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Effects of pCO_2 on the interaction between an excavating sponge, *Cliona varians,* and a hermatypic coral, *Porites furcata*

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Abstract Rising dissolved pCO_2 is a mounting threat to coral reef ecosystems. While the biological and physiological impacts of increased pCO_2 are well documented for many hermatypic corals, the potential effects on bioerosion processes remain largely unknown. Increases in pCO_2 are likely to modify the direct interactions between corals and bioeroders, such as excavating sponges, with broad implications for the balance between biologically mediated deposition and erosion of carbonate in reef communities. This study investigated the effects of three levels of CO_2 (present-day, mid-century and end-of-century projections) on the direct interaction between a bioeroding sponge, *Cliona varians,* and a Caribbean coral, *Porites furcata*. Increased pCO_2 concentrations had no effect on the attachment rates of *C. varians* to the corals, and we observed no significant impact of pCO_2 on the survival of either the coral or sponges. However, exposure to end-of-century levels of CO_2-dosing (~750 µatm) reduced calcification in *P. furcata* and led to a significant increase in sponge-mediated erosion of *P. furcata*. These findings demonstrate that pCO_2 can enhance erosional efficiency without impacting survival or competitive vigor in these two species. While few studies have considered the influence of pCO_2 on the competitive outcomes of interactions between corals and other reef organisms, our study suggests that assessing the impacts of changing pCO_2 on species interactions is crucial to adequately predict ecosystem-level responses in the future.

Keywords Species interactions · Bioerosion · Cliona · Carbon dioxide · Acidification

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Introduction

Currently, atmospheric CO_2 levels fluctuate around 390 ppm and continue to rise at an accelerating rate (Caldeira and Wickett 2003, 2005); projected scenarios indicate that levels will approach 450–600 ppm by 2050 and 750–1,000 ppm by the end of the twenty-first century (IPCC 2007; Gattuso and Lavigne 2009). The resultant increase in dissolved seawater CO_2 is expected to reduce surface ocean pH by 0.3–0.4 units, substantially altering the carbonate chemistry of coastal marine ecosystems (Kleypas 1999; Guinotte and Fabry 2008; Doney et al. 2009). These changes in seawater pCO_2 will affect the physiological ability of organisms to precipitate calcium carbonate ($CaCO_3$) (Feely et al. 2004; Orr et al. 2005) and will therefore disproportionately impact ecosystems relying on the formation of biogenic carbonate structure, such as coral reefs (Hoegh-Guldberg et al. 2007; Andersson and Gledhill 2013).

Tropical studies investigating the effects of increasing pCO_2 have primarily focused on the biological responses of calcifying species, particularly the calcification processes of hermatypic corals and coralline algae (Gattuso et al. 1997; Kuffner et al. 2007; Anthony et al. 2008; Jokiel et al. 2008; Kurihara 2008; Albright and Langdon 2011; Diaz-Pulido et al. 2012). Based on the results of these studies, it is now widely accepted that increases in pCO_2 will reduce calcification rates across a range of taxa and,

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therefore, directly impact the net growth, stabilization and carbonate accretion processes on reefs. Increasing pCO_2 also intensifies the rate of erosional processes by physically and chemically weakening existing $CaCO_3$ structures (Kleypas 1999), thereby facilitating the biologically mediated erosion of carbonate substrates (Tribollet et al. 2009; Duckworth and Peterson 2012; Wisshak et al. 2012; Fang et al. 2013; Reyes-Nivia et al. 2013).

Biological erosion, or bioerosion, is carried out by a suite of reef organisms, such as urchins (Asgaard and Bromley 2008), fish (Bruggemann et al. 1996), algae (Reyes-Nivia et al. 2013), microbes (Tribollet et al. 2009), polychaetes (Hutchings 2008), mollusks (Kleeman 2008) and excavating sponges. Natural rates of bioerosion vary greatly among taxa; however, sponges are often regarded as the dominant (Perry 1998) and most destructive in terms of $CaCO_3$ removal on coral reefs (Neumann 1966; MacGeachy 1977; Rützler 2002; Schönberg 2002). Calcium carbonate removal rates for tropical excavating sponges can range from 0.84 to 23 kg $CaCO_3$ m^{-2} $year^{-1}$ (Hill 1996; Zundelevich et al. 2007; Nava and Carballo 2008), with some of the highest rates reported for *Cliona varians* (Hill 1996) and *Cliona lampa* (Neumann 1966) at 22.8 kg calcite m^{-2} $year^{-1}$ and 22–23 kg $CaCO_3$ m^{-2} $year^{-1}$, respectively. Excavating sponges are important to healthy reef ecosystems and perform vital functions such as recycling minerals, restructuring coral colonies (Goreau and Hartman 1963), creating new space for settlement and easing spatial competition among benthic taxa (Williams et al. 1999). In recent years, however, there has been a global increase in the prevalence of excavating sponges on threatened and impacted reefs, likely facilitated by wide-spread declines in coral health (Rose and Risk 1985; Holmes 2000; Rützler 2002; Lopez-Victoria and Zea 2004; Ward-Paige et al. 2005; Schönberg and Ortiz 2008; Carballo et al. 2013).

The increase in excavating sponge abundance, coupled with the detrimental effects of pCO_2 on accretion processes, may cause net reef bioerosion to increase in the near future. Recent studies by Wisshak et al. (2012) and Fang et al. (2013) have shown that the Indo-Pacific sponge *Cliona orientalis*, a member of the '*Cliona viridis* species complex' (Schönberg 2000), increases its boring rates on pre-infested dead coral skeleton when exposed to future pCO_2 conditions, while experiencing little to no direct negative impacts on its own physiology. Members of the '*Cliona viridis* species complex' are known to be particularly efficient bioeroders, as this group of sponges harbor symbiotic zooxanthellae that both accelerate boring rates and necessitate direct spatial competition with corals for light (Hill 1996). Studies demonstrating that erosional processes are affected by decreasing pH (Duckworth and Peterson 2012) and increasing pCO_2 (Wisshak et al. 2012; Fang et al. 2013, Wisshak et al. 2014) are important for understanding how future changes will affect substrate erosion; however, a direct evaluation of the spatial interactions and competitive outcomes occurring between these ecologically important species must also be undertaken.

Cliona varians, a member of the '*Cliona viridis* species complex,' is a prominent bioeroder on Caribbean reefs and a direct spatial competitor (Vicente 1978) with hermatypic corals (Hill 1996; Perry 1998; Rützler 2002), simultaneously overgrowing living coral tissue while eroding the skeleton beneath. To determine how varying levels of pCO_2 affect this living coral–sponge interaction, we used *C. varians* and the coral, *Porites furcata*, an abundant, opportunistic branching coral, commonly colonized by *C. varians* on shallow (<5 m) Caribbean reefs (pers obs: Bocas del Toro, Panama). We examined the effect of three levels of pCO_2 on the ability of *C. varians* to spatially compete with and subsequently erode living *P. furcata.* Hypothesizing that *C. varians* would exhibit greater success attaching to and eroding *P. furcata* in seawater with higher levels of pCO_2, we expected that a simultaneous reduction in *P. furcata* calcification and defense from pCO_2 stress would lead to an increase in attachment efficiency of *C. varians* and, therefore, an increase in erosional activity in treatments with increased pCO_2.

Materials and methods

Study species collection

Approximately 30 *Porites furcata* colonies from a continuous reef system on Isla Pastores, Panama (9°13.551′N, 82°19.538′W), served as donors for the experiment. After collection, coral specimens were placed in flow-through seawater tables; while submerged, the growing tips from healthy branches were excised to create smaller fragments (3–6 cm in length). Any fragments exhibiting necrotic tissue, bleaching, disease or an infestation of excavating sponges or other bioeroders were discarded. After 1 week of recovery, each *P. furcata* fragment was tagged, and initial buoyant weights were determined following methods of Jokiel et al. (1978) and Davies (1989). Fifteen large *Cliona varians* forma *incrustans* individuals (each >300 cm^2 surface area) were also collected at Isla Pastores; standard spicule preparations were used to confirm species identification. Sponges were cut into smaller explants (~8 cm^3) taking care to include approximately 4 cm^2 of the outer mesohyl layer where the zooxanthellae reside. Explants were allowed a 3-day recovery period to ensure that all sponges had healed over cut wounds, before being loosely secured to coral fragments with cable ties (Schönberg 2002). *P. furcata* fragments serving as controls (no sponge attached) were also supplied a cable tie to partially account

for any abrasion or shading artifacts. Fragments of corals with ($n = 5$) and without sponges ($n = 5$) were placed into experimental aquaria ($n = 30$). All coral fragments were elevated off the bottom using plastic 'egg crate' material to prevent contact with any accumulated sediment or detritus.

Flow-through system and experimental design

Using the outdoor unfiltered, seawater system at the Smithsonian Tropical Research Institute's Bocas del Toro Laboratory, a flow-through pH–stat system was constructed using 3 reservoirs (200 L each) that each fed 10 aquaria (30 L). These reservoirs allowed for three levels of pH manipulation that corresponded with current and projected levels of pCO_2 for mid-century (450 µatm) and the year 2100 (750 µatm) (based on the SRES A2 emissions scenario; IPCC 2007). Target pH values for this system were 8.0 (ambient pCO_2), 7.8 (moderate pCO_2) and 7.6 (high pCO_2). In each reservoir, pH was monitored continuously using a pH controller (Reef Fanatic) connected to a CO_2 regulator (Milwaukee MA957); whenever pH levels exceeded the target values of 7.8 and 7.6 for the moderate and high pCO_2 treatments, respectively (Anthony et al. 2008; Duckworth et al. 2012), the controller opened a valve that delivered CO_2 gas to the reservoir until target values were achieved again. No direct CO_2 manipulations occurred in the ambient pCO_2 reservoir. All reservoirs, regardless of treatment, were also bubbled with ambient air to ensure that dissolved oxygen levels were adequate. Each reservoir received water from the open flow-through system at a rate of 30 L min^{-1} and supplied 10 aquaria with treatment water at a rate of roughly 3 L min^{-1}; seawater residence time in each aquarium was ~10 min. Within the aquaria, in situ temperature, salinity and pH (calibrated daily using NIST/NBS traceable standards) were monitored daily with a hand-held YSI 85 and Oakton 35-series pH meter. Aquarium pCO_2 levels were measured on discrete samples at the onset and completion of the experiment using an Infrared Gas Analyzer EGM-4 (PPSystems) to ensure that the target pH values of the system corresponded to the desired pCO_2 levels. In addition, HOBO loggers continuously monitored temperature (°C) and light (photons) conditions in the aquaria. Finally, temperature, salinity and pH were sampled hourly during one 24 h period in all aquaria to monitor fluctuations over the course of an entire tidal and light cycle. Water chemistry parameters were calculated by inputting the values of pCO_2, pH (NBS scale), temperature and salinity into CO2SYS using the appropriate constants. The experiment ran for 51 days (October–December 2011); during this time, weekly measurements of temperature, salinity, pH and pCO_2 were also taken at the field collection site, Isla Pastores, for water chemistry comparison.

Response variables

Survival was monitored weekly for both *P. furcata* and *C. varians* individuals. To understand whether the competitive interaction between *C. varians* and *P. furcata* was affected by pCO_2, *C. varians* attachment to corals was assessed weekly for each coral–sponge pair by visually inspecting and gently prodding the sponge explant (Duckworth et al. 2012). Calcification was quantified using the percent change in skeletal weight of individual corals, obtained from the initial and final buoyant weights (Jokiel et al. 1978; Davies 1989) and hereafter referred to as percent net calcification. Percent net calcification, rather than absolute weight change, was used exclusively in data analyses due to the variation in fragment size and surface area. Coral fragments with sponges were similarly assessed, although here changes in skeletal mass were a function of both coral calcification and sponge-mediated bioerosion. At the conclusion of the experiment, *C. varians* were removed from *P. furcata* fragments, and corals were immersed in a 10 % bleach solution for 24 h to remove live tissue (sponge or coral). The fragments were then rinsed with deionized water, dried at 60 °C for 24 h and reweighed. Micro-scale sponge-induced erosion and cleavage patterns in *P. furcata* individuals with attached *C. varians* ($n = 6$; two from each treatment) were evaluated qualitatively using a scanning electron microscope (SEM); photos were taken at 225 × magnification beneath the sponge attachment site and at an area distal to the coral–sponge interaction.

Data analysis

The hierarchical design of the experiment required the use of tank means ($n = 30$) in the analysis of all response variables. All data were assessed for normality using the Shapiro–Wilk test; no transformations were necessary for survival or attachment data. Mean survival (days) for *P. furcata* fragments in each tank was analyzed using a two-way ANOVA to test for the main and interactive effects of sponge presence and CO_2 dosing on survival. Attachment times (represented as days until sponge attachment) were used to compare competitive competence in *C. varians* between CO_2 treatments using a one-way ANOVA. Percent net calcification was negatively skewed and leptokurtic, and so, these data were rank-transformed; only those tanks with two or more individuals alive at the close of the experiment were included in this analysis. A two-way analysis of variance (ANOVA) on ranked data was used to test for the main and interactive effects of CO_2 dosing and sponge presence on percent net calcification. When significant main effects were identified, Tukey's honestly significant difference (HSD) tests were used to determine treatment differences. All analyses were performed using the

Table 1 Summary of water parameters measured at the field collection site (Isla Pastores; weekly from October 5 to November 1, 2011) and within aquaria for each CO_2 dosing treatment (see text for sampling frequency)

Variable	Isla Pastores	Ambient	Moderate	High
Temperature (°C)	30.4 ± 0.3	28.8 ± 0.6	28.8 ± 0.5	28.7 ± 0.6
Salinity	32.3 ± 0.01	31.8 ± 0.04	31.8 ± 0.13	31.8 ± 0.04
pCO_2 (µatm)	341 ± 59	304 ± 34	450 ± 36	753 ± 65
pH (NBS scale)	7.99 ± 0.02	7.97 ± 0.03	7.77 ± 0.03	7.58 ± 0.05
TA (µmol kg^{-1})	1,067 ± 35.8	911.1 ± 91.9	805.1 ± 75.6	820.1 ± 79.6
HCO_3^{2-} (µmol kg^{-1})	856.5 ± 18.5	738.5 ± 77.1	697.0 ± 65.1	746.8 ± 69.2
$\Omega_{Calcite}$	1.56 ± 0.2	1.22 ± 0.2	0.73 ± 0.1	0.50 ± 0.1
$\Omega_{Aragonite}$	1.07 ± 0.2	0.83 ± 0.1	0.5 ± 0.07	0.35 ± 0.07

Measured values were pCO_2, pH (NBS scale), temperature and salinity; all other values (mean ± 1 SD) were calculated using CO2SYS

open-source statistical software, R version 2.13.2 (R Core Team 2012).

Results

Water parameters

The reservoir pH–stat system was successful at producing significantly different pCO_2 treatments ($F_{(2,22)} = 223.5$, $P < 0.001$; Table 1). Other conditions such as flow rate, temperature and salinity did not vary among pCO_2 treatments. Water chemistry parameters (both measured and calculated) within the aquaria and at the organisms' field collection site are summarized in Table 1. It is important to note that pH was measured on the NBS scale, rather than the preferred total scale. The inherent measurement uncertainties of using pH (NBS scale) and pCO_2 to calculate the remainder of the carbonate system parameters result in increased error (+1.5–15 %) of the calculated values of TA, HCO_3^{2-}, $\Omega_{Aragonite}$ and $\Omega_{Calcite}$ (Riebesell et al. 2011 and references within). Collection site pCO_2 ranged from 232 to 429 µatm and pH ranged from 7.96 to 8.01, depending on the tidal cycle. Hourly monitoring of the temperature, salinity and pH over a 24 h period within each aquarium showed that fluctuations in the flow-through treatment system paralleled natural fluctuations due to tidal and light cycles (see electronic supplemental material Fig. 1).

Survival and attachment

No *C. varians* individuals died during the experiment. Survival for *P. furcata* fragments (mean ± 1 standard deviation) in the highest CO_2 treatment was 31.0 ± 6.9 days ($n = 10$ tanks, $n = 43$ coral individuals) and 30.2 ± 12.0 days ($n = 10$ tanks, $n = 43$ coral individuals) for corals with and without sponges, respectively. Comparatively, survival in the ambient treatment was 32.9 ± 12.6 days ($n = 10$ tanks, $n = 44$ coral individuals) and 37.8 ± 10.2 days ($n = 10$ tanks, $n = 46$ coral individuals) for corals with and without sponges, respectively. No significant difference in coral survival was observed between or within any of the treatment combinations. The time to attachment of *C. varians* was independent of CO_2 treatment, with no significant difference between treatments observed. The mean days until attachment of *C.varians* to *P. furcata* was 12.1 ± 7.1 days.

Calcification and erosion

The full ANOVA model found a significant main effect of pCO_2 on percent net calcification. A post hoc Tukey HSD revealed that there was no statistically significant difference between the moderate and high CO_2 treatments. The impact of pooling the moderate and high treatments on the magnitude of the F-statistic for sponge presence (two-way ANOVA) was tested using a resampling technique (10,000 permutations, with replacement) that preserved the original sampling balance. This approach indicated that there was no statistically significant difference between the original high and resampled composite moderate–high treatments ($P > 0.124$). We, therefore, present only the results of a two-way interactive model comparing the percent net calcification of corals using two CO_2 doses (ambient and high CO_2 dosing levels * sponge presence; Table 2).

The percent net calcification was significantly affected by CO_2 dosing ($F_{(1,28)} = 24.846$, $P < 0.0001$) and sponge presence ($F_{(1,28)} = 4.690$, $P = 0.04$). Further exploration using Tukey's HSD showed that these significant main effects were driven by the significantly lower net calcification of coral fragments with *C. varians* in the highest pCO_2 treatment compared to corals with or without *C. varians* in the ambient pCO_2 treatments (Tukey HSD; $P < 0.001$ and $P < 0.0001$, respectively; Table 2). Net calcification decreased with increasing pCO_2 levels, and this decrease was exacerbated in the coral fragments with sponges due to increased bioerosion (Fig. 1), particularly in the highest

Table 2 Results of the analysis of variance (two-way ANOVA on ranks) of percent net coral calcification due to pCO_2 level and sponge presence, followed by the results of the post hoc Tukey HSD pairwise comparisons

ANOVA	df	SS	MS	*F*-value	*P*
pCO_2 level	1	1,144.5	1,144.5	24.846	<0.0001
Sponge presence	1	216.0	216.0	4.690	0.039
CO_2 * sponge	1	77.7	77.7	1.687	0.205
Residuals	28	1,289.8	46.1	–	–
Tukey's HSD		Diff	Lower 95 % conf. interval	Upper 95 % conf. interval	Adjusted *P* value
High pCO_2 versus ambient pCO_2		−11.98	−16.91	−7.06	<0.0001
No *Cliona* versus *Cliona*		5.16	0.24	10.09	0.0405
High pCO_2: *Cliona* versus ambient pCO_2: *Cliona*		−14.21	−23.21	−5.20	0.001
Ambient pCO_2: no *Cliona* versus ambient pCO_2: *Cliona*		2.35	−6.66	11.35	0.892
High pCO_2: no *Cliona* versus ambient pCO_2: *Cliona*		−5.54	−15.55	4.47	0.444
Ambient pCO_2: no *Cliona* versus high pCO_2: *Cliona*		16.56	7.82	25.29	<0.0001
High pCO_2: no *Cliona* versus high pCO_2: *Cliona*		8.67	−1.10	18.43	0.096
High pCO_2: no *Cliona* versus ambient pCO_2: no *Cliona*		−7.89	−17.66	1.88	0.146

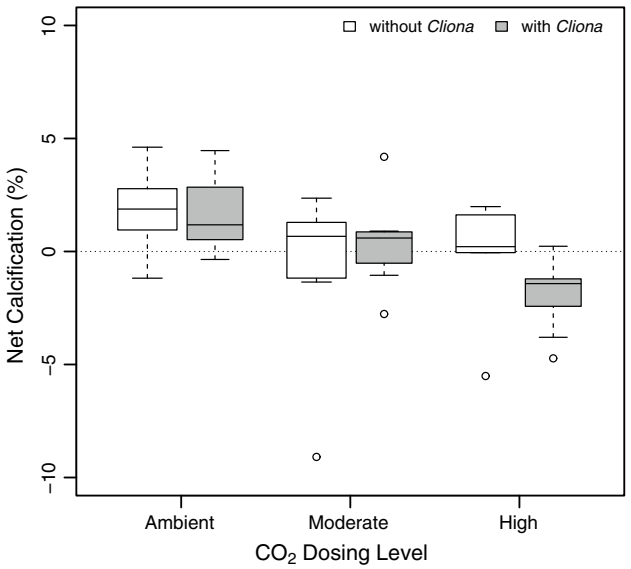

Fig. 1 Change in percent net calcification of *Porites furcata* over the 51-day experimental period in specimens with (*gray*) and without (*white*) *Cliona varians* present. *Boxplots* mark median values with a *central bar*, the first and third quartiles with a *box*, the ±1.5 interquartile ranges with 'Tukey whiskers' and *outliers* with open *circles*

pCO_2 dosing level. An increase in erosional scars in the highest pCO_2 levels was qualitatively confirmed using the SEM photographs (Fig. 2).

Discussion

Our results suggest that increasing levels of pCO_2 altered some, but not all, interactions between *P.furcata* and *C. varians*. Coral survival was not statistically related to pCO_2 treatments. It is widely assumed that future increases in temperature, rather than pCO_2 levels, will be the primary determinant of coral survivorship (Hoegh-Guldberg 1999; Fine and Tchernov 2007; Hoegh-Guldberg et al. 2007). While corals may be able to recover from a lack of growth and/or calcification (Fine and Tchernov 2007), recovery from temperature-induced bleaching is unlikely (see Hoegh-Guldberg 1999 and references within). Although corals without sponges tended to live a few days longer than corals with sponges at ambient and moderate pCO_2 conditions, these differences were not statistically, and most likely not ecologically, significant. Additionally, no sponge mortality was observed. Aerts (1998) and Aerts and van Soest (1997) described sponge–coral interactions on reefs and showed that the majority of interactions between coral and *C. varians* were limited to peripheral contact, not complete overgrowth. In our experiment, the induced colonization of *P. furcata* by *C. varians* led to coral polyp death directly underneath the attachment site; however, no further overgrowth of the coral was observed over the 51-day study period.

Unexpectedly, the time until attachment for sponges was not statistically related to pCO_2 treatment. If corals had exhibited a reduction in defensive vigor as a result of pCO_2 stress, as has been posited under most climate change scenarios (Fabry et al. 2008), we would have expected *C. varians* to exploit the stressed corals and attach at rates positively related to CO_2 treatment. It remains possible, though, that the corals were not sufficiently stressed or that *C. varians* was affected in some unmeasured way that differentially limited attachment capacity across pCO_2. In a similar species, *Cliona celata*, attachment to bivalve shells

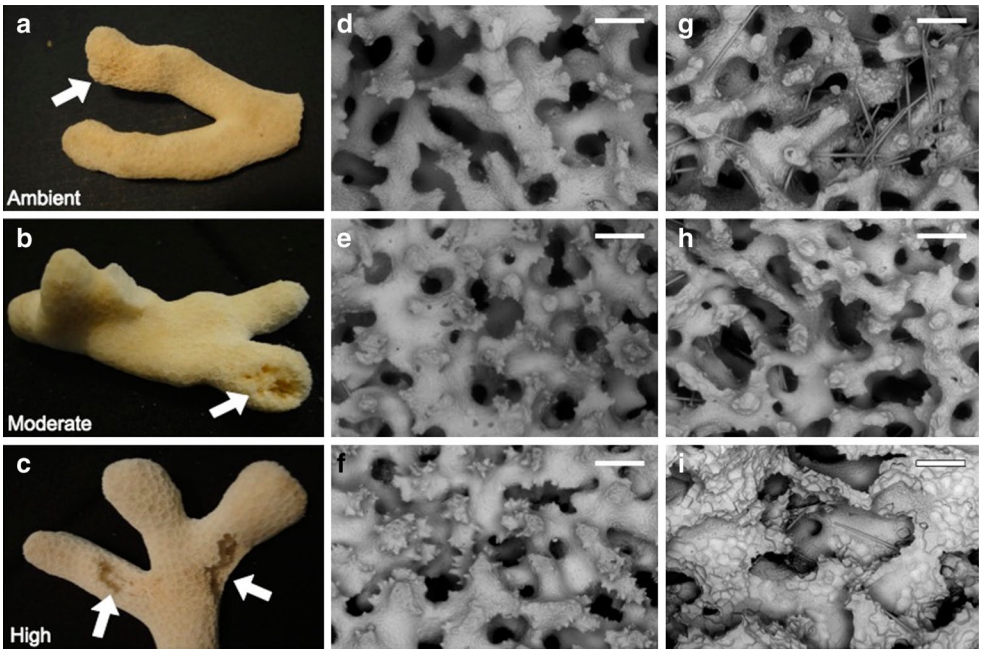

Fig. 2 Macro- and SEM images of *Porites furcata* specimens from ambient, moderate and high pCO_2 treatments. **a**, **b**, **c** *P. furcata* fragment used in subsequent SEM imaging from each of the three pCO_2 treatment levels; *arrows* indicate regions of *Cliona varians* attachment and erosion. SEM images (**d**, **e**, **f**) are of *P. furcata* skeletal regions that were free of *C. varians* infestation throughout the entirety of the experiment. **g**, **h**, **i** SEM images of *C. varians* attachment sites and sponge erosional scars on *P. furcata* from each pCO_2 level, as previously indicated by *arrows* in **a**, **b**, **c** (sponge removed for imaging purpose). *Scale bars* from all SEM images **d**, **e**, **f**, **g**, **h**, **i**) are 250 μm

was slower in reduced pH treatments, and survival slightly depressed (Duckworth and Peterson 2012); however, this study lowered pH using hydrochloric acid, not by injecting CO_2. It is possible that the reduced pH might have had a negative physiological effect on the sponges themselves, although there was no observed sponge mortality in this study, and others have reported limited impacts of pCO_2 on sponge physiology (Duckworth et al. 2012; Wisshak et al. 2012; Fang et al. 2013). Despite no significant differences in attachment rates among treatments, sponge bioerosion was significantly increased in the high pCO_2 treatments. Thus, we might conservatively expect that this sponge–coral interaction will continue to intensify in the future.

Percent net calcification in corals with attached *C. varians* was significantly reduced in the highest pCO_2 treatment as compared to the ambient treatment. These findings are consistent with other studies that have investigated changes in bioerosion efficiency of excavating sponges (albeit on nonliving biogenic substrate) to lowered pH (Duckworth and Peterson 2012) and increased pCO_2 (Wisshak et al. 2012; Fang et al. 2013). No difference in net calcification was found between coral fragments with and without sponges in ambient CO_2 treatments, indicating that the accretion and erosion processes were still in balance at this pCO_2 level.

The limited response of the corals with and without sponges to the moderate treatment (Fig. 1) may be related to the biotic history of the corals. Putnam and Edmunds (2011) and Dufault et al. (2012) demonstrated that corals from sites that experienced large daily fluctuations in temperature or pCO_2 were often unaffected by elevated levels of these parameters in experimental conditions. The *P. furcata* fragments used in this experiment were collected from a reef tract on Isla Pastores that, like most reefs inside the archipelago of Bocas del Toro, Panama, lies directly adjacent to a large mangrove habitat (<10 m distance). Mangrove habitats typically experience large diel variations in pCO_2 and temperature due to the shallow waters and high level of organic matter decomposition within the sediments (Borges 2003; Zablocki et al. 2011). CO_2-enriched seawater from mangrove habitats is then tidally exported to adjacent environments before being mixed and diluted. Zablocki et al. (2011) found that the maximum diel range of pCO_2 in mangrove habitats of Bermuda was from 268 to 4,823 μatm, far beyond the range experienced in a controlled experiment designed to manipulate pCO_2 at certain target levels. The pCO_2 values at Isla Pastores ranged from 213 to 430 μatm; however, measurements were taken weekly during the mid-morning hours, and therefore, a full diel range is not represented by these data. It may be that

the coral used in this experiment had already been acclimated to large fluctuations in CO_2 and that the calcification responses were therefore dampened in all but the highest experimentally altered level of pCO_2.

The precise mechanisms underlying the observed increase in sponge-mediated erosion in high CO_2-dosing are still unclear. Excavating sponges remove coralline substrate through a combination of chemical (etching agents are used to weaken the $CaCO_3$ matrix) and mechanical (etching cells physically chip away at the substrate) erosion, although the exact contributions of each process are not fully understood (Hatch 1980; Pomponi 1980; Zundelevich et al. 2007; Nava and Carballo 2008). The possibility remains that increased sponge erosion was (1) an opportunistic response to an overall weaker coral skeleton, (2) a response to a decreased dissolution gradient between the surrounding seawater and the sponge–substrate interface that lowered the metabolic cost of excavation (Wisshak et al. 2012; Fang et al. 2013) or (3) a synergistic response of acidified water augmenting the sponges' natural exudates, easing substratum resistance to etching cells without additional metabolic costs. Determining which of these might be responsible for the observed increase in bioerosion was beyond the scope of this study and warrants future consideration. The result, however, was plainly evident: the erosion efficiency of *C. varians* increased in the highest CO_2 treatment, which represented projections for the end of the century in the SRES A2 scenario (IPCC 2007).

Previous studies have independently shown that (1) excavating sponges are increasing in abundance (Rose and Risk 1985; Ward-Paige et al. 2005; Chiappone et al. 2007), (2) bioerosion efficiency of dead substrate increases with increasing pCO_2 (Wisshak et al. 2012; Fang et al. 2013) and (3) across-taxa reductions in calcification occur with increased pCO_2 (Anthony et al. 2008; Andersson and Gledhill 2013). However, none of these studies have taken into account the ability of interspecific interactions to amplify detrimental effects of increasing pCO_2. This is the first study that has used living coral and excavating sponges in tandem to assess how future changes in pCO_2 may affect this common reef interaction. We have established that competitive outcomes between *P. furcata* and *C. varians* do not change under different pCO_2 regimes and that the bioerosion efficiency of *C. varians* increases with increasing pCO_2, despite the stress of constant peripheral interaction with a living coral. This suggests that as pCO_2 rises in shallow coastal waters, the mode and efficiency of *C. varians* invasion will remain the same, while a simultaneous reduction in coral calcification and an increase in sponge-mediated bioerosion will accelerate reef structural degradation and net erosion. Further investigations of this interaction that include temperature manipulations are necessary, as many excavating sponges grow faster in higher temperatures (Siegrist et al. 1992), which may further exacerbate their competitive advantage. We demonstrate here and further argue that assessing the impact of changing pCO_2 on species interactions is crucial to adequately predict ecosystem-level responses in the future.

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