Science of the Total Environment 808 (2022) 151594

Contents lists available at ScienceDirect

Science of the Total Environment

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

Who wins or loses matters: Strongly interacting consumers drive seagrass resistance under ocean acidification

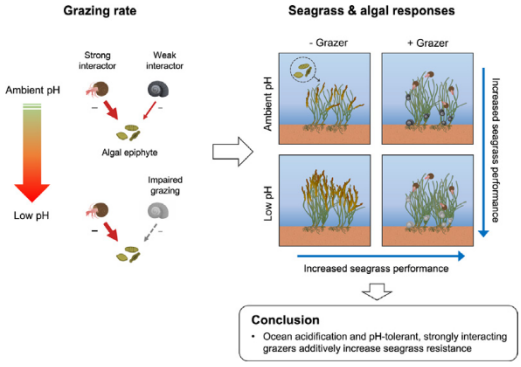
Juhyung Lee [a,*,1], Brent B. Hughes [b,2], Kristy J. Kroeker [c], Ava Owens [d,3], Candace Wong [d,4], Fiorenza Micheli [a,e]

[a] Hopkins Marine Station of Stanford University, 120 Ocean View Blvd, Pacific Grove, CA 93950, USA
[b] Nicholas School of the Environment, Duke University, Beaufort, NC 28516, USA
[c] Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA
[d] Santa Catalina School, Monterey, CA 93940, USA
[e] Stanford Center for Ocean Solutions, 120 Ocean View Blvd, Pacific Grove, CA 93950, USA

HIGHLIGHTS

- Ocean acidification (OA) directly facilitated algal epiphyte and seagrass.
- Co-occurring grazers variably controlled algal overgrowth on seagrass.
- pH-tolerant, strongly interacting grazers maintained overall grazing pressure.
- Grazing and OA additively increased seagrass productivity.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 6 September 2021
Received in revised form 3 November 2021
Accepted 6 November 2021
Available online 24 November 2021

Editor: Jay Gan

Keywords:
Global change
Ocean acidification
Ecosystem resistance
Functional role
Response variability
Seagrass-grazer interaction

ABSTRACT

Global stressors are increasingly altering ecosystem resistance, resilience, and functioning by reorganizing vital species interactions. However, our predictive understanding of these changes is hindered by failures to consider species-specific functional roles and stress responses within communities. Stressor-driven loss or reduced performance of strongly interacting species may generate abrupt shifts in ecosystem states and functions. Yet, empirical support for this prediction is scarce, especially in marine climate change research. Using a marine assemblage comprising a habitat-forming seagrass (*Phyllospadix torreyi*), its algal competitor, and three consumer species (algal grazers) with potentially different functional roles and pH tolerance, we investigated how ocean acidification (OA) may, directly and indirectly, alter community resistance. In the field and laboratory, hermit crabs (*Pagurus granosimanus* and *P. hirsutiusculus*) and snails (*Tegula funebralis*) displayed distinct microhabitat use, with hermit crabs more frequently grazing in the area of high algal colonization (i.e., surfgrass canopy). In mesocosms, this behavioral difference led to hermit crabs exerting ~2 times greater per capita impact on algal epiphyte biomass than snails. Exposure to OA variably affected the grazers: snails showed reduced feeding and growth under extreme pH (7.3 and 7.5), whereas hermit crabs (*P. granosimanus*) maintained a similar grazing rate under all pH levels (pH 7.3, 7.5, 7.7, and 7.95). Epiphyte biomass increased more rapidly under extreme OA (pH 7.3 and 7.5), but natural densities of snails and hermit crabs prevented algal overgrowth irrespective of pH treatments. Finally, grazers and acidification additively increased

* Corresponding author.
E-mail address: juh.lee@northeastern.edu (J. Lee).
[1] Present Address: Marine Science Center, Northeastern University, Nahant, MA 01908, USA.
[2] Present Address: Department of Biology, Sonoma State University, Rohnert Park, CA 94928, USA.
[3] Present Address: College of Natural Sciences and Mathematics, University of Denver, Denver, CO 80210, USA.
[4] Present Address: Department of Engineering Science, University of California, Berkeley, CA 94720, USA.

http://dx.doi.org/10.1016/j.scitotenv.2021.151594

surfgrass productivity and delayed the shoot senescence. Hence, although OA impaired the function of the most abundant consumers (snails), strongly interacting and pH-tolerant species (hermit crabs) largely maintained the top-down pressure to facilitate seagrass dominance. Our study highlights significant within-community variation in species functional and response traits and shows that this variation has important ecosystem consequences under anthropogenic stressors.

1. Introduction

Anthropogenic stressors are degrading important biogenic habitats and ecosystem functions they provide (Atwood et al., 2015; González-Varo et al., 2013; Hoegh-Guldberg et al., 2007). These impacts are often caused by stressors directly modifying habitat-forming organisms' physiology and performances. Yet, they are also driven by stressors altering how these organisms interact with surrounding communities (Hughes, 2000). Stressors can modify biodiversity and community composition of habitat-associated species (Haddad et al., 2015; Kroeker et al., 2011) as well as ecological interactions vital to sustaining habitat-forming species (Connell et al., 2017; Niu and Wan, 2008). Furthermore, these changes can combine additively and even synergistically to drive abrupt and non-linear alterations in ecosystem states and functioning (Crain et al., 2008; Silliman and He, 2018).

Assessing such ecologically mediated stressor effects is challenging because of the complexity of stress responses and multiple interaction pathways. Communities comprise species that play different functional roles or contribute differentially to the same collective function (Blüthgen and Klein, 2011). Stressors also cause variable organismal responses within communities, producing winners and losers (Elmqvist et al., 2003). Theory and empirical studies suggest that the functional consequences of stressor-driven species loss are dependent on how species' functions and stressor sensitivities are correlated in given communities (i.e., the response-and-effect framework; Suding et al., 2008). For instance, if strongly interacting species (i.e., species with large functional contributions) are more sensitive to external stressors than weakly interacting ones (i.e., species with small functional contributions), stressor-driven species losses could initially cause a significant reduction in ecosystem functioning (Hooper et al., 2012; Larsen et al., 2005). If such species are more resistant to stressors than the others, species losses may have negligible or even positive effects on ecosystem functioning (Smith and Knapp, 2003; Winfree et al., 2015).

It remains less clear how stress-induced changes in the performance (e.g., feeding, growth, and survival) of strongly and weakly interacting species scale to ecosystem dynamics. This is a critical oversight, considering that (a) stressors may not necessarily lead to species losses, and (b) changes in individual species performances are often sufficient to significantly alter ecosystem functions (Hawlena and Schmitz, 2010; Post et al., 1999). By assessing altogether how stressors affect the performances of strong and weak interactors within communities and overall ecosystem functioning, we can better understand mechanistically how stress responses of individual species combine to alter ecosystem dynamics.

We used a marine community comprising a habitat former (seagrass), its competitor (epiphytic algae), and three dominant consumer species (algae grazers) to test how strongly and weakly interacting consumers modulate ecosystem resistance – i.e., the ability to withstand disturbance (Pimm, 1984) – under increasing stress (ocean acidification). For our purpose, we define strongly and weakly interacting consumers as species that have relatively large and small per capita effects on shared resources, respectively (Berlow, 1999). Seagrasses represent one of the most productive ecosystems on the planet and provide a suite of vital services (e.g., carbon sequestration, coastal protection, and fishery production) (Nordlund et al., 2016). However, these habitats are declining globally (Waycott et al., 2009), commonly due to increased competition with ephemeral algae that thrive in human-perturbed coastal environments (Orth et al., 2006). In healthy seagrass ecosystems, algal overgrowth is controlled by mesograzers (e.g., small crustaceans, mollusks, and fishes) that preferably consume algae over seagrass (Williams and Ruckelshaus, 1993). However, impaired grazing function and increased algal dominance can negatively impact seagrass productivity and resilience (Hughes et al., 2013; Reynolds et al., 2014).

Ocean acidification (OA), i.e., the enrichment of seawater with anthropogenic CO_2, has the potential to modify seagrass community dynamics by altering the physiology, behavior, and performance of interacting species (Kroeker et al., 2011). However, predicting the community-level outcomes of OA has proven to be difficult due to the variable effects of OA on different components of seagrass communities. Studies show OA could facilitate seagrass and algae through increased availability of CO_2 and bicarbonate ion concentrations (Hughes et al., 2018; Palacios and Zimmerman, 2007) but drive negative and more variable responses among grazers (Eklöf et al., 2012; Hughes et al., 2018). OA-driven changes in seagrass community dynamics could be further complicated because grazer species can exert a varying degree of control over algae due to different morpho-behavioral adaptations (Best and Stachowicz, 2012; Duffy et al., 2001). Elucidating how OA affects strong and weak interactors within grazer assemblages and overall grazing pressure can help predict when and where seagrass ecosystems would be most vulnerable to the stressor.

We experimentally assessed how acidification modifies seagrass-algae-grazer interactions in and resistance of surfgrass ecosystems (*Phyllospadix torreyi*). Surfgrasses are ubiquitous foundation species on the Pacific coast of North America (Phillips and Menez, 1988) that have several important functions, including habitat provision for juvenile and adult marine organisms and amelioration of physical stressors (Castañeda-Fernández De Lara et al., 2005; Galst and Anderson, 2008; Shelton, 2010). In intertidal and shallow subtidal rocky shores, surfgrasses are commonly associated with gastropod (turban snail *Tegula funebralis*) and crustacean grazers (hermit crab *Pagurus granosimanus* and *P. hirsutiusculus*) (Pearse et al., 2015) that consume algae growing on and around seagrass shoots (Figs. 1A and S1). Increased algal growth is associated with reduced surfgrass productivity and deteriorated bed health (Honig et al., 2017). Our goals were (a) to examine if and how OA variably influences the two dominant grazer groups and (b) to evaluate how the grazer responses scale up to the community-level processes, including grazer-control of algae and grazer-facilitation of surfgrass productivity.

We first hypothesized that grazers would vary in their effectiveness for controlling algae due to different microhabitat uses and feeding behaviors. Based on our initial observations that hermit crabs frequently feed within surfgrass canopy, where intense algal recruitments usually occur (Willcocks, 1982), we predicted the species would exert greater top-down effects on algae. Snails were commonly observed in shoot bases or the seafloor and were expected to play a weaker functional role. Second, we hypothesized OA would negatively but variably affect grazer species. We predicted a stronger negative effect of OA on snails, which are generally more calcified and less effective in maintaining intracellular pH than crustaceans (Kroeker et al., 2011). Third, we hypothesized OA would directly facilitate algae and seagrass productivity via increased resource availability (Koch et al., 2013). Finally, we hypothesized that grazer-control of algae and facilitation of seagrass resistance under OA would depend on how strongly interacting grazers (hermit crabs) respond to the stressor. That is, if strongly interacting grazers show decreased performance under OA, increased algal loading will overwhelm grazing to the extent that seagrass production will no longer be sustained (P_1 and P_2; Fig. 1B). Alternatively, if the species are tolerant of OA, sufficiently high grazing pressure will be maintained – irrespective of how OA affects weakly interacting grazers – to suppress algae and to sustain or enhance seagrass production (P_3 and P_4; Fig. 1B).

We combined field surveys and laboratory experiments to assess the microhabitat associations and varying effectiveness of snail (*T. funebralis*)

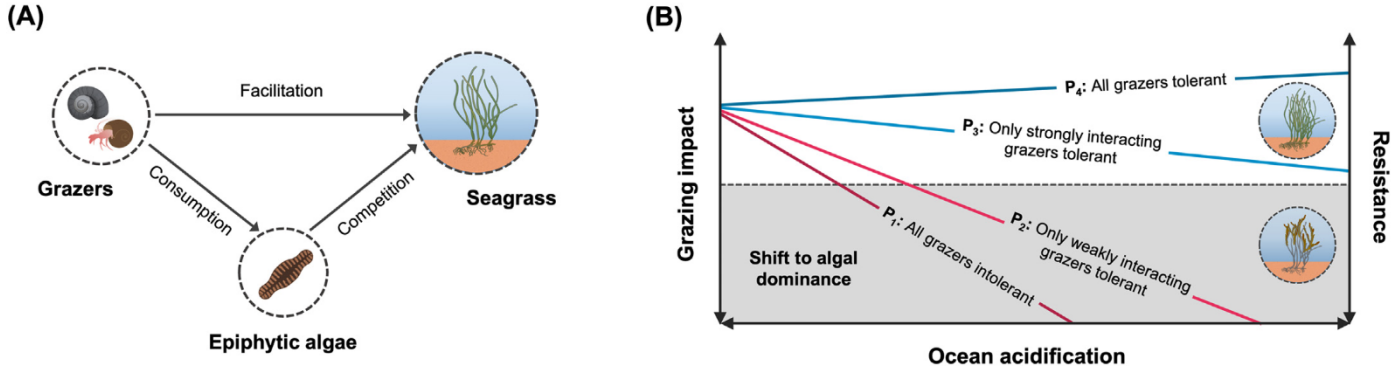


Fig. 1. Hypothesized changes in seagrass ecosystem dynamics under ocean acidification. (A) Conceptual diagrams of interspecific interactions among seagrass, epiphytic algae, and grazer assemblage. These include trophic interaction between grazers and algae, competition between algae and seagrass, and non-trophic, facilitative interaction between grazers and seagrass. (B) Hypothesized changes in seagrass ecosystem resistance under ocean acidification (OA). We predicted, if strongly interacting grazers are susceptible to OA, increased algal recruitment and growth will overwhelm grazing to the extent that seagrass production will no longer be sustained (P_1 and P_2). If the species are tolerant of OA, sufficiently high grazing pressure will be maintained – regardless of how OA influences weakly interacting grazers – to sustain or enhance seagrass productivity and resistance (P_3 and P_4). Images: snail (Tracy Sutton), hermit crab (Lantapix), and seagrass (Tracey Saxby, IAN Image Library).

and hermit crab grazers (*P. granosimanus* and *P. hirsutiusculus*) in controlling algae. We then investigated under mesocosms the effects of different seawater pH (pH 7.3, 7.5, 7.7, and 7.95) on the growth, survival, and feeding rate of different grazer species. Finally, we mimicked a shallow water surfgrass community in outdoor mesocosms and tested how snails and hermit crabs, at their natural densities, control algae and seagrass productivity under OA. The extreme pH treatments (pH 7.3 and 7.5), which are well beyond the projected IPCC scenario (Bopp et al., 2013; Gattuso et al., 2015; Pachauri et al., 2014), represented the conditions surfgrass communities experience only temporarily in their natural habitats (e.g., diel pH fluctuations in tide pool surfgrass habitats ranging from pH 7.22 to 9.0) (Jellison et al., 2016; Kwiatkowski et al., 2016; Tharaldson, 2018). However, we used the semi-regression design to understand better the functional relationship between seawater pH and the community processes of our interest across a broad OA spectrum.

2. Methods and materials

2.1. Interspecific variation in grazer function (field survey and Experiment 1)

Between the summer of 2018 and the spring of 2020, we surveyed surfgrass grazer communities at seven intertidal sites (Fig. S2) across Central California, USA: Stillwater Cove (36°33′57.9″ N, 121°56′38.0″ W), Hopkins Marine Station (36°37′14.4″ N, 121°54′11.4″ W), Pleasure Point (36°57′27.1″ N, 121°58′07.6″ W), Opal Cliff (36°57′33.6″ N, 121°57′53.5″ W), Scotts Creek (37°02′30.4″ N 122°13′58.4″ W), Davenport Landing (37°01′18.9″ N, 122°12′56.0″ W), and Waddell Creek (37°06′11.8″ N, 122°17′16.7″ W). Grazers were surveyed within two different habitat types: surfgrass beds in exposed intertidal flats and the beds within tide pools or channels that remain submerged through most tidal cycles. In exposed beds, we placed 11 to 27 randomly spaced quadrats (1 m^2) along 20–50 m transects laid perpendicularly to the shoreline in the low and mid-intertidal zone. We estimated % seagrass cover and counted all visible crustaceans (i.e., decapods and isopods) and snail grazers within each quadrat. Although amphipod and limpet grazers are also common in surfgrass, they were not included in the survey due to their cryptic nature. The surveys on exposed surfgrass beds were conducted in all study sites, except in Hopkins Marine Station. At Scott's Creek, Davenport Landing, and Hopkins Marine Station, we randomly placed five additional quadrats over surfgrass patches within tide pools and channels (depth > 10 cm). Here, we used smaller quadrats (0.25 m^2) because of the higher grazer density found in these habitats.

We investigated the microhabitat association of dominant grazers (i.e., turban snails *Tegula* spp. and hermit crabs *Pagurus* spp.) in surfgrass beds at Hopkins Marine Station. We placed eight random quadrats (0.25 m^2) across tide pools and channel areas at the site (depth > 20 cm). Within each quadrat, we vertically partitioned the habitats into shoot canopy (a shoot section approximately > 10 cm from the seafloor) vs. bottom (i.e., seafloor and shoot section < 10 cm from the seafloor) and counted all snails and hermit crabs found in each microhabitat.

To experimentally test the microhabitat association and top-down control of algae by grazers, we conducted an outdoor-mesocosm experiment comprising thirty 5-liter tanks at the Hopkins Marine Station. Experimental tanks were constructed from white, semi-transparent paint buckets (30 cm diam., 45 cm height) and were placed on an outdoor seawater table (1.5 m × 3.5 m). Each tank was continuously flooded with sand-filtered (nominal 20 μm) seawater. Grazers and surfgrasses were manually collected from Hopkins Marine Station during July 2019. Collected grazers included black turban snail *T. funebralis* and two species of hermit crab, *P. granosimanus* and *P. hirsutiusculus*. While these species actively consume various algae, including diatoms and macroalgae (Erlandson et al., 2015; Ruesink, 2000), our observations suggest they do not consume live seagrass tissue. Surfgrasses were collected in clumps to include aboveground shoots and undamaged rhizomes. These clumps were then divided into smaller units (approximately 5–7 cm diameter cores) with standardized shoot density (65–70 individual blades per core) and length (~43 cm). We planted a single core into each tank containing a layer of coarse sand. We randomly assigned ten mesocosm tanks to each of the three treatments: without grazer, with snails (4 *T. funebralis*; mean blotted wet mass ± 1 SE = 5.63 ± 0.09 g), and with hermit crabs (2 *P. granosimanus* and 2 *P. hirsutiusculus*; mean blotted wet mass ± 1 SE = 5.57 ± 0.03 g including shell). Grazer biomass and density in each tank were well within their natural range in the field (see Fig. 2).

We monitored grazer microhabitat usage every 2–3 days. During each session, an observer counted the number of snail and hermit crab grazers that had climbed on surfgrass > 10 cm above the sand bottom. After 21 days, we harvested all seagrass, separated aboveground shoots from the rhizome, and scraped off all epiphytic materials from the seagrass blades using pre-weighed pieces of paper towel. We also sampled all visible macroalgae (mainly *Ulva* spp.) growing inside the mesocosms. Seagrass shoot, epiphyte, and macroalgae were dried at 65 °C for 72 h before weighing. We finally dried and weighed all surviving snails and hermit crabs (extracted from the shell).

2.2. Grazer growth, survival, and feeding under ocean acidification (Experiment 2)

We investigated the effect of experimental OA on the growth, survival, and feeding rate of snail and hermit crab grazers at the Long Marine

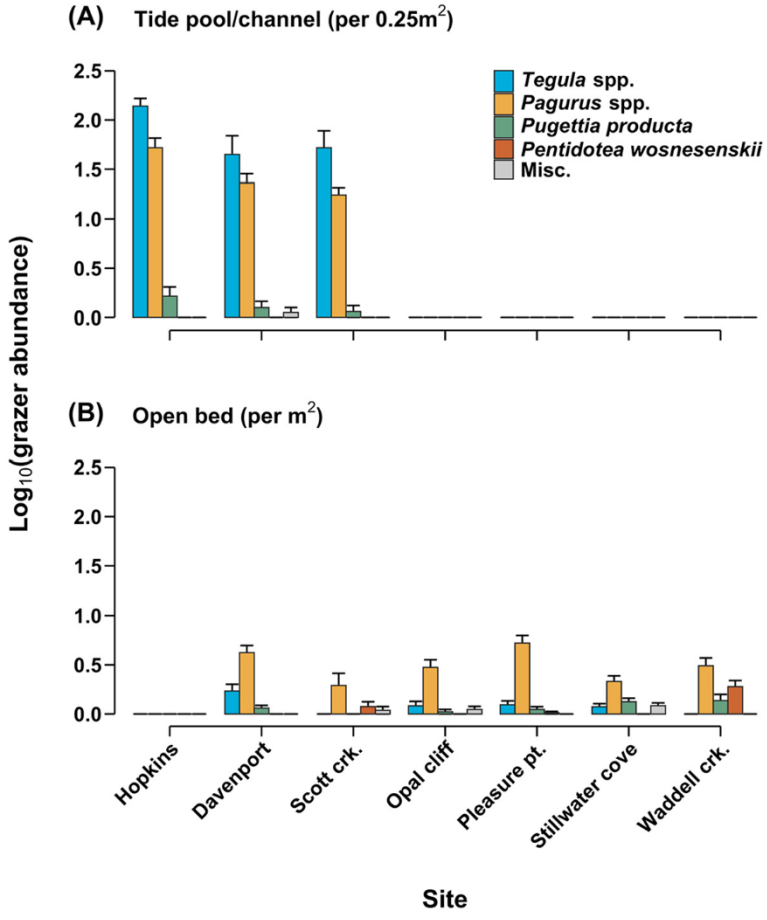


Fig. 2. Field abundance of seagrass-associated mesograzers. Mean log-densities (per 0.25 or 1 m^2) of invertebrate grazers associated with seagrass *Phyllospadix torreyi* in (A) tide pools and channels and (B) open, exposed beds in intertidal sites across Central California (n = 5 plots per site for tidal pools/channels and n = 11–27 for open beds). Field surveys were conducted in July–September 2018 for open beds and in February 2020 for tide pools and channels. When pooled across all sites and habitat types, *T. funebralis* accounted for >95% of total *Tegula* abundance, and *P. granosimanus* and *P. hirsutiusculus* accounted for >96% of total *Pagurus* abundance. Note that grazer densities were measured using different quadrat sizes (0.25 m^2 for tide pool/channels and 1 m^2 for open beds). Error bars indicate 1 SE. Different colors indicate different species groups.

Laboratory (University of California Santa Cruz). Our experiment consisted of four outdoor 200-liter mesocosm tanks (60 cm diam., 90 cm height), each receiving seawater with manipulated carbonate chemistry from four individual header barrels (200 L). We adjusted the pH level in each header barrel (pH 7.3, 7.5, 7.7, and 7.95) by mixing filtered seawater with CO_2 enriched seawater (pH 5.7–6.0) created in a separate recirculating tank through direct bubbling of CO_2. The mixing process was regulated with a custom-built control system, which consisted of pH sensors, controllers, and relays (Hughes et al., 2018). Seawater pH and temperature in each header barrel was monitored every 10 s by a Durafet pH sensor connected to a UDA controller (Honeywell Inc.) with the preprogrammed set point. When the header barrel pH reached values higher than the setpoint (pH 7.35, 7.55, 7.75, and 8.0), a relay switch in the controller was activated to release the low pH seawater (pH 5.7–6.0) into the barrel via a solenoid valve. The manipulated seawater was then gravity fed into each of four experimental mesocosm tanks from the four independent header barrels at consistent rates.

In November 2016, we collected the two most abundant grazer species (*T. funebralis* and *P. granosimanus*) from surfgrass beds adjacent to Hopkins Marine Station. For snails, we measured the shell length and blotted wet mass (BWM; g) after removing excess water from its mantle (by gently pushing the operculum into the shell). We also marked the margin of each snail shell aperture with a thin layer of white paint and superglue to track the shell growth. For hermit crabs, we extracted each individual from its shell by applying mild heat to the shell apex and measured its carapace length and BWM. Snails (n = 72) and hermit crabs (n = 72) were then haphazardly assigned to four pH treatments (pH 7.3, 7.5, 7.7, and 7.95) so that each pH treatment group had 18 snails and 18 hermit crabs. The average body mass of snails (mean snail BWM ± 1 SE = 1.34 ± 0.1 g for all pH groups) and hermit crabs (mean hermit crab BWM without shell ± 1 SE = 0.06 ± 0.01 g for all pH groups) were nearly identical among different pH groups. We constructed a total of 72 rearing chambers (n = 18 per pH group), each consisting of a 120 mL plastic container (8 cm diam., 7 cm height), cobblestone, and mesh lid (3 mm opening). In each rearing chamber, we introduced one snail and one hermit crab. We placed 18 rearing chambers at the bottom of each tank (see Fig. S3A for the experimental design and set-up) and gradually reduced seawater pH to desired levels over 24 h. Grazers were fed dried *Ulva* every other day. Experiment 2 lasted a total of 17 days, during which we monitored seawater pH and temperature in experimental tanks with Durafet pH sensors (every 10 s) and a YSI Pro Plus hand-held sensor (twice daily). We also collected discrete water samples from experimental tanks every 4–5 days and measured them for total alkalinity (TA) using closed-cell titration (Metrohm, 905 Titrando).

To test the effects of prolonged OA exposure on grazing rates, we settled algal epiphytes onto artificial substrates or "cards". We utilized two different substrates for algal recruitment, considering different feeding biomechanics. For a snail, which is more specialized for scraping food items off hard surfaces using its radula, algae were settled onto transparent glass

slides (2.5 cm × 7.6 cm). For a hermit crab, which uses its claws to pick food items off substrates, algae were settled onto fiberglass mesh screens (6 cm × 8 cm, 1 mm opening), which helped minimize the algal mass loss caused by the scraping motions in leg movements. During the culture, all cards were placed inside shallow plastic bins, which received a continuous flow of ambient pH seawater. Both card types were extensively colonized by epiphytic algae (primarily diatoms) after two weeks. We dried all algae cards at 45 °C for 12 h before weighing them.

Grazing trials were conducted two days before terminating Experiment 2. We relocated grazers from the rearing chambers to independent feeding chambers (120 mL; with a mesh lid) so that each feeding chamber contained either a single snail or hermit crab. We then returned all grazers to their original mesocosm tanks, placed inside their respective feeding chambers. Due to the loss of few grazers during the rearing period, we carried out the trials with 16 individuals per species per pH treatment. Grazers were allowed to feed on the cards for 36 h. To examine whether algal mass loss that is not attributed to grazing varied with pH treatments, we set up 12 additional feeding chambers per tank, each containing an algae card without grazers (n = 6 per card type per pH group). After the trial has ended, we collected all algae cards and grazers from mesocosm tanks. We re-weighed all algae cards and determined grazer wet and dry mass (shells removed for all hermit crabs) and snail shell growths (i.e., the maximum distance between the newly formed margin of shell aperture and the outer margin of the painted surface). Snails exhibited limited shell growth (<0.5 mm) during the experiment due to their slow-growing nature (Barclay et al., 2019) and the short duration of the experiment. We measured snail shell growth under a dissecting microscope using a digital caliper (to 0.01 mm). We finally calculated the mass-specific grazing rate by dividing the mass change of each algae card by the grazer dry mass.

2.3. Grazer-control of algal epiphytes and seagrass performances under ocean acidification (Experiment 3)

We investigated the effects of experimental acidification and grazer assemblage on algal epiphytes and seagrass performance. We manipulated the carbonate chemistry in eight 200-liter header barrels, allotting two barrels to each of four pH treatments (pH 7.3, 7.5, 7.7, and 7.95). Each header barrel was connected to two 200-liter mesocosm tanks, of which each was assigned to different grazer treatments (i.e., with vs. without grazers). Hence, our experiment comprised a total of sixteen mesocosm tanks, with two replicate tanks assigned to different pH × grazer treatment groups (see Fig. S3B for the experimental design and set-up). We added to each mesocosm 16 terracotta pots (diameter = 10 cm), each planted with five pre-weighed surfgrass shoots (20 cm in shoot length, 1.5 cm in rhizome length) (Fig. S3B). We fixed surfgrass shoots with plastic cable ties to a cobblestone covered in nylon mesh, which simulated rhizome matrix and hard surfaces for root attachments. For each tank assigned to the grazer treatment, we added the following density and biomass of grazers: 24 *T. funebralis* (32.1 ± 0.2 g [1 SE]) and mixed *Pagurus* spp. comprising 12 *P. granosimanus* and 6 *P. hirsutiusculus* (11.9 ± 0.01 g [1 SE]). Grazer density and biomass in each tank were well within their natural range in the tide pool and channel habitats (i.e., 60–146 individuals and 84–143 g wet mass/0.25 m^2 for snails; 17–57 individuals and 13–81 g wet mass/0.25 m^2 for hermit crabs; see Fig. 2A).

We conducted Experiment 3 over 23 days, during which we continuously monitored seawater pH and temperature in header barrels with Durafet pH sensors (every 10 s). Additionally, we monitored seawater pH and temperature in experimental tanks with a YSI Pro Plus hand-held sensor twice daily and collected discrete water samples from the tanks every 3–4 days for total alkalinity measurements. Extensive algal proliferation occurred midway through the experiment. To examine whether the magnitude of algal recruitment and growth during the bloom varies with pH, we randomly sampled four pots from each tank on day-12 (n = 8 per pH × grazer treatment group). We counted all surviving surfgrass shoots and scraped all the epiphytic materials from surfgrass blades using pre-weighed cotton pads. We measured the length of the longest blade in each shoot and separated rhizome and brown or senescent tissues from living shoot tissues to estimate the magnitude of shoot senescence. Algae and seagrass samples were dried at 65 °C for 72 h before weighing. We repeated the process with the remaining seagrass units on day 23. We also counted all dead or missing grazers from each mesocosm.

2.4. Statistical analyses

We used a generalized linear model (GLM) with a quasi-Poisson error distribution for over-dispersed data (Bolker et al., 2009) to compare field grazer densities in different surfgrass microhabitats for snails and hermit crabs. For analyzing the number of snail and hermit crabs feeding within surfgrass canopy during Experiment 1, we averaged multiple observation values for each of 10 tanks assigned to the same treatment group and analyzed the data using one-way analysis of variance (ANOVA). We used the same test to examine the effect of grazer treatments on total algal mass (i.e., combining epiphyte and macroalgae) and absolute epiphytic biomass at the end of Experiment 1 (both log-transformed for data normalization). We used GLM with Gamma error distribution and log link to analyze standardized epiphyte biomass, which measured the relative intensity of algal recruitment and growth (i.e., epiphytic mass per gram of seagrass shoot mass). Data on macroalgal biomass was continuous, positive, and zero-inflated, so we used a two-part hurdle model incorporating two generalized linear models. The first model assessed the effect of grazers on the frequency in which macroalgae colonized mesocosms (binomial GLM). Then, the second model evaluated the effects on macroalgal biomass if the algal colonization occurred (Gamma GLM).

Due to logistical constraints, we placed multiple grazer-rearing chambers inside mesocosm tanks in Experiment 2 (n = 1 tank for each treatment group), which is a pseudo-replicated design (Hurlbert, 1984). However, we treated each chamber as a replicate because carbonate chemistry and other environmental parameters (e.g., temperature, water flow, and salinity) were tightly controlled across mesocosms (summarized in Table 1). Also, large tank volume (200 L), constant water flow, and individual chambers likely prevented grazers from affecting others through direct interaction or metabolism (besides the individuals placed in the same chamber). We used one-way ANOVA to analyze how pH levels (four levels, fixed) affect percentage changes in individual snail and hermit crab BWM and mass-specific grazing intensity at the end of Experiment 2. For snail shell growth, we again implemented a two-part hurdle model to test the effect of pH on the proportion of individuals showing any shell growth (binomial GLM) and on maximal growth (mm) along the painted shell margin (Gaussian GLM), to account for zero-inflated data.

We used linear mixed-effects models (LME) to test the effect of grazers, pH, sampling period (day 12 vs. 23), and their interactions on standardized epiphytic biomass and seagrass morphometrics (shoot mass, rhizome mass, the ratio of live to detrital shoot mass, and shoot

Table 1
Measured and estimated environmental parameters during Experiment 2. Chemical and physical characteristics of seawater during the 17-day mesocosm experiment on grazer growth, survival, and feeding rate. pH_T value was calculated as the mean seawater pH (±1 SD) within each mesocosm. Temperature and pH_T were measured every 10 s with Durafet sensors. Salinity measurements (YSI sensor) and total alkalinity (TA) samples were taken every 4–5 days (n = 4 per treatment group). Partial pressure of carbon dioxide (pCO_2) and dissolved inorganic carbon (DIC) were derived from Durafet pH and laboratory measurements of discrete TA using R package *Seacarb* (version 3.2.13).

pH treatment	7.3–7.35	7.5–7.55	7.7–7.75	7.95–8.0
pH_T	7.34(0.15)	7.53(0.11)	7.71(0.05)	7.96(0.03)
Temp (°C)	11.9(0.37)	11.8(0.39)	11.8(0.38)	11.8(0.38)
TA (μM/kg SW)	2179.2(24.7)	2179.9(22.7)	2178.6(21.3)	2180.8(24.5)
pCO_2 (μatm)	2430.9(154.2)	1513.7(104.2)	915.2(33.9)	478.1(11.1)
DIC (μM/kg SW)	2242.4(32.0)	2183.2(26.4)	2123.1(21.0)	2040.7(17.0)
Salinity (ppt)	32.3(0.8)	32.2(0.8)	32.3(0.8)	32.3(0.8)

elongation) in Experiment 3. As with the previous experiment, we placed multiple seagrass units (i.e., individual pots) in each mesocosm tank ($n = 2$ tanks for each treatment group) in Experiment 3. To account for potential pseudo-replication issues, we included Tank IDs as a nested random variable in all models. All data were normalized using log (shoot mass, rhizome mass, and the ratio of live to detrital shoot mass) or square root (standardized epiphyte mass) transformations prior to the analysis. For shoot survival (i.e., number of surviving shoots per pot), we used a Poisson generalized linear mixed model (GLMM) with the same fixed and nested random variables as specified above. Linear mixed-effects models and generalized linear mixed models were implemented using packages *nlme* (Pinheiro et al., 2020) and *lme4* (Bates et al., 2015) in R (version 3.6.3, R Core Team, 2020), respectively. For multiple comparisons in GLMs or one-way ANOVA outputs, we used Holms-corrected post-hoc tests (package *multcomp*).

3. Results

3.1. Interspecific variation in grazer function (field surveys and Experiment 1)

Hermit crabs (*Pagurus* spp.) and snails (*Tegula* spp.) were the two most abundant grazer groups, especially in surfgrass beds within tide pools and channels (Fig. 2A), where their densities averaged 33 ± 6.4 individuals/0.25 m^2 and 89 ± 15 individuals/0.25 m^2, respectively (mean hermit crab densities ranging 17–57 individuals/0.25 m^2 and mean snail densities ranging 61–146 individuals/0.25 m^2 across three survey sites). Open beds had much lower grazer abundance and were dominated by hermit crabs (Fig. 2B). When pooled across all sites and habitat types, *T. funebralis* accounted for >95% of total snail abundance, and *P. granosimanus* and *P. hirsutiusculus* accounted for >96% of total hermit crab abundance. In tide pool surfgrass beds, snails and hermit crabs showed different spatial distribution, with snail grazers mostly occupying shoot bases and the seafloor (GLM, $F_{1, 14} = 40.69$, $p < 0.0001$) and hermit crab grazers occupying the upper portion of surfgrass shoots (GLM, $F_{1, 14} = 16.65$, $p = 0.001$) (Fig. 3A and B).

We found similar grazer microhabitat-use patterns during Experiment 1. Hermit crabs were, on average, ~4 times more likely to be found among surfgrass canopy compared to snails when time-averaged across nine observations (One-way ANOVA, $F_{1, 18} = 11.85$, $p = 0.003$; Fig. 3C). Both hermit crab and snail treatments had significantly reduced total algal biomass (One-way ANOVA, $F_{2, 26} = 20.99$, $p < 0.0001$; Fig. 4A) relative to the control groups; and hermit crabs also had much stronger effects on total algal mass than snails (Holm-corrected post-hoc contrasts, $p < 0.05$). Grazer treatments significantly affected the absolute biomass of epiphytic algae (One-way ANOVA, $F_{2, 26} = 11.64$, $p < 0.001$) as well as epiphytic biomass standardized by seagrass shoot mass (GLM, $F_{2, 26} = 8.64$, $p = 0.001$; Fig. 4B). Hermit crabs exerted stronger effects on absolute and standardized epiphytic biomass relative to snails (Holm-corrected post-hoc contrasts, $p < 0.05$; Fig. 4B). Snails marginally reduced absolute and standardized epiphytic biomasses relative to the control group (Holm-corrected post-hoc contrasts, both $p < 0.1$; Fig. 4B). Grazers significantly affected the frequency of macroalgal recruitment (GLM, Likelihood Ratio $\chi^2 = 7.19$, df = 2, $p = 0.03$) but had only marginal effects on macroalgal mass (GLM, $F_{2, 16} = 2.81$, $p = 0.09$). Holm-corrected post-hoc contrasts revealed that hermit crabs and snails weakly reduced or did not affect the frequency of macroalgal recruitment ($p < 0.07$ for hermit crabs, $p = 0.28$ for snails) and macroalgal biomass ($p = 0.18$ for hermit crabs, $p < 0.08$ for snails).

3.2. Environmental parameters during ocean acidification experiments (Experiment 2 and 3)

The mean seawater pH (on the total scale, pH_T) in experimental mesocosms (Experiment 2 and 3) and header barrels (Experiment 3 only) generally followed the prescribed pH conditions (see Tables 1 and 2 for the complete summary of carbonate chemistry in Experiment 2 and 3, respectively). In Experiment 3, pH_T was slightly elevated in experimental mesocosms than in header barrels, possibly due to the increased photosynthesis by seagrass and epiphytic algae. Temperature, salinity, and total alkalinity (TA) were comparable among treatment groups in both experiments (Tables 1 and 2).

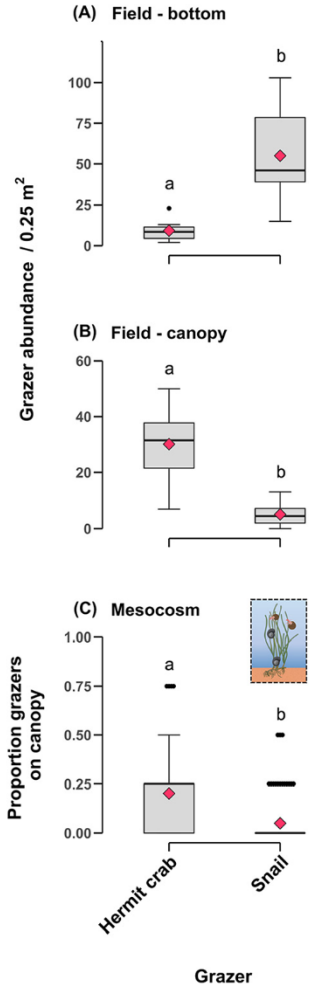


Fig. 3. Microhabitat usages of dominant seagrass-associated mesograzers. Box plots illustrating the densities of hermit crab and snail grazers in different seagrass microhabitats, including (A) bottom (shoot bases and seafloor) and (B) canopy (upper portion of seagrass shoots). Grazer microhabitat use was surveyed in tidal channels nearby Hopkins Marine Station ($n = 8$ per species). (C) The proportion of hermit crab and snail grazers feeding in seagrass canopy area during Experiment 1 ($n = 10$ per species). In box plots, mean values are represented by red diamond symbols. Different letters indicate significant difference ($p < 0.05$) based on Holm-adjusted post-hoc contrasts. Images: snail (Tracy Sutton), hermit crab (Lantapix), and seagrass (Tracey Saxby, IAN Image Library).

3.3. Grazer growth, survival, and feeding under ocean acidification (Experiment 2)

Acidification negatively impacted the somatic growth of snails (Mean % increase BWM ± 1 SE, pH 7.95 = 1.8 ± 0.3%, pH 7.7 = 1.2 ± 0.1%, pH 7.5 = 0.5 ± 0.3%, pH 7.3 = −0.2 ± 0.2%; One-way ANOVA, $F_{3, 68} = 15.51$, $p < 0.0001$) and hermit crabs (Mean % increase BWM ± 1 SE, pH 7.95 = 22.3 ± 1.9%, pH 7.7 = 20.0 ± 2.5%, pH 7.5 = 21.2 ± 2.1%, pH 7.3 = 12.2 ± 2.0%; One-way ANOVA, $F_{3, 62} = 4.53$, $p < 0.01$). Percentage growth in snail body mass decreased significantly at pH 7.3 and 7.5 (Fig. 5B), whereas the growth rate of hermit crabs was only affected at pH 7.3 (Fig. 5A). Overall, snails grew at a much slower

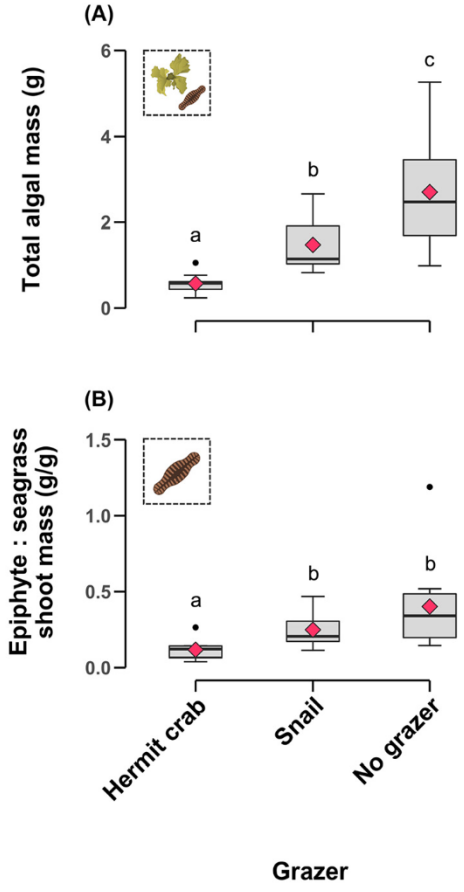


Fig. 4. Species-specific grazing impacts on ephemeral algae (Experiment 1). Box plots illustrating algal biomass on seagrass after the 21-day experiment in the presence of hermit crabs or snails and in the absence of grazers. Measured are (A) total algal biomass combining benthic macroalgae (e.g., *Ulva* spp.) and algal epiphytes and (B) standardized epiphyte biomass (i.e., the ratio between epiphyte mass and seagrass shoot mass). In box plots, mean values are represented by red diamond symbols. Different letters indicate significant difference ($p < 0.05$) based on Holm-adjusted post-hoc contrasts. Macroalgae image: Tracey Saxby (IAN Image Library).

pace than hermit crabs during the experiment. Acidification did not affect the probability (GLM, Likelihood Ratio $\chi^2 = 5.77$, df = 3, $p = 0.12$) nor the magnitude (Mean ± 1 SE shell growth, pH 7.95 = 0.22 ± 0.04 mm, pH 7.7 = 0.12 ± 0.02 mm, pH 7.5 = 0.18 ± 0.05 mm, pH 7.3 = 0.11 ± 0.01 mm; GLM, $F_{3,\ 16} = 1.95$, $p = 0.16$) of new shell formation in snails. Hermit crab mortality (6–11%) did not vary with pH, while no mortality occurred in snails. In grazing trials, hermit crabs displayed constant feeding rates under all pH levels (One-way ANOVA, $F_{3,\ 60} = 1.34$, $p = 0.27$) (Fig. 5C). In contrast, snail feeding was significantly altered by acidification ($F_{3,\ 60} = 4.10$, $p = 0.01$) and showed marked decreases at pH 7.3 and 7.5 (Fig. 5D). Mass changes in algae cards not subjected to grazing (i.e., control cards) did not vary among pH treatments.

3.4. Grazer-control of algal epiphytes and seagrass performance under ocean acidification (Experiment 3)

Standardized epiphyte biomass increased significantly with acidification (LME, $F_{3,\ 8} = 4.55$, $p = 0.04$), whereas grazers reduced these average values by 74% ($F_{1,\ 8} = 206.88$, $p < 0.0001$) (Fig. 6A). There was also a strong pH × sampling (time) effect on standardized epiphyte biomass ($F_{3,\ 229} = 9.78$, $p < 0.0001$). Acidification significantly increased standardized epiphyte biomass in mid-experiment (day-12 sampling; $F_{1,\ 8} = 31.48$, $p < 0.0001$) but did not affect the final biomass (day-23 sampling; $F_{1,\ 8} = 0.57$, $p = 0.65$) (Fig. S4). Mean aboveground biomass of surviving shoots increased with acidification ($F_{3,\ 8} = 8.35$, $p < 0.01$), in the presence of grazers ($F_{1,\ 8} = 18.30$, $p < 0.01$), and through time ($F_{1,\ 229} = 17.73$, $p < 0.001$) (Fig. 6B). The ratio between live and detrital shoot mass decreased with time ($F_{1,\ 229} = 121.90$, $p < 0.0001$) but increased with acidification ($F_{3,\ 8} = 22.52$, $p < 0.001$) and grazer addition ($F_{1,\ 8} = 132.23$, $p < 0.0001$) (Fig. 6C). There was also a significant grazer × time effect on the live to detrital shoot mass ratio ($F_{1,\ 229} = 20.77$, $p < 0.0001$). Shoot elongation was significantly affected by grazers ($F_{1,\ 8} = 15.49$, $p = 0.004$), increasing time ($F_{1,\ 229} = 4.09$, $p = 0.04$), and a two-way interaction between grazer addition and time ($F_{1,\ 229} = 6.74$, $p = 0.01$). Mean rhizome biomass (Fig. 6D) and number of surviving shoots were not affected by any of the experimental variables.

4. Discussion

Recent advances in global change research have highlighted the importance of considering within-community variations in species functions and stressor sensitivities and their relationship in scaling from individual to ecosystem dynamics (Enquist et al., 2015; Suding et al., 2008). We utilized this framework to examine how OA variably modifies the performances of strongly and weakly interacting consumers within seagrass communities and how these changes combine to modulate seagrass resistance.

Although snails dominated the grazer assemblage in focal surfgrass habitats (i.e., tide pools and channels), hermit crabs exerted much stronger control over algal production per capita (~74%, on average). Snail grazing and growth deteriorated under extreme pH (pH 7.3 and 7.5), but hermit crabs exhibited a constant grazing rate across all pH levels. This high pH

Table 2
Measured and estimated environmental parameters during Experiment 3. Chemical and physical characteristics of seawater during the 23-day mesocosm experiment on grazer-control of algae and seagrass performance. The range of pH treatment represents the target pH levels set for header barrels ($n = 2$ per each pH × grazer treatment group). For grazer treatment, + Grazer represents the addition of mixed assembly of hermit crab and turban snails, and − Grazer represents treatments without any grazers. Durafet pH_T was calculated as the mean seawater pH (±1 SD) in header barrels during the 23-day experiment period. All other environmental parameters were measured directly from experimental mesocosms. YSI pH_T, temperature, and salinity were measured every day, and total alkalinity (TA) samples were taken from each mesocosm tank every 3–4 days ($n = 7$ per treatment group). Partial pressure of carbon dioxide (pCO_2) and dissolved inorganic carbon (DIC) were derived from YSI pH_T and laboratory measurements of discrete TA using R package *Seacarb* (version 3.2.13).

Treatment	pH 7.3–7.35		pH 7.5–7.55		pH 7.7–7.75		pH 7.95–8.0	
	+ Grazer	− Grazer	+ Grazer	− Grazer	+ Grazer	− Grazer	+ Grazer	− Grazer
Durafet pH_T	7.32(0.1)		7.51(0.07)		7.70(0.04)		7.92(0.02)	
YSI pH_T	7.38(0.08)	7.40(0.09)	7.54(0.02)	7.54(0.04)	7.72(0.02)	7.76(0.04)	7.92(0.07)	7.94(0.06)
TA (μM/kg SW)	2219(28)	2214(39)	2219(31)	2213(31)	2220(26)	2220(33)	2223(22)	2223(23)
pCO_2 (μatm)	2071(140)	1877(204)	1327(139)	1276(172)	851(84)	767(104)	492(36)	453(48)
DIC (μM/kg SW)	2252(30)	2234(39)	2196(39)	2185(38)	2142(30)	2127(38)	2068(22)	2055(30)
Temp (°C)	13.0(0.52)	13.1(0.50)	13.0(0.57)	13.1(0.52)	13.1(0.53)	13(0.54)	13.1(0.50)	13.0(0.52)
Salinity (ppt)	34.1(0.06)	34.1(0.07)	34.1(0.06)	34.1(0.06)	34.1(0.06)	34.1(0.05)	34.1(0.06)	34.1(0.06)

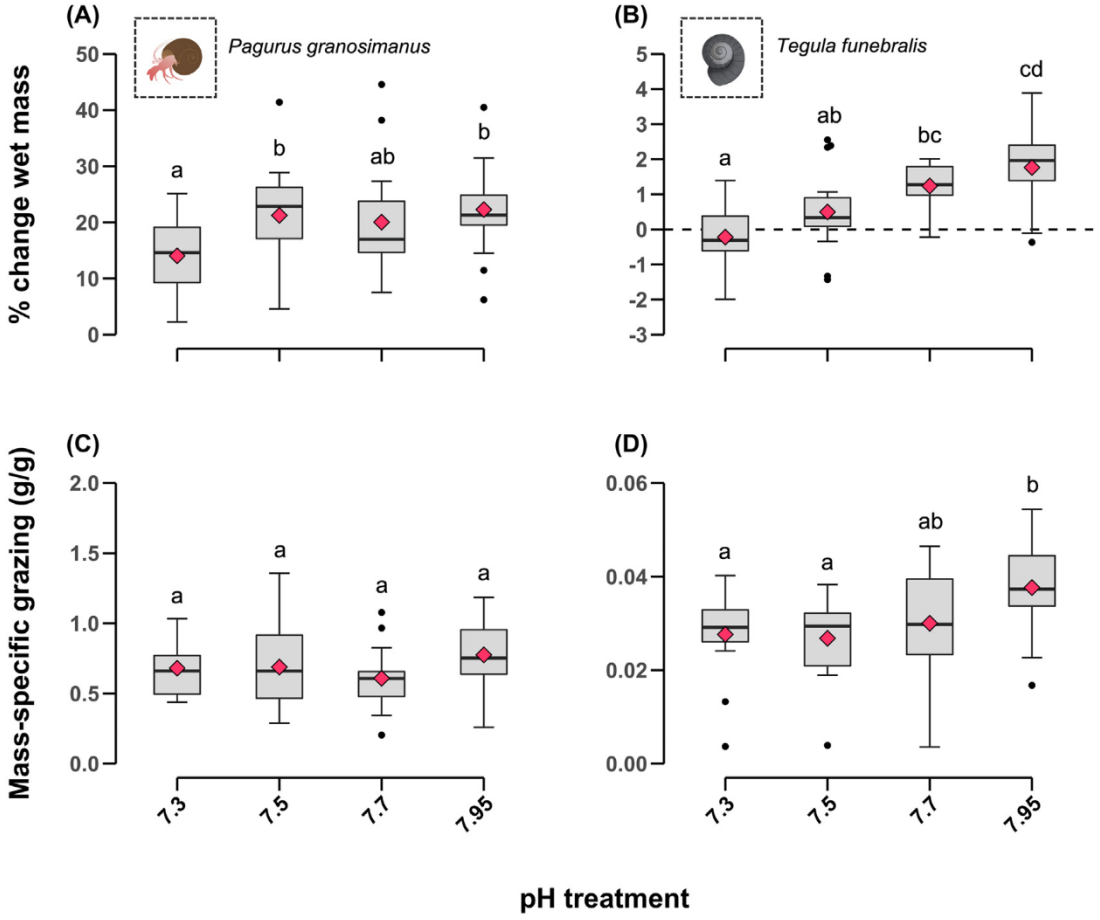


Fig. 5. Effects of ocean acidification on grazer feeding and growth rate (Experiment 2). Box plots showing percent changes in grazer blotted wet mass (panel A: hermit crab, B: snail) and feeding rate (panel C: hermit crab, D: snail) under the varying pH conditions (pH 7.3, 7.5, 7.7, and 7.95). The grazer feeding rate was estimated as dry algal mass loss per grazer biomass for each feeding chamber unit. The scale of Y-axis differs between the grazer species because experimental snails weighed significantly more than hermit crabs (>15 times) and showed limited growth during Experiment 2. In box plots, mean values are represented by red diamond symbols. Different letters indicate a significant difference ($p < 0.05$) based on Holm-adjusted post-hoc contrasts. Images: snail (Tracy Sutton) and hermit crab (Lantapix).

tolerance of hermit crabs was likely critical to the maintenance of community-level grazing pressure under acidification. Ultimately, the strong top-down control of algae under OA, combined with the positive effects of altered carbonate chemistry on surfgrass, resulted in grazers and acidification additively increasing surfgrass performances. These results corroborate previous findings that seagrass communities are generally resilient to OA (Eklöf et al., 2012; Hughes et al., 2018). More broadly, they highlight how resilient, strongly interacting species could drive community dynamics under global change and the importance of considering direct and indirect effects in scaling the impacts of anthropogenic stressors.

Numerous examples from terrestrial and aquatic communities show that different morpho-behavioral adaptations in species (e.g., feeding biomechanics and behaviors, and body sizes) underlie complementarity in ecological functions (Bueno et al., 2013; Burkepile and Hay, 2008). The differential grazing impacts of snails and hermit crabs on algal epiphytes could be explained by their varying abilities to forage in surfgrass canopy. Both grazers were capable of feeding throughout different surfgrass microhabitats. However, hermit crabs are better suited to climbing and clinging onto narrow blades of surfgrass owing to their articulated appendages, whereas snails are more specialized in grazing over hard flat surfaces. In Experiment 1, hermit crabs were ~4 times more likely to be found in surfgrass canopy than snails. Likewise, in the field, hermit crabs showed >6 times greater density than snails in the canopy, whereas snails showed >6 times greater density than hermit crabs near the shoot base and seafloor. Hence, these grazers likely play complementary, rather than redundant, roles (Micheli and Halpern, 2005), with hermit crabs more effectively controlling algal epiphytes growing on seagrass, and snails exerting potentially stronger effects on benthic macroalgae (Nielsen, 2001). Both grazers weakly affected macroalgal growth in Experiment 1. However, this is because macroalgae recruiting to mesocosms were mostly free-floating *Ulva*, which grazers could not feed effectively.

Greater pH tolerance of hermit crab vs. snail grazers was expected based on previous findings (e.g., Kroeker et al., 2010, 2011). Compared to shell-forming mollusks, crustaceans may better tolerate acidification due to relatively lower $CaCO_3$ body composition and ability to effectively maintain intracellular pH through ion-transport regulation (Wheatly and Henry, 1992). Studies have also shown that the snail species is prone to extreme pH (e.g., 0.5 to 1.1 decrease in mean seawater pH) and can display altered anti-predatory or feeding behaviors and reduced growth under acidification (Barclay et al., 2019; Jellison and Gaylord, 2019; Jellison et al., 2016). Granted, reduced grazer performances were found only under extreme pH (pH 7.3 and 7.5) that are well beyond the projected oceanic pH by the end of the 21st century (Bopp et al., 2013; Gattuso et al., 2015; Pachauri et al., 2014). However, these pH values reflect conditions surfgrass communities regularly face – albeit temporarily – in their habitats. For example, tide pools inhabited by surfgrass can exhibit substantial diel pH fluctuations (e.g., pH 7.22–9.0) due to intense respiration during night-time and photosynthetic activities during mid-day (Jellison et al., 2016; Kwiatkowski et al., 2016; Tharaldson, 2018). The strong environmental fluctuation inherent in intertidal systems could partly explain the

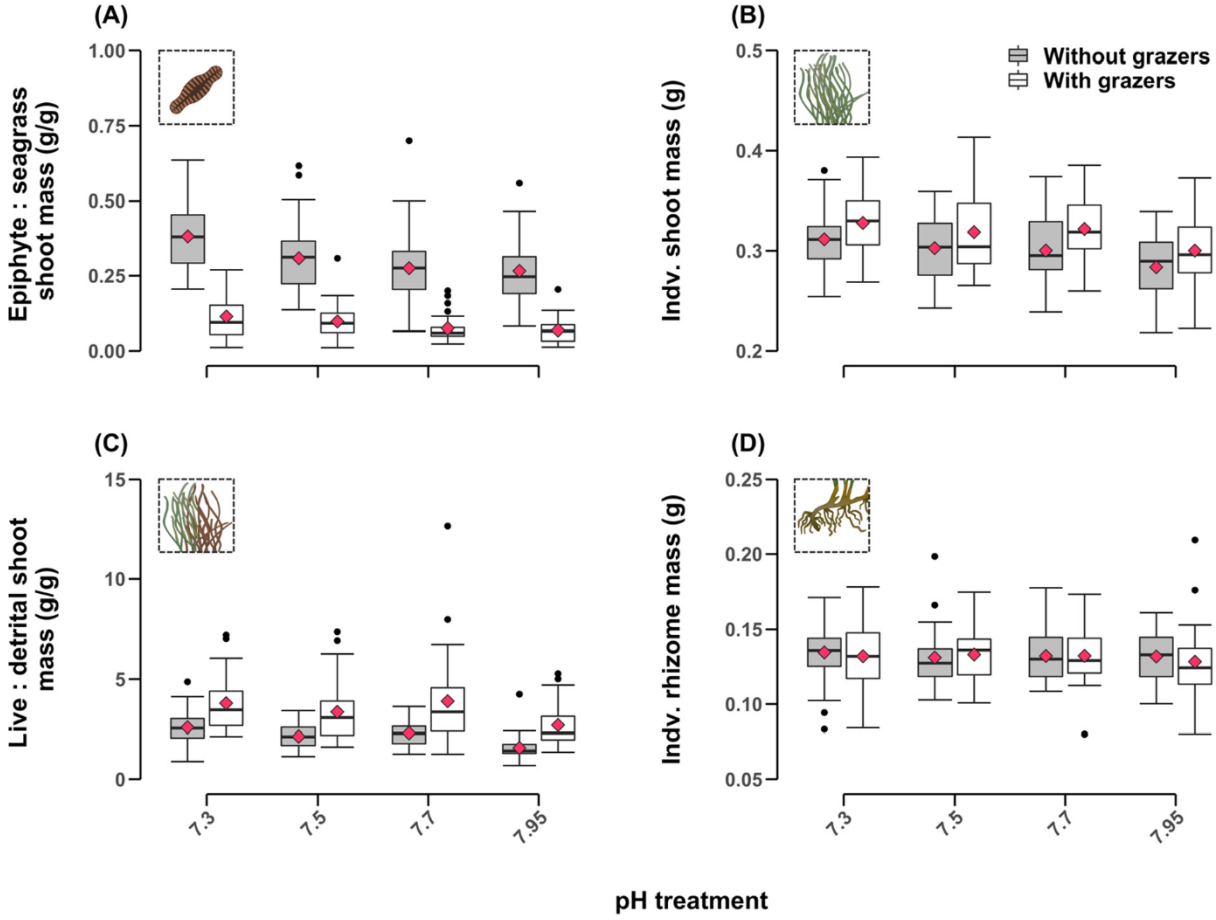


Fig. 6. Effects of grazer and ocean acidification on epiphyte biomass and seagrass performances (Experiment 3). Box plots showing (A) standardized epiphyte biomass, (B) average aboveground biomass of individual seagrass shoots surviving the experiment, (C) the ratio between live and detrital shoot mass, and (D) average biomass of individual seagrass rhizomes under the varying pH conditions (pH 7.3, 7.5, 7.7, and 7.95) and in the presence or absence of grazers. Algal and seagrass measurements on day-12 and 23 are pooled for data visualization. In box plots, mean values are represented by red diamond symbols. Different colors indicate different grazer treatment groups. Seagrass image: Tracey Saxby (IAN Image Library).

absence of acute responses among the grazers (e.g., OA-driven mortality) and their functional resilience under extreme OA.

Consistent with a previous study (Hughes et al., 2018), recruitment and growth of epiphytic algae increased with acidification, imposing a greater competition for seagrass. This effect was pronounced during the initial phase of Experiment 3 (by day-12), as the bloom more rapidly increased algal mass and overwhelmed grazing under extreme OA (pH 7.3 and 7.5). By day-23, however, grazers had reduced the algal mass to the minimum level in all treatment groups, which explained the strong sampling (time) × pH effects on algal biomass. Several mechanisms likely contributed to the maintenance of overall grazing pressure under OA, despite increased algal loading and reduced performance in one of the key grazer species. First, because snails play a significantly weaker role in controlling algal epiphytes, their reduced grazing may have led to relatively small changes in overall grazing pressure. Second, whereas OA can cause compensatory feeding in some marine consumers (e.g., Ghedini et al., 2015), we did not observe changes in hermit crab's feeding rate or behavior under OA that would have compensated for reduced snail grazing. Nonetheless, it is still possible that reduced competition with or interference from snails may have enhanced the per-capita grazing impact of hermit crabs (e.g., Eklöv and Werner, 2000). Third, our experiment simulated a moderate-to-high grazer density found in pristine tide pool habitats. Perhaps, a sufficiently high grazer density allowed the grazer assemblage as a whole to control algae effectively despite reduced grazing pressure exerted by snails. It is unclear whether acidification may have further modified the top-down control of epiphytes through changes in algal palatability. Altered carbonate chemistry may change the community composition and physicochemical properties (e.g., chemical defense, nutrient contents) of marine algae, which, in turn, could directly affect grazer consumption (Duarte et al., 2016; Fieber and Bourdeau, 2021; Kroeker et al., 2013). Further investigation is thus needed on if and how OA alters algal traits or species composition and how these changes might influence grazer-algae interactions and surfgrass community dynamics.

We predicted OA would favor algal epiphytes over seagrass, and that, in the absence of grazers, intensified competition from algae would offset any physiological benefits seagrass gains from elevated CO_2. However, even without grazers and under increased algal loading, surfgrass exhibited a higher growth rate and delayed senescence under OA, which is consistent with previous findings in other seagrass species (e.g., Hughes et al., 2018). This resistance is likely related to increased resource availability directly enhancing seagrass productivity (Koch et al., 2013; Zimmerman et al., 2015) and shifting the strength of interspecific competitions (Hughes et al., 2018). We further show that acidification and grazing have independent, positive effects on surfgrass performances, with surfgrass attaining the highest growth rate under the lowest pH and in the presence of grazers. This additive effect of OA and grazing highlights the importance of considering multiple interaction pathways (i.e., direct vs. indirect and bottom-up vs. top-down effects) when assessing the community consequence of global stressors.

Although our findings point to the resistance of seagrass communities to OA, more research is needed to establish the general relationship between

this stressor and seagrass ecosystem dynamics. First, we only assessed the short-term effects of OA on grazer feeding, growth, and survival. Our grazer-rearing experiment (Experiment 2) lasted 17 days, which may have been too short for adequately assessing the growth response of slow-growing species such as *T. funebralis* (Barclay et al., 2019). Moreover, it remains uncertain how OA-induced changes in grazers' growth and feeding rate might affect their long-term fitness and population success. A more in-depth examination of grazers' life-history performances (e.g., food consumption and assimilation, survival, and reproduction) over prolonged OA-exposure would provide valuable insights into the long-term shifts in seagrass community dynamics (Hughes et al., 2018). Second, to test our hypotheses, we employed a simplified experimental assemblage comprised of only the most abundant and conspicuous consumers. However, seagrasses often host taxonomically and functionally diverse grazer species (Duffy et al., 2001; Eklöf et al., 2012), and grazer communities can vary a great deal in time and space (Gullström et al., 2012). Thus, future research would benefit from employing a study design that considers these natural community variabilities. Third, because we only focused on the interaction between grazers and epiphytic algae, further investigation is needed on how OA influences other algal components in surfgrass communities. For instance, elevated CO_2 and reduced snail grazing under OA could release benthic macroalgae (e.g., *Ulva* spp.) (Kang et al., 2021), which may negatively impact surfgrass performances. Finally, OA will likely affect surfgrass communities in conjunction with other stressors, such as warming and eutrophication (Hughes et al., 2018; Koch et al., 2013). As stressors can interact with one another to drive complex changes in ecological processes (Low and Micheli, 2020; Ng and Micheli, 2020), predictions on surfgrass community dynamics should incorporate these multiple stressor perspectives.

Our study points to the importance of strongly interacting species in modulating community and ecosystem dynamics under stressors. This may be especially true for low-diversity communities where individual species or traits have disproportionately large contributions to ecosystem functioning (Arenas et al., 2006; Schweiger et al., 2018; Smith and Knapp, 2003). In our study system, strongly interacting grazers were also highly stressor-tolerant; and these species played a crucial role in maintaining top-down pressure and enhancing community resistance under increasing stress. However, in other communities, species functions and stressor sensitivities could be correlated in ways that such species are more susceptible to external stressors (Larsen et al., 2005; Suding et al., 2008). As strong species interactions deteriorate and are not adequately compensated, the likelihood of reaching tipping points and ecosystem collapse may increase drastically.

Predicting and managing ecosystem thresholds, resistance, and resilience in the face of global change remains challenging for scientists, managers, and policymakers. We show that the processes governing ecosystem dynamics may shift less predictably due to response variabilities within functional groups. Our findings emphasize the importance of understanding the natural history of focal communities in global change research and ecosystem management. Only through examining heterogeneous relationships between species functions and stressor-sensitivities in each ecological assemblage of interest may we start making relevant predictions for future ecosystem changes.

CRediT authorship contribution statement

JL, FM, and KK designed all ocean acidification experiments (Exp. 2 and 3). BH and KK built the control system used for the ocean acidification experiment. JL, CW, and AO designed Experiment 1 and CW and JL conducted Experiment 1. JL analyzed the data. JL, FM, KK, and BH wrote the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Kairi Tezuka, Audrey Bennet, Freya Chay, Cheryl Butner, Min-Sun Lee, and Nathan Myers for their assistance with field surveys and laboratory experiments. We also thank Emily Donham for helping to operate and maintain the pH control system. We are grateful to James Watanabe, Mark Denny, and Kabir Peay for their insightful comments on the manuscript. Our work was funded by Arthur C. Giese Award (Hopkins Marine Station Graduate Student Award). Finally, we dedicate this paper to the late John Pearse, whose life-long work has been inspirational to this study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.151594.

References

Arenas, F., Sánchez, I., Hawkins, S.J., Jenkins, S.R., 2006. The invasibility of marine algal assemblages: role of functional diversity and identity. Ecology 87, 2851–2861.
Atwood, T.B., Connolly, R.M., Ritchie, E.G., Lovelock, C.E., Heithaus, M.R., Hays, G.C., Fourqurean, J.W., Macreadie, P.I., 2015. Predators help protect carbon stocks in blue carbon ecosystems. Nat. Clim. Chang. 5, 1038–1045.
Barclay, K.M., Gaylord, B., Jellison, B.M., Shukla, P., Sanford, E., Leighton, L.R., 2019. Variation in the effects of ocean acidification on shell growth and strength in two intertidal gastropods. Mar. Ecol. Prog. Ser. 626, 109–121.
Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.
Berlow, E.L., 1999. Strong effects of weak interactions in ecological communities. Nature 398, 330–334.
Best, R.J., Stachowicz, J.J., 2012. Trophic cascades in seagrass meadows depend on mesograzer variation in feeding rates, predation susceptibility, and abundance. Mar. Ecol. Prog. Ser. 456, 29–42.
Blüthgen, N., Klein, A.M., 2011. Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. Basic Appl. Ecol. 12, 282–291.
Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127–135.
Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Seferian, R., 2013. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. Biogeosciences 10, 6225–6245.
Bueno, R.S., Guevara, R., Ribeiro, M.C., Culot, L., Bufalo, F.S., Galetti, M., 2013. Functional redundancy and complementarities of seed dispersal by the last neotropical megafrugivores. PLoS One 8, e56252.
Burkepile, D.E., Hay, M.E., 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc. Natl. Acad. Sci. 105, 16201–16206.
Castañeda-Fernández De Lara, V., Butler, M., Hernández-Vázquez, S., GuzmdndelProo, S., Serviere-Zaragoza, E., 2005. Determination of preferred habitats of early benthic juvenile California spiny lobster, Panulirus interruptus, on the Pacific coast of Baja California Sur, Mexico. Mar. Freshw. Res. 56, 1037–1045.
Connell, S.D., Doubleday, Z.A., Hamlyn, S.B., Foster, N.R., Harley, C.D., Helmuth, B., Kelaher, B.P., Nagelkerken, I., Sarà, G., Russell, B.D., 2017. How ocean acidification can benefit calcifiers. Curr. Biol. 27, R95–R96.
Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. 11, 1304–1315.
Duarte, C., López, J., Benítez, S., Manríquez, P.H., Navarro, J.M., Bonta, C.C., Torres, R., Quijón, P., 2016. Ocean acidification induces changes in algal palatability and herbivore feeding behavior and performance. Oecologia 180, 453–462.
Duffy, J.E., Macdonald, K.S., Rhode, J.M., Parker, J.D., 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. Ecology 82, 2417–2434.
Eklöf, J.S., Alsterberg, C., Havenhand, J.N., Sundbäck, K., Wood, H.L., Gamfeldt, L., 2012. Experimental climate change weakens the insurance effect of biodiversity. Ecol. Lett. 15, 864–872.
Eklöv, P., Werner, E.E., 2000. Multiple predator effects on size-dependent behavior and mortality of two species of anuran larvae. Oikos 88, 250–258.
Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change, and resilience. Front. Ecol. Environ. 1, 488–494.
Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., Sloat, L.L., Savage, V.M., 2015. Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. Adv. Ecol. Res. 52, 249–318.
Erlandson, J.M., Ainis, A.F., Braje, T.J., Jew, N.P., McVey, M., Rick, T.C., Vellanoweth, R.L., Watts, J., 2015. 12,000 years of human predation on black turban snails (Tegula funebralis) on Alta California's northern Channel Islands. Calif. Archaeol. 7, 59–91.
Fieber, A.M., Bourdeau, P.E., 2021. Elevated pCO2 reinforces preference among intertidal algae in both a specialist and generalist herbivore. Mar. Pollut. Bull. 168, 112377.
Galst, C.J., Anderson, T.W., 2008. Fish–habitat associations and the role of disturbance in surfgrass beds. Mar. Ecol. Prog. Ser. 365, 177–186.

Gattuso, J.-P., Magnan, A., Billé, R., Cheung, W.W., Howes, E.L., Joos, F., Allemand, D., Bopp, L., Cooley, S.R., Eakin, C.M., 2015. Contrasting futures for ocean and society from different anthropogenic CO2 emissions scenarios. Science 349, aac4722.
Ghedini, G., Russell, B.D., Connell, S.D., 2015. Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances. Ecol. Lett. 18, 182–187.
González-Varo, J.P., Biesmeijer, J.C., Bommarco, R., Potts, S.G., Schweiger, O., Smith, H.G., Steffan-Dewenter, I., Szentgyörgyi, H., Woyciechowski, M., Vilà, M., 2013. Combined effects of global change pressures on animal-mediated pollination. Trends Ecol. Evol. 28, 524–530.
Gullström, M., Baden, S., Lindegarth, M., 2012. Spatial patterns and environmental correlates in leaf-associated epifaunal assemblages of temperate seagrass (Zostera marina) meadows. Mar. Biol. 159, 413–425.
Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, e1500052.
Hawlena, D., Schmitz, O.J., 2010. Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. Proc. Natl. Acad. Sci. 107, 15503–15507.
Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., 2007. Coral reefs under rapid climate change and ocean acidification. Science 318, 1737–1742.
Honig, S.E., Mahoney, B., Glanz, J.S., Hughes, B.B., 2017. Are seagrass beds indicators of anthropogenic nutrient stress in the rocky intertidal? Mar. Pollut. Bull. 114, 539–546.
Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., O'Connor, M.I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486, 105–108.
Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? Trends Ecol.Evol. 15, 56–61.
Hughes, B.B., Eby, R., Van Dyke, E., Tinker, M.T., Marks, C.I., Johnson, K.S., Wasson, K., 2013. Recovery of a top predator mediates negative eutrophic effects on seagrass. Proc. Natl. Acad. Sci. 110, 15313–15318.
Hughes, B.B., Lummis, S.C., Anderson, S.C., Kroeker, K.J., 2018. Unexpected resilience of a seagrass system exposed to global stressors. Glob. Chang. Biol. 24, 224–234.
Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.
Jellison, B.M., Gaylord, B., 2019. Shifts in seawater chemistry disrupt trophic links within a simple shoreline food web. Oecologia 190, 955–967.
Jellison, B.M., Ninokawa, A.T., Hill, T.M., Sanford, E., Gaylord, B., 2016. Ocean acidification alters the response of intertidal snails to a key sea star predator. Proc. R. Soc. B. 283, 20160890.
Kang, E.J., Han, A.R., Kim, J.H., Kim, I.N., Lee, S., Min, J.O., Nam, B.R., Choi, Y.J., Edwards, M.S., Diaz-Pulido, G., 2021. Evaluating bloom potential of the green-tide forming alga Ulva ohnoi under ocean acidification and warming. Sci. Total Environ. 769, 144443.
Koch, M., Bowes, G., Ross, C., Zhang, X.H., 2013. Climate change and ocean acidification effects on seagrasses and marine macroalgae. Glob. Chang. Biol. 19, 103–132.
Kroeker, K.J., Kordas, R.L., Crim, R.N., Singh, G.G., 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecol. Lett. 13, 1419–1434.
Kroeker, K.J., Micheli, F., Gambi, M.C., Martz, T.R., 2011. Divergent ecosystem responses within a benthic marine community to ocean acidification. Proc. Natl. Acad. Sci. 108, 14515–14520.
Kroeker, K.J., Micheli, F., Gambi, M.C., 2013. Ocean acidification causes ecosystem shifts via altered competitive interactions. Nat. Clim. Chang. 3, 156–159.
Kwiatkowski, L., Gaylord, B., Hill, T., Hosfelt, J., Kroeker, K.J., Nebuchina, Y., Ninokawa, A., Russell, A.D., Rivest, E.B., Sesboüé, M., 2016. Nighttime dissolution in a temperate coastal ocean ecosystem increases under acidification. Sci. Rep. 6, 22984.
Larsen, T.H., Williams, N.M., Kremen, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecol. Lett. 8, 538–547.
Low, N.H., Micheli, F., 2020. Short- and long-term impacts of variable hypoxia exposures on kelp forest sea urchins. Sci. Rep. 10, 1–9.
Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett. 8, 391–400.
Ng, C.A., Micheli, F., 2020. Short-term effects of hypoxia are more important than effects of ocean acidification on grazing interactions with juvenile giant kelp (Macrocystis pyrifera). Sci. Rep. 10, 1–11.
Nielsen, K.J., 2001. Bottom-up and top-down forces in tide pools: test of a food chain model in an intertidal community. Ecol. Monogr. 71, 187–217.
Niu, S., Wan, S., 2008. Warming changes plant competitive hierarchy in a temperate steppe in northern China. J. Plant Ecol. 1, 103–110.
Nordlund, L.M., Koch, E.W., Barbier, E.B., Creed, J.C., 2016. Seagrass ecosystem services and their variability across genera and geographical regions. PLoS One 11, e0163091.
Orth, R.J., Carruthers, T.J., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., 2006. A global crisis for seagrass ecosystems. Bioscience 56, 987–996.
Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., Church, J.A., Clarke, L., Dahe, Q., Dasgupta, P., Dubash, N.K., 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, Switzerland.
Palacios, S.L., Zimmerman, R.C., 2007. Response of eelgrass Zostera marina to CO2 enrichment: possible impacts of climate change and potential for remediation of coastal habitats. Mar. Ecol. Prog. Ser. 344, 1–13.
Pearse, J.S., Doyle, W.T., Pearse, V.B., Gowing, M.M., Pennington, J.T., Danner, E., Wasser, A., 2015. Long-term Monitoring of Surfgrass Meadows in the Monterey Bay National Marine Sanctuary: Recovery Followed by Stability After the Termination of a Domestic Sewage Discharge. Marine Sanctuaries Conservation Series ONMS-15-10. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries.
Phillips, R.C., Menez, E.G., 1988. Seagrasses. Smithson. Contrib. Mar. Sci. 34, 1–104.
Pimm, S.L., 1984. The complexity and stability of ecosystems. Nature 307, 321–326.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2020. nlme: linear and nonlinear mixed effects models. R package version 3.1-145. https://CRAN.R-project.org/package=nlme.
Post, E., Peterson, R.O., Stenseth, N.C., McLaren, B.E., 1999. Ecosystem consequences of wolf behavioural response to climate. Nature 401, 905–907.
R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Reynolds, P.L., Richardson, J.P., Duffy, J.E., 2014. Field experimental evidence that grazers mediate transition between microalgal and seagrass dominance. Limnol. Oceanogr. 59, 1053–1064.
Ruesink, J.L., 2000. Intertidal mesograzers in field microcosms: linking laboratory feeding rates to community dynamics. J. Exp. Mar. Biol. Ecol. 248, 163–176.
Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Hobbie, S.E., Madritch, M.D., Wang, R., Tilman, D., Gamon, J.A., 2018. Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. Nat. Ecol. Evol. 2, 976–982.
Shelton, A.O., 2010. Temperature and community consequences of the loss of foundation species: surfgrass (Phyllospadix spp., Hooker) in tidepools. J. Exp. Mar. Biol. Ecol. 391, 35–42.
Silliman, B.R., He, Q., 2018. Physical stress, consumer control, and new theory in ecology. Trends Ecol. Evol. 33, 492–503.
Smith, M.D., Knapp, A.K., 2003. Dominant species maintain ecosystem function with non-random species loss. Ecol. Lett. 6, 509–517.
Suding, K.N., Lavorel, S., Chapin Iii, F.S., Cornelissen, J.H., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., Navas, M.L., 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Glob. Chang. Biol. 14, 1125–1140.
Tharaldson, T.M., 2018. The Ability of Phyllospadix spp., A Pair of Intertidal Foundation Species, to Maintain Biodiversity And Ameliorate CO2 Stress in Rocky Shore Tidepools. Humboldt State University Master Dissertation.
Waycott, M., Duarte, C.M., Carruthers, T.J., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. 106, 12377–12381.
Wheatly, M.G., Henry, R.P., 1992. Extracellular and intracellular acid-base regulation in crustaceans. J. Exp. Zool. 263, 127–142.
Willcocks, P.A., 1982. Colonization and distribution of the red algal epiphytes Melobesia mediocris and Smithora naiadum on the seagrass Phyllospadix torreyi. Aquat. Bot. 12, 365–373.
Williams, S.L., Ruckelshaus, M.H., 1993. Effects of nitrogen availability and herbivory on eelgrass (Zostera marina) and epiphytes. Ecology 74, 904–918.
Winfree, R., Fox, J.W., Williams, N.M., Reilly, J.R., Cariveau, D.P., 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecol. Lett. 18, 626–635 Master Dissertation.
Zimmerman, R.C., Hill, V.J., Gallegos, C.L., 2015. Predicting effects of ocean warming, acidification, and water quality on Chesapeake region eelgrass. Limnol. Oceanogr. 60, 1781–1804.