* grown under ambient or elevated pCO_2 with and without nutrient additions ('Co-effects of pCO_2 and nutrients') or under treatment pCO_2 levels with nutrient additions ('pCO_2 dose response'; Table 2)

Experiment	Treatment	Tissue C	Tissue N	C:N
Co-effects of pCO_2 and nutrients	Control	0.32 ± 0.01	0.0104 ± 0.0004	30.5 ± 2.4
	Nutrients	0.33 ± 0.01	0.0109 ± 0.0007	29.6 ± 2.4
	CO_2	0.33 ± 0.00	0.0098 ± 0.0005	33.7 ± 1.7
	CO_2/Nutrients	0.33 ± 0.02	0.0095 ± 0.0011	35.2 ± 4.8
pCO_2 dose response	Ambient pCO_2	0.33 ± 0.01	0.0160 ± 0.0032	21.4 ± 4.4
	Low pCO_2	0.33 ± 0.02	0.0160 ± 0.0036	21.6 ± 6.7
	Medium pCO_2	0.33 ± 0.02	0.0169 ± 0.0022	19.8 ± 4.0
	High pCO_2	0.34 ± 0.01	0.0148 ± 0.0018	22.9 ± 3.3

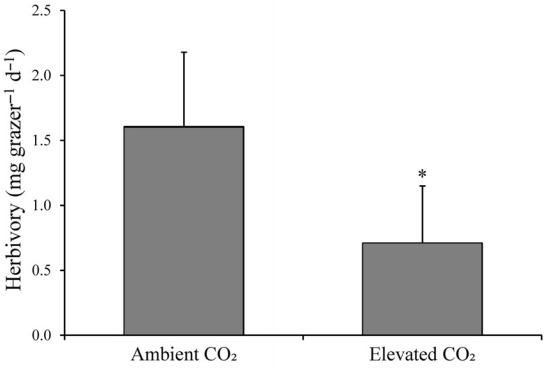

Fig. 4. Mean (SD) herbivory rates of *Lacuna vincta* starved and allowed to graze on *Saccharina latissima* under ambient and elevated pCO_2 levels for 48 h ('Effects of high and low pCO_2 on herbivory'; Table 2). Statistical analyses: 1-way ANOVA performed for the 48 h grazing period (n = 4 for all treatments); *p < 0.05

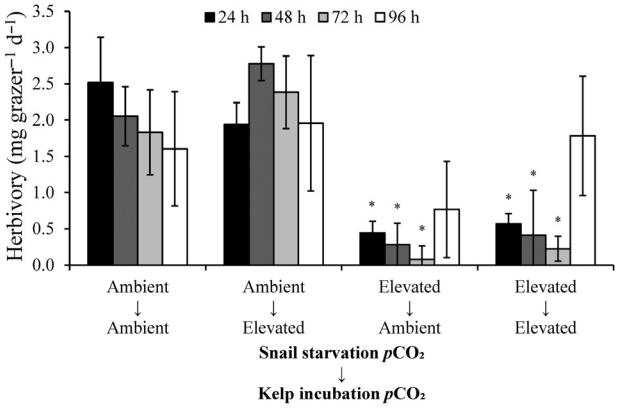

Fig. 5. Mean (±SD) herbivory rates of *Lacuna vincta* grazing on *Saccharina latissima* under ambient or elevated pCO_2 levels with *S. latissima* pre-incubated for 1 wk under ambient or elevated pCO_2 ('Direct vs. indirect effects of elevated pCO_2 on herbivory'; Table 2). Statistical analyses: 2-way ANOVA and post hoc Tukey's HSD tests performed for each 24 h grazing period (n = 4 for all treatments). *p < 0.05 between treatments for each 24 h grazing period relative to the control (ambient pCO_2 snail starvation → ambient pCO_2 kelp incubation)

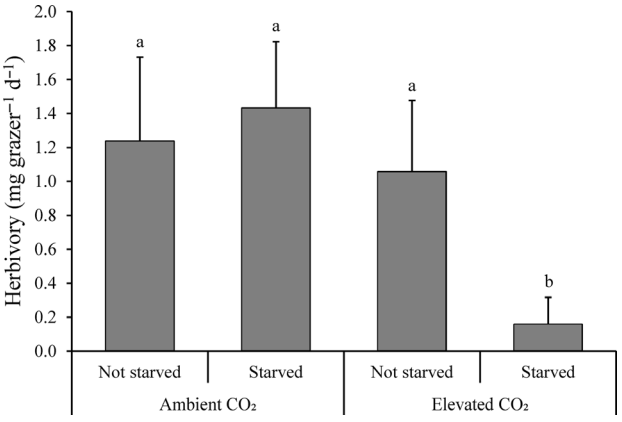

Fig. 6. Mean (SD) herbivory rates of *Lacuna vincta* either starved or not starved for 24 h under ambient or elevated pCO_2 levels and allowed to graze on *Saccharina latissima* for 24 h ('Co-effects of elevated pCO_2 and food restriction on herbivory'; Table 2). Statistical analyses: 2-way ANOVA and post hoc Tukey's HSD tests (n = 4 for all treatments); significant differences (p < 0.05) between treatments indicated by letters

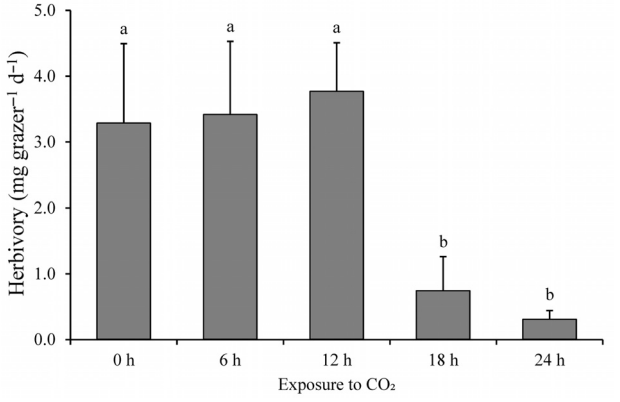

Fig. 7. Mean (SD) herbivory rates of *Lacuna vincta* starved for various lengths of time under ambient and elevated pCO_2 levels and allowed to graze on *Saccharina latissima* under ambient pCO_2 for 24 h ('Effective minimum exposure duration'; Table 2). Statistical analyses: 1-way ANOVA and post hoc Tukey's HSD tests (n = 4 for all treatments); significant differences (p < 0.05) between treatments indicated by letters

or 12 h did not alter herbivory rates compared to the control (1-way ANOVA and Tukey's HSD, p > 0.05 for all; Fig. 7, Tables S14 & S15) but 18 and 24 h exposure did, yielding rates significantly lower than the 0, 6, and 12 h exposure treatments (1-way ANOVA and Tukey's HSD, p < 0.05 for all; Fig. 7, Tables S14 & S15). There was no significant difference in herbivory between the 18 and 24 h exposure treatments (1-way ANOVA and Tukey's HSD, p < 0.05; Fig. 7, Tables S14 & S15).

Finally, during the 'effective minimum dose' experiment, pCO_2 concentrations reduced herbivory rates of *L. vincta* feeding on *S. latissima* in a dose-dependent manner. Herbivory rates within the ~830, ~1420, and ~2450 µatm pCO_2 treatments were all significantly lower than in the ambient (~450 µatm) $pCO2$ treatment (1-way ANOVA and Tukey's HSD, p < 0.05 for all; Fig. 8, Tables S16 & S17). While herbivory rates in the ~830 µatm pCO_2 treatment were significantly higher than in the ~1420 and ~2450 µatm pCO_2 treatments (1-way ANOVA and Tukey's HSD, p < 0.05 for both; Fig. 8, Tables S16 & S17), there was no significant difference in herbivory between the 1420 and 2450 µatm pCO_2 treatments (1-way ANOVA and Tukey's HSD, $p > 0.05$; Fig. 8, Tables S16 & S17).

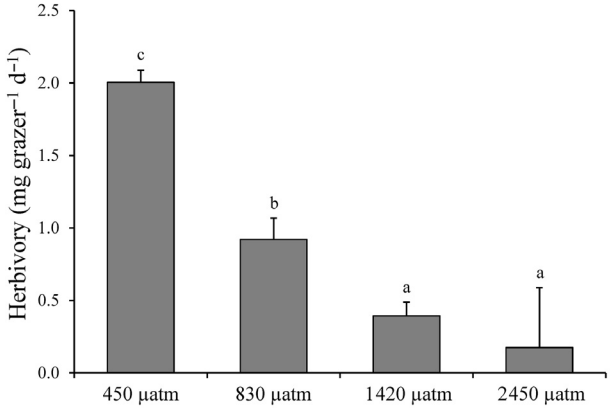

Fig. 8. Mean (SD) herbivory rates of *Lacuna vincta* starved for 24 h and allowed to graze on *Saccharina latissima* for 24 h under treatment pCO_2 levels ('Effective minimum dose'; Table 2). Statistical analyses: 1-way ANOVA and post hoc Tukey's HSD (n = 4 for all treatments); significant differences ($p < 0.05$) between treatments indicated by letters

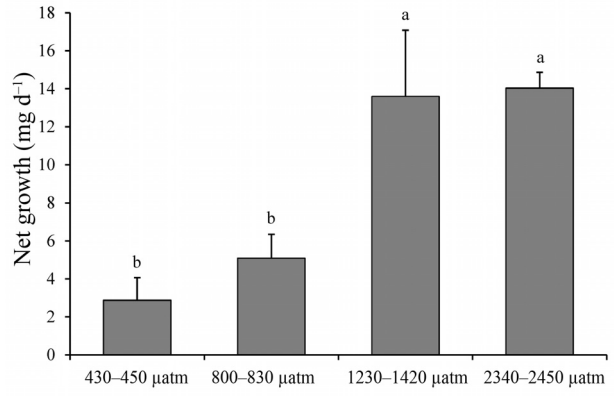

Fig. 9. Mean (SD) net growth rates of *Saccharina latissima* grown under treatment pCO_2 levels following grazing by *Lacuna vincta* under the same pCO_2 conditions. The net growth rates consider the growth rates of *S. latissima* and herbivory rates of *L. vincta* from the 'pCO_2 dose response' and 'Effective minimum dose' experiments, respectively (Table 2). Statistical analyses: 1-way ANOVA and post hoc Tukey's HSD tests (n = 4 for all treatments); significant differences ($p < 0.05$) between treatments indicated by letters

3.4. Net growth rates

Net growth rates of *S. latissima* (growth − grazing) were determined by considering growth under the range of pCO_2 levels in the 'pCO_2 dose response' experiment and herbivory rates of *L. vincta* grazing on *S. latissima* under approximately the same pCO_2 conditions in the 'effective minimum dose' experiment. Net growth rates increased as pCO_2 levels increased above 1200 µatm. At 1230–1420 and 2340–2450 µatm pCO_2 levels, net growth (~14 mg d^{-1}) was significantly higher than the ambient (3 mg d^{-1} at 430–450 µatm) and 800–830 µatm (5 mg d^{-1}) pCO_2 levels by more than 4- and 2-fold, respectively (1-way ANOVA and Tukey's HSD, $p < 0.05$ for all; Fig. 9, Tables S18 & S19). There were no significant differences in net growth between the 430–450 and 800–830 µatm pCO_2 treatments or between the 1230–1420 and 2340–2450 µatm pCO_2 treatments (1-way ANOVA and Tukey's HSD, $p > 0.05$ for all; Fig. 9, Tables S18 & S19).

4. DISCUSSION

Ocean acidification is restructuring the function of coastal ecosystems. Given the potential for elevated pCO_2 to promote the growth of some autotrophs and to negatively affect some calcifying organisms, interactions between herbivorous calcifiers and macroalgae may be significantly altered by ocean acidification. During the present study, growth rates of the ecologically and economically important kelp species *Saccharina latissima* were enhanced by elevated pCO_2 levels, while herbivory rates of *Lacuna vincta* grazing on *S. latissima* were reduced when exposed to elevated pCO_2 and deprived of food prior to exposure. This study demonstrates, to our knowledge for the first time, the ability of ocean acidification to benefit the growth of a macrophyte by concurrently altering both top-down (herbivory) and bottom-up (growth) processes.

During this study, *S. latissima* growth was significantly increased under elevated pCO_2, an outcome consistent with prior studies (Hepburn et al. 2011, Olischläger et al. 2012, Zhang et al. 2020). While these effects could have been temperature-dependent, our use of *in situ* temperatures from our study site did not allow for detection of such trends. The physiological response of macroalgae to elevated pCO_2 levels is largely dependent on its mode of carbon uptake and the extent to which its inorganic carbon uptake is substrate-saturated at current pCO_2 levels (Koch et al. 2013). When exposed to elevated pCO_2 levels, macroalgae may be relived of C limitation and/or may downregulate carbon-concentrating mechanisms that convert HCO_3^- to CO_2, allowing for more energy to be available for vegetative growth (Mercado et al. 1998, Koch et al. 2013). The tissue $\delta^{13}C$ content of macroalgae can indicate the form of inorganic carbon used for photosynthesis, with values of −10‰ indicative sole use of HCO_3^-, values of −10 to −30‰ indicative use of both HCO_3^- and CO_2, and values of −30‰ or lower representing sole use of

CO_2 (Maberly et al. 1992, Raven et al. 2002, Hepburn et al. 2011). In the present study, *S. latissima* had $\delta^{13}C$ signatures that ranged from −16 to −18‰ when exposed to normal conditions, suggesting it primarily, but not exclusively, uses HCO_3^- as a C source under ambient pCO_2 conditions (Maberly et al. 1992, Raven et al. 2002, Hepburn et al. 2011). Exposure to elevated pCO_2 significantly lowered $\delta^{13}C$ signatures (−18 to −29‰) of *S. latissima*, indicating that when exposed to higher pCO_2 levels, this alga obtained a larger fraction of its C from CO_2, an observation consistent with previous studies of stable carbon isotope discrimination of *S. latissima* and other laminarian kelp species (Maberly et al. 1992, Fernández et al. 2015). Furthermore, in the present study, growth rates increased under increasing pCO_2 levels up to ~1200 µatm, suggesting that *S. latissima* may become substrate-saturated at this concentration. While this level of pCO_2 is not predicted to occur in open ocean regions for more than a century, it can occur regularly in some coastal systems (Feely et al. 2008, Melzner et al. 2013, Wallace et al. 2014). Be it in the future or due to present day coastal processes, elevated pCO_2 levels may directly benefit the growth of laminarian kelp species such as *S. latissima*.

Nutrients also increased *S. latissima* growth rates, although there was no interaction with pCO_2 levels. Eutrophication can initiate phase shifts in coastal ecosystems whereby turf algae benefit from the overloading of nutrients and cover substrate onto which kelp may grow and recruit, causing declines in kelp forests (Eriksson et al. 2002, Gorgula & Connell 2004, Connell et al. 2008). However, kelps including *S. latissima* can grow robustly using aquaculture approaches in eutrophic ecosystems (Kim et al. 2015, Jiang et al. 2020), and the results shown here demonstrate that, without competition, elevated nutrients can benefit *S. latissima* via enhanced growth rates.

Beyond growth, herbivory on *S. latissima* also changed under elevated pCO_2. The effects of elevated pCO_2 and the absence of food on the herbivory rates of *L. vincta* are consistent with prior observations regarding the manner in which acidification alters herbivory by this gastropod grazing on the green alga, *Ulva* (Young et al. 2019). In the present study, herbivory by *L. vincta* on *S. latissima* was even more sensitive to acidification, with food limitation decreasing herbivory rates at 830 µatm, slightly lower than the level at which *L. vincta* grazing on *Ulva* was reduced (850 µatm; Young et al. 2019). Exposure to elevated pCO_2 levels may cause a state of acidosis that can disrupt metabolism and homeostatic function, thus diverting energy from critical functions such shell and somatic growth, shell repair, and gametogenesis (Lindinger et al. 1984, Pörtner et al. 1998, Hendriks et al. 2010). *L. vincta* exposed to elevated pCO_2 and starved display lower respiration rates (Young et al. 2019), a finding interpreted as metabolic depression within other marine gastropods during periods of food limitation (Maas et al. 2011). The ability of acidification alone to slow the metabolism of gastropods has also been previously reported (Hendriks et al. 2010, Melatunan et al. 2011), which may serve as a survival strategy to match lowered energy supply (Bishop & Brand 2000) and may result in an increased reliance on anaerobic respiration (Pörtner et al. 1998, Melatunan et al. 2011). Reductions in herbivory under elevated pCO_2 were not observed when *L. vincta* was fed ad libitum, however. Similarly, when provided with an adequate food source, some other calcifying organisms (Melzner et al. 2011, Thomsen et al. 2013, Pansch et al. 2014) and early life stage fish (Gobler et al. 2018) are resistant to acidification.

In an ecosystem setting, kelp beds may provide a refuge to grazers by simultaneously buffering carbonate chemistry and providing ample quantities of food. Previous studies have demonstrated the ability of macroalgae to buffer carbonate chemistry and promote the growth and survival of calcifying organisms (Wahl et al. 2018, Young & Gobler 2018). However, such a buffering effect can be species- and/or site-specific (Rivest et al. 2017). Daytime primary productivity within kelp beds has been shown to significantly reduce pCO_2 compared to outside the bed on diel and even seasonal timescales (Delille et al. 2000, 2009). Furthermore, vertical gradients in pCO_2 can also form in kelp canopies due to enhanced primary productivity in surface waters (Hofmann et al. 2011). The lower quantities of food and relatively higher levels of pCO_2 on the vertical or horizontal margins of the kelp beds may be the regions more likely to facilitate disruption of gastropod herbivory. Similarly, acidified regions with low-density kelp blades could similarly be disruptive to snail grazing. All these conditions would be exacerbated by nocturnal acidification (Wallace et al. 2014, Tomasetti & Gobler 2020).

While the pCO_2 levels in the present study are not expected for the open ocean for decades or centuries to come, eutrophication, upwelling, riverine discharge, and other coastal processes may result in the diurnal and/or seasonal accumulation of CO_2 in coastal zones that can produce the pCO_2 and nutrient levels shown here to accelerate the growth of, and reduce grazing on, *S. latissima* (Feely et al. 2008,

Melzner et al. 2013, Wallace et al. 2014). In the present study, 18 h of exposure to elevated pCO_2 in the absence of food suppressed *L. vincta* herbivory, with this effect persisting for 72 h. In an ecosystem context, *L. vincta* and other gastropods and grazers sensitive to elevated pCO_2 may be vulnerable to diurnal and seasonal shifts in pH and pCO_2. During nighttime and/or low tides, eutrophic estuaries can become strongly net heterotrophic and produce acidified conditions that can persist >18 h (Wallace et al. 2014, Baumann et al. 2015). These conditions are mostly likely to occur in temperate estuaries during the late summer, when microbial respiration rates accelerate acidification, and may persist into the fall (Wallace et al. 2014), which is the beginning of the growing season for numerous kelp species (Kim et al. 2015, Augyte et al. 2017). Aside from the diurnal and seasonal shifts in pCO_2, acidified conditions often co-occur with low oxygen conditions in estuaries (Tomasetti & Gobler 2020), and the combination of hypoxia and acidification has been shown to additively and synergistically disrupt grazing by *L vincta* (Young & Gobler 2020). Finally, the elevated nutrients associated with eutrophication may also affect herbivory rates by *L. vincta* and growth by *S. latissima*. Nutrient enrichment can reduce the abundance of common estuarine grazers, including *Lacuna*, due to potentially toxic concentrations of ammonia (Atalah & Crowe 2012). While eutrophication indirectly harms *S. latissima* via reduced light availability and overgrowth by epiphytic and filamentous algae (Moy & Christie 2012), the alga can directly benefit from the increased nutrient concentrations (Boderskov et al. 2016, this study) and the acidification wrought from eutrophication (this study).

Despite the potential benefits that ocean acidification may provide to some primary producers (Koch et al. 2013, Hattenrath-Lehmann et al. 2015, Young & Gobler 2016), grazing pressure by common herbivores, such as gastropods, may limit the extent of these benefits through top-down controls on growth (Baggini et al. 2015). Among the factors that limit kelp abundance, overgrazing is a major biotic driver of kelp loss via consumption of kelp blades, inhibition of new recruitment, and/or grazing damage causing blade breakage (Steneck et al. 2002, Molis et al. 2010, Filbee-Dexter & Wernberg 2018). As *L. vincta* is the primary mesograzer of *S. latissima* macroscopic kelp sporophytes in the Northwest Atlantic (Brady-Campbell et al. 1984, Johnson & Mann 1986), large population increases in the gastropod can consume significant quantities of kelp biomass, which can result in significant losses of kelp canopy biomass due to wave action (Krumhansl & Scheibling 2011). Studies have shown that *L. vincta* grazing of kelp can remove up to 10% of the total surface area of blades in natural settings (Molis et al. 2010, Krumhansl & Scheibling 2011) and larger amounts (>40%) in experimental settings (Chenelot & Konar 2007). In the present study, *L. vincta* displayed significantly reduced herbivory when exposed to elevated pCO_2 and prior food restriction, while *S. latissima* growth was significantly increased under elevated pCO_2. When considering the responses of *S. latissima* across a pCO_2 gradient, net growth rates increased more than 4-fold from under ambient pCO_2 to ~1200 µatm (Fig. 9). *L. vincta* had the potential to consume 70% *S. latissima* productivity per day under ambient pCO_2, but only 38 and 9% at 800 and 1300 µatm, respectively, meaning that as pCO_2 levels rise, *L. vincta*, and other gastropods that experience reduced herbivory rates under elevated pCO_2, may become incapable of controlling kelp proliferation.

Beyond growth and grazing, competition with other algae will also influence the fate of *S. latissima* populations in high-CO_2 environments (Young & Gobler 2017). During the last decade, turf-forming algae have begun to replace kelp beds in many ecosystems, primarily due to warming and eutrophication (Moy & Christie 2012, Filbee-Dexter & Wernberg 2018). In regions with naturally occurring high CO_2 conditions from volcanic vents, however, turf algal communities decline in diversity and abundance with decreasing pH and increasing pCO_2 (Porzio et al. 2011). Hence, beyond the ability of high pCO_2 to foster higher net growth rates in *S. latissima*, these conditions may also allow it to maintain dominance in regions where it may be competing with turf-forming algae, possibly off-setting losses associated with other anthropogenic processes.

Within the northwestern Atlantic, *L. vincta* can reproduce year-round on kelp in cooler climates (Maney & Ebersole 1990), with a distinctive peak in spawning during January and February (Johnson & Mann 1986), larval recruitment and hatching occurring thereafter, followed by a summer maxima (Southgate 1982). Within the same regions, kelp species such as *S. latissima* begin their growing season during the fall, grow rapidly in spring, and experience rapid decay and mortality during the summer as thermal thresholds are surpassed (Krumhansl & Scheibling 2011, Kim et al. 2015, Augyte et al. 2017). The emergence of marine gastropod grazers with the onset of the warmer summer weather accelerates the seasonal demise of kelp (Johnson & Mann 1986, Krumhansl & Scheibling 2011). As coastal waters sea-

sonally warm, accelerating rates of ecosystem metabolism can cause a supersaturation of pCO_2 (Wallace et al. 2014, Baumann et al. 2015) that may enhance the net growth rates of *S. latissima* and prolong the growing season of the kelp that might otherwise slow due to warmer temperatures and grazing (Wernberg et al. 2010, Filbee-Dexter et al. 2016). In the future, as climate change intensifies acidification, shortened growing seasons due to warming may be offset by increased net growth due to higher pCO_2. Future experiments should consider the interactive effects of temperature and pCO_2 on the growth of *S. latissima*.

5. CONCLUSIONS

Elevated levels of pCO_2 have a dual benefit for the kelp *Saccharina latissima*. The net growth rates of *S. latissima* at higher pCO_2 (>1200 µatm) exceeded those at ambient pCO_2 by 4-fold due to both accelerated growth by *S. latissima* and suppressed herbivory by the gastropod *Lacuna vincta*. The pCO_2 conditions that elicited reduced herbivory (~830 µatm) and enhanced kelp growth (~1200 µatm pCO_2) are seasonally found in many estuaries today and will become more common in the future as climate change accelerates. Eutrophication associated with coastal acidification may benefit *S. latissima* directly through nutrient- and CO_2-enhanced growth rates and may further reduce herbivore grazing due to hypoxia and/or high ammonia levels. Since only 18 h of acidification suppressed herbivory by *L. vincta*, nocturnal acidification associated with eutrophication (Wallace et al. 2014) may further suppress herbivore grazing. While *S. latissima* may buffer carbonate chemistry to the benefit of calcifying organisms such as *L. vincta*, these benefits may only be realized in the center of dense kelp beds as opposed to horizontal and vertical margins where acidification and gastropod starvation may become more common. Lastly, given that turf-forming algae may not directly benefit from increased pCO_2, the combination of increased growth and suppressed herbivory experienced by *S. latissima* may allow the alga to maintain dominance facilitated by high-CO_2 conditions.

Acknowledgements. We thank Brooke Morrell and Marissa Velasquez for their efforts in growing and collecting the *Saccharina latissima* used in the present study, and Andrew Lundstrom for assistance with the analysis of samples for DIC. We thank Paul McCormick at the Great Gun Shellfish Farm in Moriches Bay for use of his farm and assistance in cultivating kelp used in these experiments. We are appreciative of the logistic support provided by the Stony Brook Southampton Marine Science Center staff throughout this study. This work was supported by funding from The Chicago Community Trust, the New York Farm Viability Institute, and New York Sea Grant (R-FBM-38).

LITERATURE CITED

Atalah J, Crowe TP (2012) Nutrient enrichment and variation in community structure on rocky shores: the potential of molluscan assemblages for biomonitoring. Estuar Coast Shelf Sci 99:162–170

Augyte S, Yarish C, Redmond S, Kim JK (2017) Cultivation of a morphologically distinct strain of the sugar kelp, *Saccharina latissima* forma *angustissima*, from coastal Maine, USA, with implications for ecosystems services. J Appl Phycol 29:1967–1976

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

Baumann H, Wallace RB, Tagliaferri T, Gobler CJ (2015) Large natural pH, CO_2 and O_2 fluctuations in a temperate tidal salt marsh on diel, seasonal, and interannual time scales. Estuaries Coasts 38:220–231

Bishop T, Brand MD (2000) Processes contributing to metabolic depression in hepatopancreas cells from the snail *Helix aspersa*. J Exp Biol 203:3603–3612

Boderskov T, Schmedes PS, Bruhn A, Rasmussen MB, Nielsen MM, Pedersen MF (2016) The effect of light and nutrient availability on growth, nitrogen, and pigment contents of *Saccharina latissima* (Phaeophyceae) grown in outdoor tanks, under natural variation of sunlight and temperature, during autumn and early winter in Denmark. J Appl Phycol 28:1153–1165

Brady-Campbell MM, Campbell DB, Harlin MM (1984) Productivity of kelp (*Laminaria* spp.) near the southern limit in the Northwestern Atlantic Ocean. Mar Ecol Prog Ser 18:79–88

Brinkhuis BH, Breda VA, Tobin S, Macler BA (1983) New York marine biomass program-culture of *Laminaria saccharina*. J World Maric Soc 14:360–379

Chavanich S, Harris LG (2002) The influence of macroalgae on seasonal abundance and feeding preference of a subtidal snail, *Lacuna vincta* (Montagu) (Littorinidae) in the Gulf of Maine. J Molluscan Stud 68:73–78

Chenelot H, Konar B (2007) *Lacuna vincta* (Mollusca, Neotaenioglossa) herbivory on juvenile and adult *Nereocystis luetkeana* (Heterokontophyta, Laminariales). Hydrobiologia 583:107–118

Chung IK, Oak JH, Lee JA, Shin JA, Kim JG, Park KS (2013) Installing kelp forests/seaweed beds for mitigation and adaptation against global warming: Korean project overview. ICES J Mar Sci 70:1038–1044

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 277:1409–1415

Connell SD, Russell BD, Turner DJ, Shepherd SA and others (2008) Recovering a lost baseline: missing kelp forests from a metropolitan coast. Mar Ecol Prog Ser 360:63–72

Delille B, Delille D, Fiala M, Prevost C, Frankignoulle M (2000) Seasonal changes of pCO_2 over a subantarctic *Macrocystis* kelp bed. Polar Biol 23:706–716

Delille B, Borges AV, Delille D (2009) Influence of giant kelp beds (*Macrocystis pyrifera*) on diel cycles of pCO_2 and

DIC in the sub-Antarctic coastal area. Estuar Coast Shelf Sci 81:114–122

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO_2 problem. Annu Rev Mar Sci 1:169–192

Dubois A, Iken K (2012) Seasonal variation in kelp phlorotannins in relation to grazer abundance and environmental variables in the Alaskan sublittoral zone. Algae 27:9–19

Duffy E, Stachowicz J, Hovel K, Reynolds P (2014) *Zostera* experimental network handbook, v1. Smithsonian Environmental Research Center, Edgewater, MD

Eriksson BK, Johansson G, Snoeijs P (2002) Long-term changes in the macroalgal vegetation of the inner Gullmar Fjord, Swedish Skagerrak coast. J Phycol 38:284–296

Feely RA, Sabine CL, Hernandez-Ayon JM, Ianson D, Hales B (2008) Evidence for upwelling of corrosive 'acidified' water onto the continental shelf. Science 320:1490–1492

Feely RA, Doney SC, Cooley SR (2009) Ocean acidification: present conditions and future changes in a high-CO_2 world. Oceanography (Wash DC) 22:36–47

Fernández PA, Roleda MY, Hurd CL (2015) Effects of ocean acidification on the photosynthetic performance, carbonic anhydrase activity and growth of the giant kelp *Macrocystis pyrifera*. Photosynth Res 124:293–304

Filbee-Dexter K, Wernberg T (2018) Rise of turfs: a new battlefront for globally declining kelp forests. Bioscience 68: 64–76

Filbee-Dexter K, Feehan CJ, Scheibling RE (2016) Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. Mar Ecol Prog Ser 543:141–152

Gobler CJ, Buck NJ, Sieracki ME, Sañudo-Wilhelmy SA (2006) Nitrogen and silicon limitation of phytoplankton communities across an urban estuary: the East River–Long Island Sound system. Estuar Coast Shelf Sci 68: 127–138

Gobler CJ, Berry DL, Dyhrman ST, Wilhelm SW and others (2011) Niche of harmful alga *Aureococcus anophagefferens* revealed through ecogenomics. Proc Natl Acad Sci USA 108:4352–4357

Gobler CJ, Merlo LR, Morell BK, Griffith AW (2018) Temperature, acidification, and food supply interact to negatively affect the growth and survival of the forage fish, *Menidia beryllina* (inland silverside) and *Cyprinodon variegatus* (sheepshed minnow). Front Mar Sci 5:86

Gorgula SK, Connell SD (2004) Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. Mar Biol 145:613–619

Hattenrath-Lehmann TK, Smith JL, Wallace RB, Merlo LR and others (2015) The effects of elevated CO_2 on the growth and toxicity of field populations and cultures of the saxitoxin-producing dinoflagellate, *Alexandrium fundyense.* Limnol Oceanogr 60:198–214

Hendriks IE, Duarte CM, Álvarez M (2010) Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. Estuar Coast Shelf Sci 86:157–164

Hepburn CD, Pritchard DW, Cornwall CE, McLeod RJ, Beardall J, Raven JA (2011) Diversity of carbon use strategies in a kelp forest community: implications for a high CO_2 ocean. Glob Change Biol 17:2488–2497

Hofmann GE, Smith JE, Johnson KS, Send U and others (2011) High-frequency dynamics of ocean pH: a multi-ecosystem comparison. PLOS ONE 6:e28983

IPCC (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II, and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva

Janiak DS, Whitlatch RB (2012) Epifaunal and algal assemblages associated with the native *Chondrus crispus* (Stackhouse) and the non-native *Grateloupia turuturu* (Yamada) in eastern Long Island Sound. J Exp Mar Biol Ecol 413:38–44

Jiang Z, Liu J, Li S, Chen Y and others (2020) Kelp cultivation effectively improves water quality and regulates phytoplankton community in a turbid, highly eutrophic bay. Sci Total Environ 707:135561

Johnson CR, Mann KH (1986) The importance of plant defence abilities to the structure of subtidal seaweed communities: the kelp *Lamanaria longicruris* de la Pylaie survives grazing by the snail *Lacuna vincta* (Montagu) at high population densities. J Exp Mar Biol Ecol 97:231–267

Johnson KM, Wills KD, Butler DB, Johnson WK, Wong CS (1993) Coulometric total carbon dioxide analysis for marine studies: maximizing the performance of an automated gas extraction system and coulometric detector. Mar Chem 44:167–187

Kim JK, Kraemer GP, Yarish C (2015) Use of sugar kelp aquaculture in Long Island Sound and the Bronx River Estuary for nutrient extraction. Mar Ecol Prog Ser 531: 155–166

Koch M, Bowes G, Ross C, Zhang XH (2013) Climate change and ocean acidification effects on seagrasses and marine macroalgae. Glob Change Biol 19:103–132

Krumhansl KA, Scheibling RE (2011) Spatial and temporal variation in grazing damage by the gastropod *Lacuna vincta* in Nova Scotian kelp beds. Aquat Biol 13:163–173

Lindinger MI, Lauren DJ, McDonald DG (1984) Acid–base balance in the sea mussel, *Mytilus edulis*. III. Effects of environmental hypercapnia on intra- and extracellular acid-base balance. Mar Biol Lett 5:371–381

Maas AE, Elder LE, Dierssen HM, Seibel BA (2011) Metabolic response of Antarctic pteropods (Mollusca: Gastropoda) to food deprivation and regional productivity. Mar Ecol Prog Ser 441:129–139

Maberly SC, Raven JA, Johnston AM (1992) Discrimination between ^{12}C and ^{13}C by marine plants. Oecologia 91: 481–492

Maney EJ, Ebersole JP (1990) Continuous reproduction and episodic recruitment of *Lacuna vincta* (Montagu, 1803) in the Gulf of Maine. Veliger 33:215–221

Marinho G, Holdt SL, Birkeland MJ, Angelidaki I (2015) Commercial cultivation and bioremediation potential of sugar kelp, *Saccharina latissima*, in Danish waters. J Appl Phycol 27:1963–1973

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

Melzner F, Stange P, Trübenbach K, Thomsen J and others (2011) Food supply and seawater pCO_2 impact calcification and internal shell dissolution in the blue mussel *Mytilus edulis.* PLOS ONE 6:e24223

Melzner F, Jörn T, Koeve W, Oschlies A and others (2013) Future ocean acidification will be amplified by hypoxia in coastal habitats. Mar Biol 160:1875–1888

Mercado JM, Gordillo FJL, Niella FX, Figueroa FL (1998) External carbonic anhydrase and affinity for inorganic carbon in intertidal macroalgae. J Exp Mar Biol Ecol 221: 209–220

Millero FJ (2010) History of the equation of state of seawater. Oceanography (Wash DC) 23:18–33
Molis M, Enge A, Karsten U (2010) Grazing impact of, and indirect interactions between mesograzers associated with kelp (*Laminaria digitata*). J Phycol 46:76–84
Moy FE, Christie H (2012) Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. Mar Biol Res 8:309–321
Nelson TA, Haberlin K, Nelson AV, Ribarich H and others (2008) Ecological and physiological controls of species composition in green macroalgal blooms. Ecology 89: 1287–1298
Norderhaug KM, Christie HC (2009) Sea urchin grazing and kelp re-vegetation in the NE Atlantic. Mar Biol Res 5: 515–528
Norderhaug KM, Christie H, Fosså JH, Fredriksen S (2005) Fish–macrofauna interactions in a kelp (*Laminaria hyperborea*) forest. J Mar Biol Assoc UK 85:1279–1286
O'Brien JM, Scheibling RE (2016) Nipped in the bud: mesograzer feeding preference contributes to kelp decline. Ecology 97:1873–1886
Olischläger M, Bartsch I, Gutow L, Wiencke C (2012) Effects of ocean acidification on different life-cycle stages of the kelp *Laminaria hyperborea* (Phaeophyceae). Bot Mar 55: 511–525
Pansch C, Schaub I, Havenhand J, Wahl M (2014) Habitat traits and food availability determine the response of marine invertebrates to ocean acidification. Glob Change Biol 20:765–777
Poloczanska ES, Burrows MT, Brown CJ, Molinos JG and others (2016) Responses of marine organisms to climate change across oceans. Front Mar Sci 3:62
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
Porzio L, Buia MC, Hall-Spencer JM (2011) Effects of ocean acidification on macroalgal communities. J Exp Mar Biol Ecol 400:278–287
R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org
Raven JA, Johnston AM, Kübler JE, Korb R and others (2002) Mechanistic interpretation of carbon isotope discrimination by marine macroalgae and seagrasses. Funct Plant Biol 29:355–378
Raven JA, Gobler CJ, Hansen PJ (2020) Dynamic CO_2 and pH levels in coastal, estuarine, and inland waters: theoretical and observed effects on harmful algal blooms. Harmful Algae 91:101594
Rivest EB, Comeau S, Cornwall CE (2017) The role of natural variability in shaping the response of coral reef organisms to climate change. Curr Clim Change Rep 3:271–281
RStudio Team (2020) RStudio: integrated development for R. RStudio, PBC, Boston, MA. http://rstudio.com/
Scheibling RE, Hennigar AW, Balch T (1999) Destructive grazing, epiphytism, and disease: the dynamics of sea urchin–kelp interactions in Nova Scotia. Can J Fish Aquat Sci 56:2300–2314
Sivertsen K, Bjørge A (2015) On the brink of the Arctic: unusual intertidal sub-Arctic kelp associations in the Porsangerfjord, North Norway. Mar Biol Res 11:405–413
Smale DA, Burrows MT, Moore P, O'Connor N, Hawkins SJ (2013) Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. Ecol Evol 3:4016–4038
Southgate T (1982) A comparative study of *Lacuna vincta* and *Lacuna pallidula* (Gastropoda: Prosobranchia) in littoral algal turfs. J Molluscan Stud 48:302–309
Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29:436–459
Sunda WG, Cai WJ (2012) Eutrophication induced CO_2-acidification of subsurface coastal waters: interactive effects of temperature, salinity, and atmospheric pCO_2. Environ Sci Technol 46:10651–10659
Talmage SC, Gobler CJ (2010) Effects of past, present, and future ocean carbon dioxide concentrations on the growth and survival of larval shellfish. Proc Natl Acad Sci USA 107:17246–17251
Thomsen J, Casties I, Pansch C, Körtzinger A, Melzner F (2013) Food availability outweighs ocean acidification effects in juvenile *Mytilus edulis*: laboratory and field experiments. Glob Change Biol 19:1017–1027
Tomasetti SJ, Gobler CJ (2020) Dissolved oxygen and pH criteria leave fisheries at risk. Science 368:372–373
Vargas CA, Contreras PY, Pérez CA, Sobarzo M, Saldías GS, Salisbury J (2016) Influences of riverine and upwelling waters on the coastal carbonate system off Central Chile and their ocean acidification implications. J Geophys Res Biogeosci 121:1468–1483
Wahl M, Schneider Covachã S, Saderne V, Hiebenthal C, Müller JD, Pansch C, Sawall Y (2018) Macroalgae may mitigate ocean acidification effects on mussel calcification by increasing pH and its fluctuations. Limnol Oceanogr 63:3–21
Wakefield RL, Murray SN (1998) Factors influencing food choice by the seaweed-eating marine snail *Norrisia norrisi* (Trochidae). Mar Biol 130:631–642
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
Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecol Lett 13: 685–694
Young CS, Gobler CJ (2016) Ocean acidification accelerates the growth of two bloom-forming macroalgae. PLOS ONE 11:e0155152
Young CS, Gobler CJ (2017) The organizing effects of elevated CO_2 on competition among estuarine primary producers. Sci Rep 7:7667
Young CS, Gobler CJ (2018) The ability of macroalgae to mitigate the negative effects of ocean acidification on four species of North Atlantic bivalve. Biogeosciences 15: 6167–6183
Young CS, Gobler CJ (2020) Hypoxia and acidification, individually and in combination, disrupt herbivory and reduce survivorship of the gastropod, *Lacuna vincta.* Front Mar Sci 7:547276
Young CS, Lowell A, Peterson BJ, Gobler CJ (2019) Ocean acidification and food limitation combine to suppress herbivory by the gastropod *Lacuna vincta.* Mar Ecol Prog Ser 627:83–94
Zhang X, Xu D, Guan Z, Wang S and others (2020) Elevated CO_2 concentrations promote growth and photosynthesis of the brown alga *Saccharina japonica*. J Appl Phycol 32: 1949–1959

Editorial responsibility: Adriana Vergés, Sydney, New South Wales, Australia
Reviewed by: 3 anonymous referees

Submitted: August 17, 2020
Accepted: February 5, 2021
Proofs received from author(s): April 2, 2021