



NOTE

Macroalgal presence decreases coral calcification rates more than ocean acidification

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Abstract Global coral reef degradation has precipitated phase shifts toward macroalgal-dominated communities. Despite the negative repercussions for reefs, higher abundances of primary producers have the potential to positively impact the physicochemical environment and mitigate negative impacts of ocean acidification (OA). In this study, we investigated the influence of macroalgal (cf. *Sargassum vulgare*) density on coral (*Acropora millepora* and *A. hemprichii*) calcification rates under current and future OA conditions. Corals were resistant to OA up to ~1100 μatm , with no changes in calcification rates. However, the presence of

(low and high density) algae reduced calcification rates by ~41.8%, suggesting either a chemical defense response due to algal metabolites or potential physical impacts from shading or abrasion. Documented beneficial buffering effects of macroalgae in OA may also elicit negative impacts on coral calcification, suggesting further work is needed to elucidate how species interactions influence responses to projected climate change.

Keywords Calcification · Ocean acidification · Coral · Acropora · Macroalgae · Sargassum

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Introduction

Coral reef ecosystem degradation due to climate change impacts can alter reef community structure, potentially causing phase shifts toward macroalgal-dominated reefs (Graham et al. 2015). As a result, coral cover continues to decline in most reef ecosystems worldwide, resulting from the combination of local and global disturbances (Sully et al. 2022). Local disturbances on coral reefs include point source pollution, sedimentation, eutrophication, extreme weather events (Fabricius et al. 2008), and predator outbreaks (Ban et al. 2014). Global stressors include warming seawater temperatures due to elevated atmospheric CO₂ that ultimately lead to higher disease prevalence and weakened coral immunity responses, as well as causing global bleaching events (Ban et al. 2014). However, the potential for local and global stressors to interact is particularly alarming due to the likelihood that compounding effects could exacerbate the deterioration of coral reef structural integrity (Tebbett et al. 2023).

Evidence shows decadal scale recovery stimulated through coral larval recruitment is possible (Gilmour et al. 2013). However, repeated disturbances across a short

temporal scale impede recovery trajectories (Hughes et al. 2018). Fleshy macroalgae, in particular, outcompete slower-growing corals for resources (e.g., nutrients, light, and space) by rapid colonization of bare substrata post-disturbance events (McManus and Polsenberg 2004).

Elevated $p\text{CO}_2$ from anthropogenic sources are generally associated with increased growth rates in fleshy macroalgal species (Johnson et al. 2014). Algae tend to benefit from increased CO_2 and associated OA conditions, while flexible HCO_3^- users are less affected by fluctuations in chemical conditions (Ho et al. 2020). From a larger ecological perspective, understanding of the effects of OA on reefs that have shifted to dominance by macroalgae is still limited. Specifically, there is a need to explore how species interactions might influence coral growth rates, which could be altered by the presence of fleshy macroalgae. Some evidence indicates that photosynthesizing organisms have the ability to buffer against impacts of OA by elevating localized pH in the microenvironment (Bergstrom et al. 2019; Doo et al. 2020). However, relatively little is known about the impacts of coral–macroalgal interactions on coral growth under projected OA.

The Red Sea presents a unique opportunity to understand future global change impacts on reefs as daily sea surface temperatures can exceed 31 °C in the Central region and 33 °C in the South during the summer (Chaidez et al. 2017). In addition to disturbance events due to climate change and industry (e.g., Carvalho et al. 2019), extreme temperatures also cause disturbances such as coral bleaching which occur in the region (Eladawy et al. 2022). These disturbances can lead to a decline in coral cover and an increase in macroalgal cover, resulting in more coral–macroalgal interactions. Increased competition and greater potential for macroalgal phase shifts are potential outcomes as OA intensifies. Therefore, we exposed common reef-building *Acropora* spp. from the Central Red Sea to varying densities of *Sargassum* spp. and two $p\text{CO}_2$ (475 and 1050 μatm) treatments. We simulated macroalgal-dominated reefs and future OA conditions, respectively, to quantify the potential physiological impact of macroalgae on coral calcification rates in the near future. Results from this study offer insight into how varying densities of macroalgae may interact with projected global climate change stressors (i.e., OA) to modulate calcification rates of common reef-building corals.

Methods

Colony collection and treatments

In April 2022, fragments (3–5 cm) of *Acropora* spp. (composed of species *millepora*, *hemprichii*) were collected from Al Fahal Northern Reef in Saudi Arabia (22.296863°N,

38.964912°E). A maximum of 10 nubbins were collected from each coral colony, with colonies at a minimum of 10 m apart to ensure different genotypes (Baums et al. 2006). *Sargassum* sp. (cf. *vulgare*; herein referred to as *Sargassum*) were collected from the King Abdullah Monument Reef (22.343043°N, 39.084190°E) three weeks prior to the start of the experiment. Nubbins were glued (Seachem Reef Glue) onto 5 × 5 cm white acrylic tiles and acclimated for 70 days in ambient (hereafter defined as the present day ocean conditions; i.e., no CO_2 enhancement) flow-through conditions prior to the experiment. This experiment was conducted in the indoor temperature-controlled SeaLabs aquaria space.

Incubation conditions and experimental design

Eighteen continuous flow-through mesocosm tanks (22 L volume each) were supplied with sand-filtered seawater at $\sim 600 \text{ mL min}^{-1}$. Within each tank, an elevated acrylic stand containing six coral nubbins ($N = 108$) on acrylic tiles was randomly allocated and placed on the top of each rack. Algal treatments consisted of a control treatment (NA; no algal density) and two experimental treatments (HA; high algal density or LA; low algal density). In the algal treatments, eight (HA) or four (LA) bundles of *Sargassum* were secured using zipties to the outside border of the rack. Wet weights for each algal group were calculated by placing samples in a spinner (15 revolutions) to remove excess seawater, followed by gentle blotting with a paper towel prior to weighing. Algae were weighed at the beginning and end of the 34-day experiment to determine growth rates, with initial wet weights ranging from 35.3 to 45.1 g per rack in the LA group to 57.8–70.1 g per rack in the HA group. Care was taken to minimize physical interaction of the algae with coral nubbins; however, during the experiment, algae grew and this interaction was unavoidable.

Light was provided by LED lamps (CoralCare LED Gen2 UK WH) operating on a 12:12 h light/dark photoperiod with a 6-h ramp-up and ramp-down period, and 2 h of maximum light. Maximum PAR supplied to the treatment was $\sim 230 \mu\text{mol m}^{-2} \text{ s}^{-1}$, which was measured twice per week using a 2-pi PAR sensor (Apogee Instruments MQ-500). Small aquaria pumps (AC-1020 Submersible) were placed in each replicate tank to ensure algae and coral received appropriate flow conditions.

CO_2 seawater manipulation

Seawater to all tanks was fed through one of two header tanks (155L). In the ambient sump, sand-filtered seawater was fed into the sump and circulated via an aquarium pump (Aqua Medic DC runner 3.2), which supplied ambient seawater (7.96–8.00 pH; see Table S1) to nine tanks (three NA, three LA, three HA treatments). In the elevated CO_2 sump,

an Apex Neptune Aquacontroller system was used to control the remaining nine tanks (three NA, three LA, three HA treatments) by a solenoid that supplied pure CO₂ gas to the sump. In this high CO₂ treatment, the treatment was targeted at ~0.3 pH units below the ambient (7.70 pH target) sump, correspondent to a target pCO₂ level of ~1000 µatm which is a value predicted to occur under the RCP 8.5 “business-as-usual” scenario. Seawater pH, salinity, temperature, and dissolved oxygen were measured every day using a calibrated YSI ProDSS Multiparameter Digital Water Quality Meter probe (Table S1). Total alkalinity samples were collected ~2 times a week and the accuracy/precision was evaluated using certified reference materials (CRMs; Batch #172 from A. Dickson Laboratory).

Calcification measurements

The effects of algal density on coral calcification were determined by changes in buoyant weight over the 34-day experiment. The change in buoyant weight, which represents changes in skeletal weight, was then converted to dry mass of CaCO₃ using the density of aragonite (2.93 g cm⁻³), and the density of seawater (Spencer Davies 1989).

Surface area inference

Surface area of all coral nubbins was determined by applying a constant generated from a subset of 20 acroporid corals that were buoyant weighed. Surface area was calculated by structure-from-motion and planar photographs (minimum 100 photographs per nubbin), following established methods outlined in (Lange and Perry 2020). Photographs were aligned in Agisoft Metashape, and a mesh was generated. Surface area of corals was then calculated with CloudCompare using generated mesh. Nubbin dry weight was modeled as a function of the calculated surface area (Fig. S1). A scaling factor was generated from the linear model and then applied to the entire data set to extrapolate surface area from dry weights (see Online Resource).

Statistical analysis

The effects of pCO₂ and algal density on calcification rates of *Acropora* spp. were analyzed with a blocked two-way ANOVA design. Assumptions for ANOVA were tested and met for homogeneity of variance through the Bartlett test and visual inspection of residual plots for normality. Tank was initially included in the model as a random factor and pCO₂ (ambient vs. high) and algal density (NA, LA, HA) were included as fixed factors. Tank factor was not significant ($p=0.999$) and was removed from the model, and subsequently rerun as a two-way ANOVA with pCO₂ and algal

density as fixed factors, and calcification rate as the response variable.

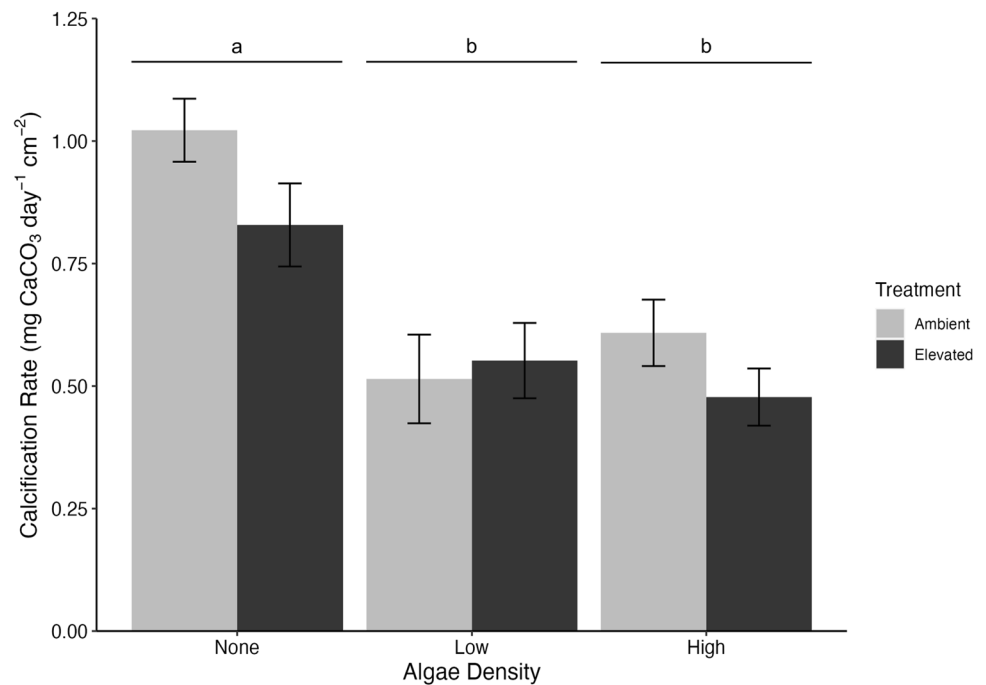
Results and discussion

An emerging paradigm in coral reef research is that macroalgae may provide refugia to corals and other calcifying species from the deleterious effects of OA, through the photosynthetic removal of CO₂ that elevates the pH of the surrounding microenvironment (Cornwall et al. 2013; Doo et al. 2020). However, we observed a trend that suggested no macroalgal buffering under OA, and contrary to previous studies on weedy acroporid species, there was no effect of pCO₂ (up to ~1100 µatm) on *A. millepora* and *A. hemprichii* calcification rates in our study (Fig. 1) ($F_{1,100}=2.92$, $p=0.091$; Table S2). Further, coral calcification decreased significantly by 41.8% in the experimental tanks with macroalgae ($F_{2,100}=18.22$, $p<0.001$; Table S2), while differences in coral calcification rate at various algal densities (LA vs. HA treatment groups) were not significantly different from each other (Fig. 1). There was no interaction between pCO₂ and algal density ($F_{2,100}=1.28$, $p=0.284$; Table S2). These patterns indicate that the mere presence of *Sargassum* was detrimental to coral calcification, showing subtle complexities that influence coral–algal competition on calcification rates that are independent of carbonate chemistry.

Many macroalgal species, including *Sargassum* used in this study, contain allelopathic chemical compounds which aid in protection against herbivory and competition (Budzałek et al. 2021), but may also result in coral bleaching (Rasher and Hay 2014; Vieira et al. 2016). Despite negative effects on coral calcification, no coral individuals exhibited visual bleaching at the end of the experiment. Macroalgae have the potential to negatively influence corals through both direct and indirect competitive mechanisms. For example, the close physical proximity of corals and macroalgae in the treatments may have increased competition for space and light, resulting in shading effects due to algal overgrowth and physical abrasions that could have affected polyp growth and mortality (McCook et al. 2001). While we could not determine the exact mechanism of how macroalgal interactions with corals decreased calcification rate, the favorable conditions resulting in macroalgal growth over the course of the experiment may have resulted in decreased photosynthetic rates thereby limiting calcification. However, it is clear that a negative interaction was present, which highlights that further work is needed to disentangle these mechanisms, specifically in regard to light availability.

A commonly observed scenario of ongoing climate change within tropical marine ecosystems is the shift from coral dominated communities to turf/macroalgal-dominated alternate stable states (Hoegh-Guldberg et al. 2007;

Fig. 1 Rates of coral calcification in the three different algal density regimes between ambient and elevated $p\text{CO}_2$ treatments. Figure indicates mean \pm SE ($n = 18$, except low algal density under ambient $p\text{CO}_2$ conditions $n = 16$), and different letters indicate significant differences between treatments



Arias-González et al. 2017). Generally, fleshy macroalgal density is expected to increase under elevated $p\text{CO}_2$ due to the potential for more substrate for photosynthesis to increase algal growth rates (Koch et al. 2013). However, in our study, growth rates of *Sargassum* increased by an average 37.7 ± 3.0 g ($n = 12$) across all treatments for the duration of the experiment but were not significantly different between ambient and high $p\text{CO}_2$ treatments ($F_{1,8} = 1.26$, $p = 0.295$; Table S3). Furthermore, algal growth rates were ~ 25 times greater in the HA compared to the LA treatment group but they did not statistically differ ($F_{1,8} = 3.88$, $p = 0.084$; Table S3), and there was no interaction between $p\text{CO}_2$ treatments on algal growth rates ($F_{1,8} = 0.01$, $p = 0.910$; Table S3). The *Sargassum* used in this study is a species which uses carbon concentrating mechanisms (CCMs) for HCO_3^- to CO_2 conversion (Kumar et al. 2017, 2020). As such, macroalgae with CCMs are not expected to benefit as much from increased CO_2 compared to those lacking CCMs (Kübler et al. 1999). The macroalgae used in this study are likely adapted to large natural fluxes in physicochemical conditions and presumably experienced optimal growth conditions in the tanks (continuous growth and no degradation of macroalgae was observed); thus, the addition of CO_2 was not beneficial to growth rates. Additionally, corals in both high and low algal density treatments exhibited similar decreases in calcification, and these results could be because the chosen algal densities were not substantially different.

The Red Sea is characterized both by naturally high salinity (> 40.0 ppt) and high variation in temperatures, and the conditions at the collection site may fluctuate by several degrees each day (Safaie et al. 2018). These

regions of naturally elevated seawater temperatures are also potential locations for coral–algal phase shifts (turf and macroalgal) to occur due to increased bleaching events (McManus and Polsenberg 2004). Although the presence of macroalgae decreased coral calcification in our experiment regardless of algal density (Fong and Todd 2021), future research could provide valuable insights on these interactions by investigating potential tipping points where coral health is adversely affected by the proximity to macroalgae. This is particularly crucial as further ecological processes such as reduced herbivory can also contribute to macroalgal dominance (Bozec et al. 2019). As coral reef ecosystems are facing escalating threats associated with climate change, the ecological trajectories (e.g., cover) of foundation species in degraded reefs is crucial to understand. In our study, potential compensatory mechanisms (e.g., Leung et al. 2017) of *Sargassum* buffering of coral calcification rates in elevated $p\text{CO}_2$ were not observed. Our results emphasize the need for a more holistic approach to understanding tipping points that encompasses bio-diverse coral communities, and how changes in species interactions may be modulated in future multi-stressor environments.

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Declarations

Conflict of interest The authors declare no competing interests.

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