Author for correspondence:
Colleen B. Bove
e-mail: colleenbove@gmail.com

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Common Caribbean corals exhibit highly variable responses to future acidification and warming

Colleen B. Bove[1], Justin B. Ries[4], Sarah W. Davies[2,5], Isaac T. Westfield[4], James Umbanhowar[1,3] and Karl D. Castillo[1,2]

[1]Environment, Ecology, and Energy Program, [2]Department of Marine Sciences, and [3]Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA
[4]Department of Marine and Environmental Sciences, Northeastern University, Nahant, MA, USA
[5]Department of Biology, Boston University, Boston, MA, USA

CBB, 0000-0003-0340-1371; JBR, 0000-0001-8427-206X; SWD, 0000-0002-1620-2278; JU, 0000-0002-8251-9388; KDC, 0000-0002-2508-5261

We conducted a 93-day experiment investigating the independent and combined effects of acidification ($280-3300$ µatm pCO_2) and warming ($28°C$ and $31°C$) on calcification and linear extension rates of four key Caribbean coral species (*Siderastrea siderea*, *Pseudodiploria strigosa*, *Porites astreoides*, *Undaria tenuifolia*) from inshore and offshore reefs on the Belize Mesoamerican Barrier Reef System. All species exhibited nonlinear declines in calcification rate with increasing pCO_2. Warming only reduced calcification in *Ps. strigosa*. Of the species tested, only *S. siderea* maintained positive calcification in the aragonite-undersaturated treatment. Temperature and pCO_2 had no effect on the linear extension of *S. siderea* and *Po. astreoides*, and natal reef environment did not impact any parameter examined. Results suggest that *S. siderea* is the most resilient of these corals to warming and acidification owing to its ability to maintain positive calcification in all treatments, *Ps. strigosa* and *U. tenuifolia* are the least resilient, and *Po. astreoides* falls in the middle. These results highlight the diversity of calcification responses of Caribbean corals to projected global change.

1. Introduction

Increasing carbon dioxide (CO_2) from anthropogenic sources is of growing concern as global average atmospheric pCO_2 has now increased from a pre-industrial level of 280 µatm to 410 µatm [1]. This rapid change has resulted in negative and often irreversible impacts on both terrestrial and marine ecosystems [2,3]. In terrestrial ecosystems, rising surface temperatures pose serious threats to animals and plants that are unable to cope with hotter, longer and more frequent thermal stress events [4,5]. Marine ecosystems are under similarly intense pressure from ocean warming and acidification [6], affecting everything from biogeochemical cycling to habitat and population structure [7].

Ocean warming is a major concern for marine organisms, especially at lower latitudes where sea surface temperature is predicted by the Intergovernmental Panel on Climate Change (IPCC) to rise between $0.6°C$ and $3.0°C$ by the end of the twenty-first century [8]. Reef-building corals in these low-latitude regions, including the Caribbean, are already living within a degree of their thermal maxima [9] and are therefore considered to be at particular risk [10]. Abnormally high seawater temperatures disrupt the symbiosis between the coral animal and its algal endosymbiont (Symbiodiniaceae) [11] through a process known as 'coral bleaching' [12], resulting in deterioration of corals' physiological processes [9,13,14]. Mortality rates increase because of the strong dependence of corals on their endosymbionts, which contribute up to 100% of their daily metabolic requirements [15], impacting the corals' ability to withstand additional environmental stress.

Table 1. Treatment conditions measured either every other day (T, pH, salinity) or every 10 days (pCO$_2$, TA, DIC, Ω_A).

treatment	T (°C)	pCO$_2$ (μatm)	pH	TA (μM)	DIC (μM)	Ω_A	salinity
1	27.9 ± 0.04	311 ± 18	8.30 ± 0.01	2052 ± 8	1708 ± 15	4.0 ± 0.1	31.7 ± 0.02
2	28.0 ± 0.04	405 ± 17	8.20 ± 0.01	2081 ± 3	1788 ± 10	3.4 ± 0.1	31.8 ± 0.02
3	28.1 ± 0.05	701 ± 17	8.01 ± 0.03	2092 ± 7	1901 ± 8	2.4 ± 0.1	31.7 ± 0.02
4	28.1 ± 0.02	3309 ± 76	7.31 ± 0.01	2131 ± 5	2156 ± 6	0.7 ± 0.1	31.8 ± 0.02
5	31.0 ± 0.04	288 ± 12	8.34 ± 0.01	2101 ± 6	1710 ± 11	4.6 ± 0.1	31.7 ± 0.02
6	31.1 ± 0.05	447 ± 28	8.21 ± 0.01	2077 ± 6	1773 ± 15	3.6 ± 0.1	31.7 ± 0.02
7	30.9 ± 0.03	673 ± 19	8.00 ± 0.01	2082 ± 6	1865 ± 8	2.7 ± 0.1	31.7 ± 0.02
8	31.0 ± 0.05	3285 ± 99	7.29 ± 0.01	2123 ± 4	2135 ± 5	0.8 ± 0.1	31.7 ± 0.02

Rising atmospheric pCO$_2$ is not only warming surface seawater, but also causing more CO$_2$ to dissolve into oceans, reducing carbonate ion concentration [CO$_3^{-2}$], pH and aragonite saturation state (Ω_A) of seawater—a process known as ocean acidification [16]. The IPCC projects that atmospheric pCO$_2$ will surpass 600 μatm by 2100, which would cause surface ocean pH to decrease by 0.1–0.3 [8]. Scleractinian corals rely heavily on elevated pH and Ω_A at their site of calcification to form calcium carbonate skeletons [17–20], making it harder for some species to maintain conditions within these sites that are supportive of skeletal formation under acidification [21]. However, previous research has revealed inconsistencies in scleractinian corals' response to acidification [22,23]. Simulations of past [24] and future [25] pCO$_2$ conditions in a natural reef system on the Great Barrier Reef revealed a decrease in net community calcification with increasing pCO$_2$, while *ex situ* experiments demonstrated negative [23,26,27], threshold [28], parabolic [14] and no significant [26,27] response of corals to increased pCO$_2$. Numerous explanations for the wide array of responses include differences in experimental design [29], evolutionary divergence among corals with respect to mechanisms of calcification and/or resilience to acidification [30], and differences among coral species' physiological control of calcifying fluid chemistry [19,31–33]. Moreover, although studies have investigated the effects of increasing pCO$_2$ on coral calcification and health, few have investigated the combined effects of temperature and pCO$_2$.

In isolation, warming has been shown to more negatively impact coral calcification than pCO$_2$ [14,34–37]. However, numerous studies have observed that the combination of pCO$_2$ and temperature causes a more severe negative response in corals than either stressor alone [31,37–40], although few studies report a truly synergistic interaction between warming and acidification. This highlights the importance of studying the response of multiple coral species to global change scenarios under a common suite of conditions. Using multiple species in the same experiment minimizes differential outcomes that arise from differences in experimental design, allowing for direct comparison among species. The few studies that have investigated multiple coral species have yielded important insights into reef-community-level responses to acidification and warming, including projecting rates of whole-reef accretion under future IPCC scenarios [37].

Here, we investigate the independent and combined effects of ocean acidification and warming on four abundant and widespread Caribbean scleractinian coral species—*Siderastrea*

siderea, *Pseudodiploria strigosa*, *Porites astreoides* and *Undaria tenuifolia*—in a 93-day laboratory experiment. These four species were selected because they span a range of skeletal morphologies (foliate—domical), possess similar life-history strategies [41] and occupy similar depth and geographical ranges [42]. Corals collected from the Belize Mesoamerican Barrier Reef System (MBRS) were reared under projected temperature and pCO$_2$ stress with the aim of characterizing the effects of future global change on a suite of genetically and morphologically diverse Caribbean coral species.

2. Material and methods

(a) Experimental design

Six colonies of *S. siderea*, *Ps. strigosa*, *Po. astreoides* and *U. tenuifolia* were collected from inshore and offshore reef environments along the southern portion of the Belize MBRS (see the electronic supplementary material for details of the coral collection and figure S1). Forty-eight coral colonies were transported to Northeastern University's Marine Science Centre in Nahant, Massachusetts and sectioned into eight comparably sized fragments and placed into aquaria for a recovery period of 23 days. After recovery, temperature and pCO$_2$ were adjusted gradually over a 20-day interval until target experimental conditions were approximately achieved for each treatment (temperature: 28°C and 31°C; pCO$_2$: 280, 400, 700, 2800 μatm). Coral fragments were acclimated to treatment conditions for 30 days and then maintained in each experimental treatment for 93 days. Four pCO$_2$ treatments corresponding to pre-industrial (311/288 μatm), present-day (pCO$_2$ control; 405/447 μatm), end-of-century (701/673 μatm) and an extreme (3309/3285 μatm) pCO$_2$ were maintained at two temperatures corresponding to the corals' approximate present-day mean annual temperature (28°C; determined by over 10 years of *in situ* records [43–45]) and projected end-of-century annual mean temperature (31°C) [8]. The extreme pCO$_2$ treatment was formulated at a value approaching that predicted for the year 2500 [8] and was selected to push the corals closer to their physiological limits. Experimental tanks were illuminated on a 10 L : 14 D cycle with photosynthetically active radiation of approximately 300 μmol photons m^{-2} s^{-1} (see the electronic supplementary material for detailed experimental conditions and maintenance and figures S2 and S3).

(b) Measured and calculated parameters

Temperature, salinity and pH were measured every other day throughout the experiment (table 1). Water samples were obtained every 10 days for measurement of total alkalinity (TA) and
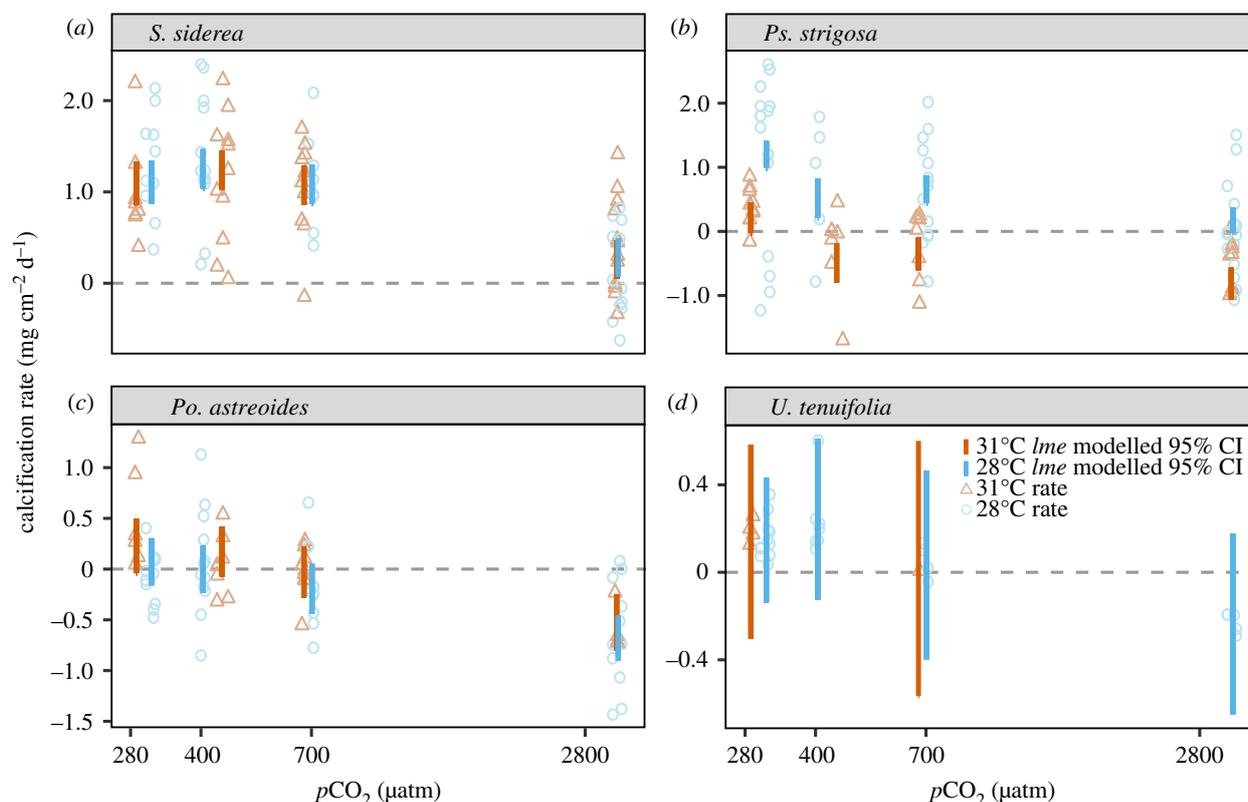
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Figure 1. Net calcification rates (mg cm^{-2} day^{-1}) for *S. siderea* (*a*), *Ps. strigosa* (*b*), *Po. astreoides* (*c*) and *U. tenuifolia* (*d*) cultured over a range of $p\mathrm{CO_2}$ and temperature conditions. Blue circles represent net calcification rates for fragments in the 28°C treatments and orange triangles represent net calcification rates for fragments in the 31°C treatments. Blue and orange vertical bars represent modelled 95% confidence intervals (CI) for each $p\mathrm{CO_2}$ treatment at 28°C and 31°C, respectively.
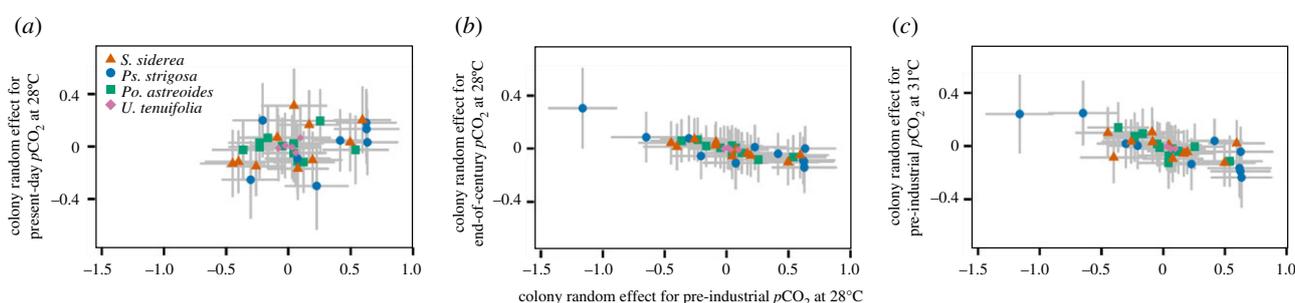

Figure 2. Estimated random effects and 95% credible intervals of colony on calcification rate of all four species under the control treatment (pre-industrial $p\mathrm{CO_2}$ at 28°C) versus random effects of colony on calcification rate under stress treatments of present-day $p\mathrm{CO_2}$ at 28°C (*a*), end-of-century $p\mathrm{CO_2}$ at 28°C (*b*) and pre-industrial $p\mathrm{CO_2}$ at 31°C (*c*).

dissolved inorganic carbon (DIC) and analysed with a VINDTA 3C (Marianda Corporation, Kiel, Germany). Temperature, salinity, TA and DIC were used to calculate carbonate parameters using CO2SYS [46] with Roy *et al.* carbonic acid constants K$_1$ and K$_2$ [47], Mucci's value for the stoichiometric aragonite solubility product [48] and an atmospheric pressure of 1.015 atm (table 1; electronic supplementary material, figure S4 and tables S2 and S3). The two temperatures at a given $p\mathrm{CO_2}$ level exhibited slight differences in carbonate chemistry because the solubility of CO$_2$ in seawater varies with temperature.

(c) Quantification of calcification and linear extension

Net calcification rates were estimated from surviving coral fragments using a buoyant weight method [49] performed at the beginning of the pre-acclimation period and every 30 days throughout the experiment (see the electronic supplementary material for empirical derivation of buoyant weight–dry weight relationships for all four coral species and for survivorship, figures S5 and S6).

Extension was quantified from vertical cross sections of the corals as the total area of skeleton above the calcein dye line

incorporated into coral skeletons at the beginning of the experiment, divided by the length of the region of active growth (see the electronic supplementary material for detailed methodology and figure S7). Linear extension was not quantified for *U. tenuifolia* or *Ps. strigosa* because their irregular skeletal morphologies rendered the method too inaccurate.

(d) Colony-level effects of basal calcification rate on calcification response to stress

Recent work has shown that coral species which calcify faster are generally more vulnerable to the effects of ocean acidification than slower calcifying species [50]—raising the possibility that similar trends exist within species among colonies with differing calcification rates. Colony-specific relationships between basal calcification rate and response to $p\mathrm{CO_2}$ and thermal stress were investigated by assessing correlation between the random effect of colony on each colony's calcification rate within the control treatment (pre-industrial $p\mathrm{CO_2}$ at 28°C) versus each colony's calcification response to $p\mathrm{CO_2}$ or thermal stress (i.e. change in
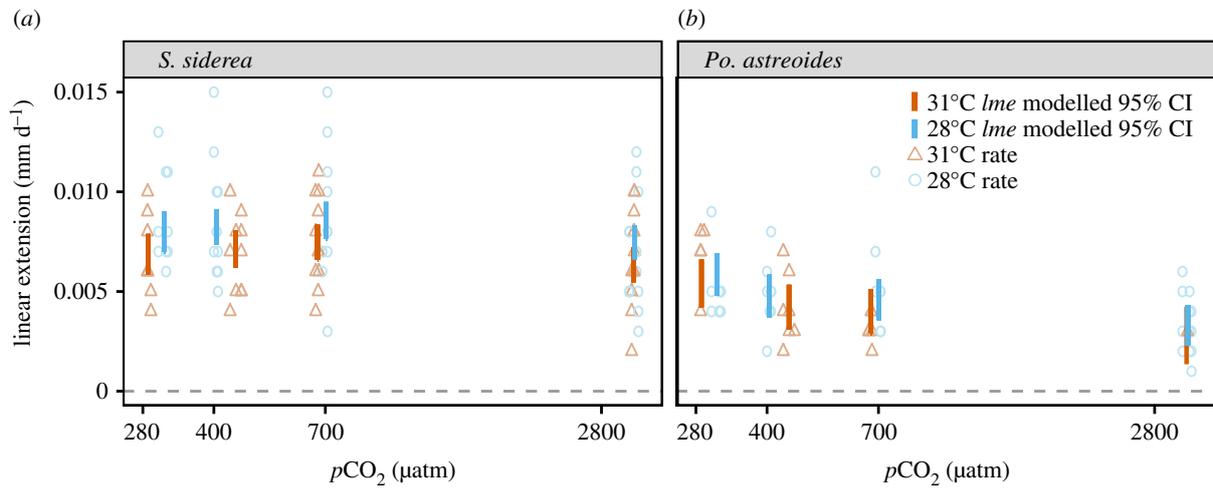
Figure 3. Linear extension rates (mm day^{-1}) for *S. siderea* (*a*) and *Po. astreoides* (*b*) cultured over a range of pCO$_2$ and temperature conditions. Blue circles represent extension rates for fragments in the 28°C treatments and orange triangles represent extension rates for fragments in the 31°C treatments. Blue and orange vertical bars represent modelled 95% confidence intervals (CI) for each pCO$_2$ treatment at 28°C and 31°C, respectively.

calcification rate between the control treatment and the stress treatments). Small sample size prevented fitting a frequentist model to estimate these colony-level effects, so a Bayesian hierarchical regression model was fitted to calculate credible intervals of the corresponding extracted correlation coefficient using R package *brms* (version 2.7.0) with default priors [51]. Random effects relating colony-specific relationships between basal calcification rate and response to pCO$_2$ and thermal stress were calculated for all species together, as the study lacked the statistical power to assess this correlation within individual species.

(e) Statistical analyses

Three-way mixed-model analyses of variance selected using Akaike information criterion (electronic supplementary material, table S4) were used to assess impacts of pCO$_2$ and temperature on calcification and linear extension (*lme4* (1.1–12)) [52]. Parametric bootstraps were performed to model 95% confidence intervals with 1500 iterations [53]. Significant differences between treatments were defined as non-overlapping 95% confidence intervals. Because reef environment was not a significant predictor of any parameter, colonies were pooled across reef environments and these effects were not further addressed (see the electronic supplementary material for detailed analyses; tables S12 and S13). To further evaluate the effects of acidification and warming on *U. tenuifolia*, survival rates were assessed using a Kaplan–Meier estimate of survival (*survfit*, survival, 2.39–5) [54]. Cox proportional hazard models, with colony nested within the tank as a random effect, were performed using *coxme* (2.2–5) [55].

3. Results

(a) Calcification rates

All four coral species exhibited nonlinear declines in calcification rate with increasing pCO$_2$ (figure 1). Notably, *S. siderea* maintained positive net calcification across all temperature and pCO$_2$ treatments (figure 1*a*), while the other species exhibited net dissolution in at least one treatment. *Pseudodiploria. strigosa* maintained net calcification at 28°C but exhibited net dissolution in all but pre-industrial pCO$_2$ at 31°C (figure 1*b*). *Porites astreoides* yielded negligible net calcification or net dissolution in all treatments except under pre-industrial pCO$_2$ at 31°C (figure 1*c*), and *U. tenuifolia* exhibited net calcification in all treatments except under the extreme pCO$_2$ treatment (figure 1*d*). Temperature had

no significant effect on *S. siderea* or *Po. astreoides* calcification rates; however, elevated temperature significantly reduced calcification rate in *Ps. strigosa* under all pCO$_2$ conditions (figure 1; electronic supplementary material, tables S5 and S6). The effect of temperature on calcification rates of *U. tenuifolia* could not be quantified owing to low survival in the elevated-temperature treatments.

(b) Colony-level calcification response to stress

A negative slope of the correlation between random effects of colony on calcification rate in the control treatment (pre-industrial pCO$_2$ at 28°C) versus those in the stress treatments (figure 2) would support the hypothesis that faster calcifying colonies (relative to the treatment mean) under control conditions calcify slower (relative to the treatment mean) under pCO$_2$ and thermal stress (figure 2). While the best estimates of these correlations were negative, only the 75% credible intervals, and not the 95% credible intervals, did not always overlap zero (electronic supplementary material, figure S8)—suggesting that the results of the current experiment provide weak evidence for the inverse correlations between basal calcification rate and calcification response to pCO$_2$ and thermal stress. However, the current study possibly lacked the statistical power to confirm the statistical significance of this correlation owing to a combination of low within-colony replication and high mortality rate.

(c) Linear extension

Siderastrea siderea and *Po. astreoides* exhibited positive linear extension rates in all treatments. Neither temperature, nor pCO$_2$, nor their interaction had a significant impact on linear extension rates of *S. siderea* or *Po. astreoides* (figure 3; electronic supplementary material, tables S7 and S8).

4. Discussion

(a) Caribbean corals exhibit nonlinear calcification responses to pCO$_2$ and temperature

All four coral species exhibited nonlinear calcification responses to pCO$_2$ driven primarily by stability in calcification rates across the three lowest pCO$_2$ treatments and

major declines under extreme pCO_2 (figure 1). One exception to this trend was *Ps. strigosa*, which exhibited an abrupt decline in calcification rate at present-day pCO_2. Similar non-linear calcification responses have been reported in previous studies for several temperate [28,56] and tropical corals [14,27,37], indicating that such pCO_2 thresholds exist for a diverse range of coral species. Interspecific differences in corals' calcification responses to pCO_2 may be influenced by differences in a coral's ability to control Ω_A at their calcification site [18,19]. It has been proposed that corals transport Ca^{2+} into the calcifying fluid from the surrounding seawater in exchange for two protons using the enzyme Ca^{2+}-ATPase [18], increasing the Ω_A by elevating $[Ca^{2+}]$ and by converting HCO_3^- to CO_3^{2-} [18,19,57]. However, this process requires energy (1 mole ATP consumed per mole of Ca^{2+}-ATPase [17]), which should increase under more acidic conditions as more protons must be removed to deprotonate HCO_3^-. This suggests that the threshold pCO_2 for maintaining stable rates of calcification is determined, at least in part, by the energetic costs of regulating ionic concentrations at the coral's site of calcification [19,36,57].

Increased temperature had no significant effect on calcification rates of either *S. siderea* or *Po. astreoides* (figure 1a,c). Similarly, in a prior study, *S. siderea* from the Florida Keys demonstrated stability in calcification rates with a temperature increase from 27°C to 30.3°C [37]. However, two studies on *S. siderea* from the Belize MBRS reported reduced calcification rates with a temperature increase from 28°C to 32°C [14,38]. Other studies have also reported reduced calcification for *Po. astreoides* under thermal stress [37,58], although the present study found that an increase in temperature from 28°C to 31°C did not significantly impact calcification rate of this species. These apparent discrepancies in coral species' calcification responses to warming may arise from evaluating temperature effects across different portions of these species' thermal performance curves. Rates of biological processes, including calcification, are known to increase with increasing temperature to a maximum before declining with continued temperature increases, resulting in a thermal performance curve [59], which is typically parabolic in shape. It is possible that the two temperatures investigated in the present experiment are symmetrically distributed about this species' optimal temperature, resulting in equivalent calcifications rates at both temperatures.

Notably, only *Ps. strigosa* exhibited reduced calcification rates under thermal stress (figure 1b), contrasting previous work on this species showing no calcification response to thermal stress [37]. Again, this discrepancy between studies may result from assessing temperature effects across different portions of this species' thermal performance curve (28–31°C versus 27.0–30.3°C in prior study). Differences in populations may also contribute to these discrepancies among studies with respect to a species' calcification responses to temperature [60] and pCO_2 [61,62].

The effect of temperature on *U. tenuifolia* calcification rate could not be fully evaluated owing to low survival at 31°C, although these results highlight the thermal sensitivity of this species—as previously observed on the Belize MBRS after thermal bleaching events [63,64] (electronic supplementary material, figure S6d and tables S9–S11). Previous studies suggest that the susceptibility of *U. tenuifolia* to thermal stress arises from lack of compensatory stress responses [65–68], including insufficient production of heat shock proteins to protect against thermal events [66] and reduced endosymbiont photosynthesis owing to oxidative stress induced by warming [67]. Owing to its reliance on endosymbiont photosynthesis over heterotrophy for energy [65], oxidative bleaching may effectively starve this species of nutrition.

The interaction between pCO_2 and temperature did not significantly impact calcification rates for any of the coral species. Absence of an interactive effect of pCO_2 and temperature on coral calcification rate is relatively common and has been observed for multiple species [37,40,69]. A previous study that exposed *S. siderea* to elevated temperature (32°C), elevated pCO_2 (approx. 900 µatm) and the combination of these two stressors found calcification rates were most negatively affected by the combined high-pCO_2/high-temperature treatment, resulting in additive, but not synergistic, effects on calcification rates [38]. Thus, the evidence to date suggests that scleractinian corals exposed to both pCO_2 and thermal stress rarely experience effects that are truly synergistic. Finally, calcification rates in the present study were generally comparable to those reported for corals from the Florida Keys [37] and Belize [38].

(b) Faster-growing colonies may be more vulnerable to pCO_2 and thermal stress

Colonies that exhibited faster calcification in the control treatment (pre-industrial pCO_2 at 28°C) tended to exhibit slower calcification in the elevated pCO_2 and elevated-temperature treatments, suggesting a trade-off in which faster calcifying colonies may be more vulnerable to the negative impacts of pCO_2 and thermal stress on calcification. Unsurprisingly, this correlation was weakest when comparing pre-industrial to present-day pCO_2 treatments—the two most similar treatments. This variation in calcification rates was evident across the four coral species, which is consistent with previous literature suggesting that divergent calcification strategies exist across populations [70–74]. Our analysis provides preliminary support for two end-member strategies of calcification: (i) fast calcifying colonies that divert more energy towards flourishing during favourable environmental regimes but flounder during periods of environmental stress (potentially owing to lack of energetic reserves); and (ii) slower calcifying colonies that store more energy during environmentally favourable conditions, yet are able to continue calcifying under environmentally stressful conditions (potentially owing to their ability to tap energy stored during environmentally favourable times).

These divergent calcification strategies within coral populations may confer stability to populations faced with environmental stress over both short and long timescales. Over short timescales, these strategies increase the probability that at least some colonies (faster calcifiers) flourish when conditions are favourable, while ensuring that there are also survivors (slower calcifiers) during unfavourable times that allow populations to persist [75]. Over longer timescales, these divergent strategies may provide a high degree of genotypic variability upon which natural selection can act, thereby facilitating the evolution of the population towards optimal weightings of these calcification strategies [74], depending on the magnitude and duration of the environmental perturbation (e.g. short-term anthropogenic cycles [76] versus medium-term glacial cycles [77] versus longer-term secular trends in pCO_2 associated with tectonics [78]).

Although populations of coral species that exhibit these divergent calcification strategies could become more tolerant of anthropogenic stressors in the future, they would also become slower growing through time. Although our current study was not designed to specifically address colony-level calcification responses, our analysis demonstrates a potential trade-off within species that may allow populations to persist under projected global change. This apparent relationship between a colony's basal calcification rate and its response to pCO_2 and thermal stress merits further investigation given its potentially far-reaching implications for corals' response to global change.

(c) All coral species, except *Siderastrea siderea*, exhibited net skeletal dissolution under the highest pCO_2

Specimens of *S. siderea* maintained positive net calcification under all treatments (figure 1a), suggesting greater resilience to pCO_2 and thermal stress compared to the other species examined [28,31,57]. Indeed, correcting net calcification rates with empirically derived gross dissolution rates [79] yields high rates of gross calcification for *S. siderea* even in undersaturated seawater conditions (electronic supplementary material, figure S9a), providing support for the assertion that *S. siderea* is able to maintain conditions supportive of aragonite precipitation at its site of calcification, despite external seawater supporting dissolution of its aragonite skeleton [14,37,38]. The combination of resilient calcification responses to thermal and pCO_2 stress with the high survival exhibited by *S. siderea* in the present study (electronic supplementary material, figure S6a and tables S9–S11), as well as in prior studies [14,37,38], suggests that *S. siderea* possesses unique physiological mechanisms for maintaining basic life processes under pCO_2 and thermal stress, and may contribute to its abundant distribution on reefs throughout the Caribbean [80].

Specimens of *Ps. strigosa*, *Po. astreoides* and *U. tenuifolia* exhibited net skeletal dissolution in at least one pCO_2–temperature treatment, with the greatest net dissolution observed under the highest pCO_2 treatment (figure 1; electronic supplementary material, figure S9b–d). *Pseudodiploria strigosa* exhibited the highest rates of net dissolution at the elevated temperature, probably owing, at least in part, to the loss of algal symbionts (i.e. partial bleaching; electronic supplementary material, figure S10) from which corals obtain a significant portion of their energy [15]. Thus, under thermal stress, reduced symbiont densities may lead to diminished photosynthate, reducing the energy available for calcification and eventually leading to thermally induced mortality as observed in the present study (electronic supplementary material, figure S6b and tables S9–S11) and previous experiments on juvenile corals [81]. Under these conditions, corals may be unable to produce enough new skeleton to counter the effects of skeletal dissolution in undersaturated conditions [79].

(d) *Siderastrea siderea* and *Porites astreoides* maintain constant rates of linear extension under pCO_2 and thermal stress

Increasing pCO_2 had no significant effect on linear extension rates of either *S. siderea* or *Po. astreoides* (figure 3), providing support for prior assertions that symbiotic corals exert strong control over the chemical milieu at their site of

calcification [18–21]. This constant rate of extension (i.e. volume addition) combined with the threshold decrease in net calcification (i.e. mass addition) with increasing pCO_2 suggests that both species produce less-dense skeletons and/ or that the gain in skeletal mass associated with the new linear extension is offset by the loss of previously formed skeletal mass via dissolution under extreme pCO_2 (figure 3; electronic supplementary material, figure S9a). Additionally, the observation that *Po. astreoides* exhibited net dissolution at both temperatures under several pCO_2 treatments, yet maintained constant rates of linear extension, suggests that dissolution, rather than decreasing skeletal density, is driving the decline in calcification rate of this species under increasing pCO_2—as the addition of new, less-dense skeleton alone could not cause a net decrease in skeletal mass (i.e. net dissolution).

Linear extension of *S. siderea* and *Po. astreoides* did not differ significantly across temperatures (figure 3). This contrasts previous reports linking historical ocean warming to reductions in the extension of wild specimens of *S. siderea*, although this decrease was observed only for forereef colonies along the southern MBRS [44]. Extension rates of *S. siderea* observed in the present study were generally comparable to those reported for wild specimens in Belize [44]. Conversely, the lack of temperature effect on the extension of *Po. astreoides* is consistent with the measured calcification response, supporting prior observations that rates of net calcification within this species is driven by the rate of linear extension, rather than by changes in skeletal density [34,82].

(e) Experiments reveal corals' differential resilience to future oceanic change

Diverse responses to pCO_2 and warming exhibited by the corals investigated here reveal a spectrum of resilience to future global oceanic change. We confirm the relatively high resilience of *S. siderea* to thermal and pCO_2 stress [37], the moderate sensitivity of *Po. astreoides* and the relatively high sensitivity of *Ps. strigosa* [80,83] and *U. tenuifolia* [64,66,67]. The results also highlight the relative resilience of the investigated species (excluding *Ps. strigosa*) to moderate pCO_2 stress, while revealing their high sensitivity to extreme pCO_2. Faster-growing colonies tended to exhibit increased vulnerability to pCO_2 and thermal stress, suggesting variability in tolerance of pCO_2 and thermal stress within populations of these corals—a potential pathway for evolutionary resilience. Collectively, these results reveal the wide spectrum of responses exhibited by four common Caribbean corals in response to changes in ocean pH and temperature, a necessary step in understanding and forecasting the response of coral reef systems to future global change.

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