Ocean acidification causes bleaching and productivity loss in coral reef builders

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Ocean acidification represents a key threat to coral reefs by reducing the calcification rate of framework builders. In addition, acidification is likely to affect the relationship between corals and their symbiotic dinoflagellates and the productivity of this association. However, little is known about how acidification impacts on the physiology of reef builders and how acidification interacts with warming. Here, we report on an 8-week study that compared bleaching, productivity, and calcification responses of crustose coralline algae (CCA) and branching (*Acropora*) and massive (*Porites*) coral species in response to acidification and warming. Using a 30-tank experimental system, we manipulated CO_2 levels to simulate doubling and three- to fourfold increases [Intergovernmental Panel on Climate Change (IPCC) projection categories IV and VI] relative to present-day levels under cool and warm scenarios. Results indicated that high CO_2 is a bleaching agent for corals and CCA under high irradiance, acting synergistically with warming to lower thermal bleaching thresholds. We propose that CO_2 induces bleaching via its impact on photoprotective mechanisms of the photosystems. Overall, acidification impacted more strongly on bleaching and productivity than on calcification. Interestingly, the intermediate, warm CO_2 scenario led to a 30% increase in productivity in *Acropora*, whereas high CO_2 lead to zero productivity in both corals. CCA were most sensitive to acidification, with high CO_2 leading to negative productivity and high rates of net dissolution. Our findings suggest that sensitive reef-building species such as CCA may be pushed beyond their thresholds for growth and survival within the next few decades whereas corals will show delayed and mixed responses.

climate change | global warming | carbon dioxide | Great Barrier Reef

The concentrations of atmospheric CO_2 predicted for this century present two major challenges for coral-reef building organisms (1). Firstly, rising sea surface temperatures associated with CO_2 increase will lead to an increased frequency and severity of coral bleaching events (large-scale disintegration of the critically important coral–dinoflagellate symbiosis) with negative consequences for coral survival, growth, and reproduction (2). Secondly, >30% of the CO_2 emitted to the atmosphere by human activities is taken up by the ocean (3, 4), lowering the pH of surface waters to levels that will potentially compromise or prevent calcium carbonate accretion by organisms including reef corals (1, 5), calcifying algae (6, 7) and a diverse range of other organisms (8). Ocean acidification research has focused mainly on the consequences of shifting ocean chemistry toward suboptimal saturation states of aragonite and calcite (9) and how this will affect the calcification processes of organisms in the pelagic (10) and benthic (11, 12) environments. Previous studies have shown dissolution of coral skeletons (13) and reduced rates of reef calcification (14) with increasing CO_2 concentrations. Ocean acidification, however, is likely to also impact on other physiological processes in key reef-building species, but little is known about these responses and their biotic consequences. Here, we investigate and compare the effects of ocean acidification on three key physiological processes in reef-building organisms. Firstly, we examine CO_2 impacts on bleaching, which is a phenomenon mainly associated with thermal stress (2, 15), although early unpublished work suggested a possible link between CO_2 and coral bleaching (16). Secondly, we investigate effects on organic productivity, which is expected to be influenced by bleaching state, and thirdly, we compare the patterns of these organic responses with effects on rates of calcification. Three groups of reef builders were used, representing some of the most common and functionally important benthic organisms on coral reefs: staghorn corals (*Acropora intermedia*), massive corals (*Porites lobata*), and crustose coralline algae (*Porolithon onkodes*). Crustose coralline algae (CCA), and in particular *P. onkodes*, play an important role in reef building and the consolidation of dead reef matrix (17, 18) and have recently demonstrated reduced growth and recruitment under elevated CO_2 (7).

The present study is based on an 8-week experiment on Heron Island (Southern Great Barrier Reef, Australia) during the austral summer of 2007 (February−March) using a system of 30 flow-through aquaria with controlled CO_2 dosing and temperature regimes. To cover the broad range of CO_2 environments projected for the century, we used experimental CO_2-dosing scenarios that represent present-day (control, 380 ppm atmospheric CO_2), intermediate (high category IV, 520–700 ppm), and high-end (above category VI, 1000–1300 ppm) CO_2 stabilization scenarios by the IPCC (19). To examine how CO_2 interacts with warming, the experimental design also incorporated two temperature treatments (25–26 °C and 28–29 °C) representing low- and high-average summer temperatures for the region. In summary, the experimental design consisted of two CO_2 dosing regimes and a control crossed with two temperature treatments, each replicated by 5 aquaria holding 3–5 specimens of each study species. The aquaria were organized randomly to control for spatial heterogeneity in light regimes, which averaged 1000 μmol photon m^{-2} s^{-1} over the day (see *Methods* for further details).

Results

Bleaching Responses. High-CO_2 dosing led to 40−50% bleaching for the CCA and *Acropora* after 8 weeks of experimentation (Fig. 1*A* and *D*). The response was highly significant as the bleaching metric (luminance scale representing variation in chlorophyll content, see *Methods*) showed low variation among the 15–25 specimens within each treatment combination [see also ANOVA results in suppporting information (SI) Table S1]. Intermediate-CO_2 dosing led to marginally more bleaching (~30% for CCA and 20% for *Acropora*) relative to 20 and 10% for controls, respectively. Interestingly, for the CCA and *Acropora*, the effect of CO_2 dosing on bleaching was stronger than the effect of

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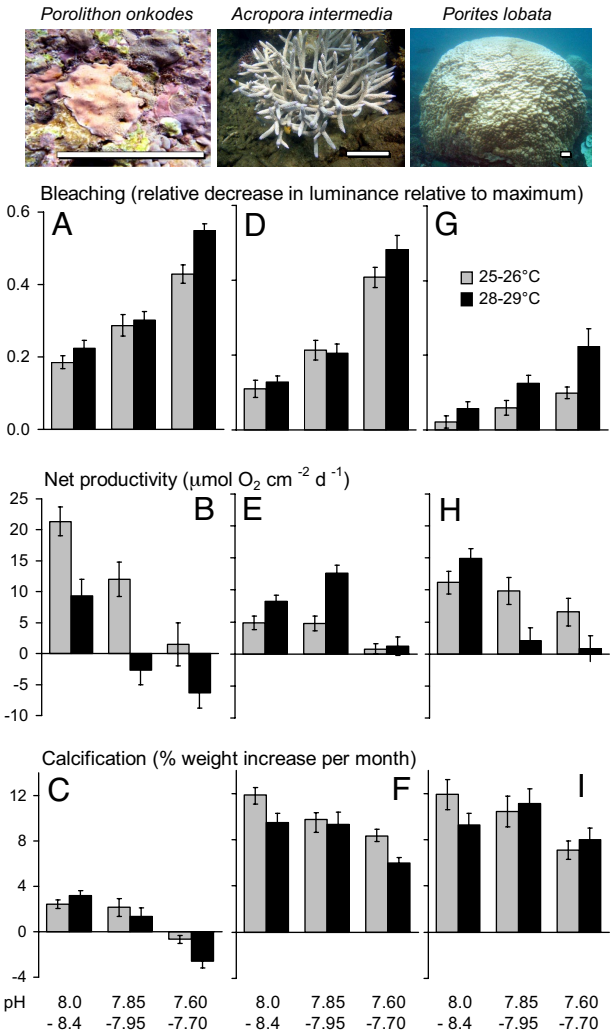

Fig. 1. Effects of experimental ocean acidification (CO_2 level) and warming on three key performance variables of three major coral reef builders: (*A–C*) crustose coralline algae (CCA, *Porolithon onkodes*), (*D–F*) branching *Acropora* (*A. intermedia*), and (*G–I*) massive *Porites* (*P. lobata*). Gray and black bars show low- and high-temperature treatments, respectively. Data are means ± SEM of $n = 15–25$ specimens for each combination of CO_2 and temperature. Levels of CO_2 represented the present-day control condition (380 ppm atmospheric CO_2) and projected scenarios for high categories IV (520–700 ppm) and VI (1000–1300 ppm) by the IPCC. See Table 1 for summary of values for water-chemistry parameters and Table S1 for results of analyses. Scale bar, 5 cm.

temperature. Specifically, high-CO_2 dosing led to a two- to threefold increase in bleaching relative to the control, whereas high temperature led to only 20% increase in bleaching for these species. *Porites* was less sensitive and bleached to a maximum of 20% in the high-CO_2/high-temperature treatment. In this species there was a strong synergy between CO_2 and temperature as the high-CO_2/low-temperature corals showed <10% bleaching (Fig. 1*G*). High temperature thus amplified the bleaching responses by 10–20% in CCA and *Acropora*, and up to 50% in *Porites*.

Productivity Responses. CO_2 dosing led to dramatic reductions in daily productivity (as hourly rates of photosynthesis minus respiration integrated over the day) of the CCA. At low temperature, intermediate-CO_2 dosing (pH 7.85–7.95) resulted in a 50% reduction in productivity relative to the control. High-CO_2 dosing (pH 7.60–7.70) led to a further reduction in productivity to near zero (Fig. 1*B*). Interestingly, acidification affected net rate of photosynthesis (daytime measurements) only, whereas rates of dark respiration varied <10% across treatments (data not shown). The acidification effect on the CCA was exacerbated by warming. At the control CO_2 (highest pH), warming led to a 45% drop in productivity, and at the warm, intermediate-CO_2 dosing scenario, productivity fell to below zero. At the highest CO_2 dosing under warm conditions, productivity of CCA was 160% reduced relative to the warm control conditions—i.e., daily rates of respiration far exceeded daily rates of photosynthesis.

Interestingly, productivity of *Acropora* was enhanced under the intermediate, warm CO_2 dosing regime but was suppressed in *Porites* (Fig. 1 *E* and *H*). Again, productivity patterns were driven by variation in net rates of photosynthesis only, and dark rate of respiration varied by <10%. In *Acropora*, intermediate-CO_2 dosing had no impact on productivity at low temperature, but was 40% increased in the warm treatment. At the highest CO_2 dosing, however, productivity dropped to near zero for both temperature groups (Fig. 1*E*). The significant interaction between CO_2 and temperature in the productivity response for *Acropora* (see ANOVA results in Table S1) was driven mainly by the high productivity maximum in the warm, intermediate-CO_2 regime. In *Porites*, productivity was marginally enhanced by warming at the control CO_2, but fell by 80% in the warm, intermediate-CO_2 group—opposite to the pattern for *Acropora* (Fig. 1*H*). High CO_2 led to a 30% drop in productivity in *Porites* (relative to the control) in cool conditions and dropped to near zero at the highest CO_2 dosing, analogous to the pattern for *Acropora*.

Calcification Responses. CCA calcification was highly sensitive to the highest CO_2 dosing and the effect was exacerbated by warming (Fig. 1*B*). Intermediate-CO_2 dosing and warming led to a 50% drop in the CCA calcification rate, but the temperature effect was not significant. High-CO_2 dosing led to 130 and 190% reductions in calcification rate relative to control conditions at low and high temperatures. Rates of calcium carbonate dissolution by CCA in the warm, high-CO_2 scenario were thus as high as their rates of accretion at present-day conditions.

Compared to their bleaching and productivity responses, the calcification responses of *Acropora* and *Porites* to CO_2 dosing were relatively weak (Fig. 1 *F* and *I*). In *Acropora*, for example, rate of calcification in the high-CO_2 dosing regime was ~40% lower than at control conditions. Warming suppressed the calcification rate of *Acropora* significantly, but only for the high-CO_2 treatment (~25%). The calcification response of *Porites* to CO_2 dosing was almost identical to that of *Acropora*, but calcification in *Porites* did not show a clear response to warming.

Discussion

Our results indicated that prolonged CO_2 dosing (representative of CO_2 stabilization categories IV and VI by the IPCC) (19) causes bleaching (loss of pigmentation) in two key groups of reef-building organisms. The bleaching results indicate that future predictions of bleaching in response to global warming must also take account of the additional effect of acidification and suggests that any potential adaptation and acclimatization by coral reef organisms to thermal stress (20, 21) may be offset or overridden by CO_2 effects. Previous studies of CO_2 enrichment and warming in corals and algae have not observed a bleaching response (22, 23). One explanation is that this study used a higher natural irradiance (average of ≈1000 μmol photons m^{-2} s^{-1}), which is a key bleaching agent in corals (24), thereby bringing organisms closer to their bleaching thresholds. Also, the experimental period of CO_2 dosing used in this experiment was longer than that of for example the study by Reynaud *et al.* (2003) (22), thereby allowing time for the buildup of physiological stress. The process by which high CO_2 induces bleaching is unknown, but

Table 1. Summary of parameter values used in the CO_2-dosing and temperature control experiment

pH	T, °C	TA, mmol·kg^{-1}	pCO_2 matm	HCO_3 mmol·kg^{-1}	CO_3 mmol·kg^{-1}	Ω_{Arag}
8.00–8.40	25.0–26.0	2375–2450	135–460	1390–1930	207–415	3.3–6.6
	28.0–29.0		130–465	1325–1885	225–440	3.6–7.1
7.85–7.95	25.0–26.0	2375–2450	520–705	1900–2050	155–200	2.5–3.2
	28.0–29.0		520–705	1860–2020	170–220	2.8–3.5
7.60–7.70	25.0–26.0	2375–2450	1010–1350	2080–2210	95–125	1.5–2.0
	28.0–29.0		1020–1360	2020–2190	105–135	1.7–2.2

The parameters pH, temperature (T), and total alkalinity (TA) and salinity (≈35 ppm) were measured, whereas the remaining carbon parameters were estimated using the program CO2SYS (39). The saturation state of aragonite (Ω_{arag}) assumes a calcium concentration of 10 mg kg SW^{-1}.

could involve a number of possible mechanisms such as changes to the carbon-concentrating mechanism (25), photorespiration (26), and/or direct impacts of acidosis (27). Results of a recent study using the same experimental conditions (A. Crawley, S.D., and K.R.N.A., unpublished data) indicate that high CO_2 and/or lowered pH disrupt the photoprotective mechanisms of coral symbionts or algal chloroplasts by lowering rates of photorespiration and the capacity for thermal dissipation. The implications are that CO_2 concentration and irradiance interact to trigger bleaching under the naturally high light level used in our experiment (noon irradiances of >1200 μmol photons m^{-2} s^{-1}). Importantly, the study by Reynaud *et al.* (2003) (22), which showed an increase in chlorophyll content under elevated CO_2, used an irradiance level of only 350 μmol photons m^{-2} s^{-1}—a third of that used in this study and potentially below the threshold for combined CO_2/irradiance-induced bleaching. Also, the study by Schneider and Erez (2006) (23) found no effect of CO_2 dosing on rates of photosynthesis and respiration, but similar to Reynaud *et al.* (2003) (22) used an experimental irradiance of only 350 μmol photons m^{-2} s^{-1}.

The productivity responses of the CCA and corals to CO_2 dosing are likely to be a result of a series of opposing mechanisms. Initial loss of pigmentation in the corals can result in increased productivity per remnant symbiont or per chlorophyll because of subtle increases in temperature or an increased internal light field (29, 30). As severe bleaching takes over, the decline in the symbiont population (or the chlorophyll pool) overrides the increased photosynthetic efficiencies, leading to a drop in areal productivity. Alternatively, CO_2 is the substrate for photosynthesis, and increasing its supply may increase rates of photosynthesis in organisms that are CO_2 limited. Many aquatic organisms however, take up HCO_3^- relatively efficiently using carbonic anhydrase to interconvert to CO_2 and bridge membranes in a carbon-concentrating mechanism that ultimately delivers CO_2 to rubisco for carbon fixation (25, 31, 32). The potential effects of increasing CO_2 and/or impacts of acidosis on inorganic carbon acquisition are likely to be highly variable in different organisms, as are the thermal thresholds that dictate whether an increase in temperature leads to a negative or positive response. In CCAs, increasing CO_2 led to a dramatic monotonic decline in productivity, and this decline was exacerbated by warming. This productivity pattern suggests that the CO_2-stabilization scenario predicted for the IPCC category IV (CO_2 peaking years 2020–2060), here represented by the warm, intermediate-CO_2 regime, will be unsustainable for CCA, and thresholds for survival of this important functional group will be far exceeded under the category VI scenario (CO_2 peaking years 2020–2090). Our data are consistent with the recent findings that elevated CO_2 leads to lowered growth and recruitment of CCA (7). A decline in CCA abundance can potentially have dramatic ecological consequences because of the roles they play in coral reefs. CCA are an important settlement cue for invertebrate larvae including corals and contribute significantly to reef accretion and cementation (33).

Interestingly, the productivity of *Acropora* was maximized at the intermediate-CO_2 regime (Fig. 1 *E* and *H*), suggesting that rate of photosynthesis is stimulated either directly by increased CO_2 supply, and/or by an increase in excitation pressure driven by bleaching-induced increases in internal light fields (34). The large drop in productivity at the highest CO_2 dosing suggests that the positive effect of high-CO_2 supply is here overridden by the disruption of photophysiological processes and as a consequence of bleaching and thereby loss of photosynthetic capacity. Low pH may interfere with the preferred pathway for CO_2 accumulation at the site of rubisco within intracellular symbionts or directly with electron transport through the destabilization of thylakoid proton gradients thereby directly affecting the ability of the individual symbionts to fix carbon. Productivity in the massive coral (*Porites*) displayed an almost opposite pattern to the branching *Acropora* with respect to temperature. Under warm conditions, productivity in *Porites* also dropped dramatically at the highest CO_2 level, but only 20% (and nonsignificantly) lower than at control conditions, suggesting a generally weaker response to acidification than *Acropora*.

Calcification responses of the CCA were analogous to their response in terms of productivity, further supporting the prediction that the niche boundaries of CCA will be exceeded under the intermediate-CO_2 scenario. One explanation for the high sensitivity of CCA is that their skeletons consist of magnesian calcite, which has higher solubility and requires a higher saturation state for deposition (and hence potentially more metabolic energy) than does aragonite and calcite (35, 36). The high rate of dissolution of CCA in the high-CO_2 dosing treatments, in combination with the low estimated saturation states for aragonite (< 2, Table 1), suggest that the CCA were approaching undersaturation in this scenario. Also, being fully autotrophic, any loss of photosynthetic capacity because of bleaching is likely to translate more directly to reduced physiological performance and mortality than in corals that have dual trophic modes (37). Our results are consistent with the productivity pattern of mixed epilithic and endolithic algal communities under elevated CO_2 (38), but also indicate that temperature is a critical covariate determining survivorship.

Calcification of *Acropora* and *Porites*, however, was less responsive to CO_2 than was bleaching and organic productivity. This is an important result as coral calcification and biogeochemistry has been used as the key response variable for predicting risks of ocean acidification to coral reefs (1, 39). The results of this study suggest that impacts of high CO_2 on the photophysiology and energy balance of reef organisms are as important in defining acidification threats to reefs as are impacts on calcification and reef geochemistry. The observation that CO_2 triggers bleaching in synergy with warming under high light, and thereby partly drives patterns of net productivity, indicates that predictions of survival thresholds for reef builders under

climate change must take account of acidification–warming interactions in the integrated biological and biogeochemical response.

Methods

Study Species. To represent three of the most important framework builders on Indo-Pacific coral reefs, we used a species of CCA commonly found on forereefs and reef-crest habitats, *P. onkodes*, and two common species of branching, *A. intermedia*, and massive, *P. lobata*, scleractinian coral. Between 125 and 220 specimens of each species were collected from the reef slope (2–3 m below lowest astronomical tide) from 3–5 different reef sites on Heron Reef. Collecting was conducted from as large an area at each site as possible to maximize the number of genotypes represented. For the CCA, we used 3 cm by 3 cm large chips chiselled off the substrate, and for *A. intermedia*, we used 6–7 cm long terminal branches. Specimens of *P. lobata* consisted of 3.5 cm diameter plugs collected by holesaw. All specimens were transferred to aquaria with running seawater and left for 6 weeks to recover from handling at light and temperature conditions similar to those in the field. *Acropora* branches were suspended from their tips by thin monofilament line, which allowed the healed tissue to completely cover their skeleton. Mortality during the acclimation phase was $<5\%$ for all species.

Experimental Setup. The experimental facility consisted of 30 flow-through aquaria (20 litres) under a natural light regime (noon irradiance ranging from 700 to 1200 μmol photons m^{-2} s^{-1}) receiving unfiltered reef seawater from six temperature-controlled CO_2 mixing tanks. Levels of acidification and temperature regimes were regulated by a custom-built CO_2 dosing (bubbling) and temperature control system (Campbell Scientific, Australia) set to pH target values of 7.85–7.95 and 7.60–7.70, corresponding to CO_2 concentrations of 520–705 ppmV and 1000–1300 ppmV for the intermediate- and high-CO_2 dosing regimes, respectively. pH was measured on seawater scale using 12 polarographic sensors ($\pm$0.01 pH unit), each connected to the logger/controller unit via a MicroChem interface (TPS Australia). The experimental CO_2 environments matched high categories IV and above VI for IPCC CO_2 stabilization scenarios, with peaking CO_2 in years 2020–2060 and 2060–2090, respectively (16). The control pH (zero CO_2 dosing, corresponding to an atmospheric CO_2 of 380 ppmV) ranged from 8.0 to 8.4, resulting in an estimated pCO_2 range of 130–465 ppm reflecting the diurnal variability of the intake water from the reef. To determine interactions with temperature in a factorial design, CO_2 treatments were crossed with two temperature regimes representing low and high average summer temperatures for the region (25–26 °C and 28–29 °C) (15). On the basis of measurements of pH, temperature, and total alkalinity [measured using the Gran alkalinity method (40) on a Mettler Toledo T50 automated titrator using 0.1M HCL for 130 g seawater samples], and salinity (measured using a Bellingham Stanley refractometer), the distribution of carbon species and aragonite saturation state were estimated for all treatments (Table 1) using the program CO2SYS (41). Five replicate tanks were used per CO_2–temperature combination, each with three CCA, five *A. intermedia*, and three *P. lobata* specimens. Corals were not fed during the acclimation and experimental phases as the running seawater directly from the reef was unfiltered.

Response Variables. Bleaching was quantified colorimetrically from digital photographs (42) at the end of the 8-week experimental period and quantified as the reduction in luminance relative to maximum (representing maximum symbiont or chlorophyll density). Ideally, chlorophyll samples should be used directly as a bleaching metric, but all biological samples from the experiment were lost in a fire. Because bleaching is a progressive response (because of gradual chlorophyll depletion over time) (43) effects on productivity were also analyzed at the end of the experiment. Net productivity was estimated from daytime assays of maximum net rates of photosynthesis (P_{NetMax}, 10 a.m.–3 p.m.) under controlled artificial lighting (200 W metal-halide lamp, AquaMedic, Germany) simulating daytime environmental irradiances of $\approx$1000 μmol photons m^{-2} s^{-1} *in situ* and nighttime assays of dark respiration (R_{dark}, 8 p.m.–2 a.m.). Photosynthesis and respiration measurements were conducted using four sealed, recirculating respirometry chambers with flow regimes simulating natural conditions (44), each chamber connected to a high-precision optical oxygen sensor (optode) and logging system (Oxy-4, Presens, Germany). Oxygen fluxes of all specimens were normalized to tissue surface area determined from geometric analyses of digital photographs (Image Tools, The University of Texas Health Science Centre). To construct daily budgets for oxygen fluxes, hourly net rates of photosynthesis were integrated over the 24-hour light-dark cycle using the hyperbolic tangent function (45)

$$P_{Net} = \int_{t=0}^{t=12} P_{Net\,Max} \tanh\left(\frac{\mathrm{E(t)}}{\mathrm{E_K}}\right)\mathrm{dt} - \int_{\mathrm{t=12}}^{\mathrm{t=24}} \mathrm{r}_{Dark}\,dt \qquad [1]$$

with irradiance at time t, $E(t)$ based on average daily light profiles from four loggers (PAR sensor, Odyssey, Dataflow Systems, New Zealand) deployed in each of four aquaria across the setup. We used subsaturation irradiances, Ek, for the three study species based on results of studies of photosynthesis in similar light habitats: *P. onkodes*, 205 μmol m^{-2} s^{-1} (18); *A. intermedia*, 350 μmol m^{-2} s^{-1} (28), and *P. lobata*, 177 μmol m^{-2} s^{-1} (46). Standard errors of the daily net rates of photosynthesis (P_{Net}) were determined using standard Monte Carlo procedure (programmed in Matlab v. 6, Mathworks) in which sets of values for P_{MaxNet} and r_{Dark} were sampled from the normal distributions specified by their parameter estimates and associated variances. The sampling procedure was repeated 1000 times for each species to produce error ranges for P_{Net} (Eq. **1**). Rate of calcification was determined as differences in buoyant (underwater) weight between the first and last days of the 8-week experiment (47). Because standardized fragment sizes were used, and because buoyant weight scales directly with skeletal weight, calcification rate was expressed as the relative monthly change in buoyant weight.

Data Analysis. All response data to CO_2 and temperature treatments were tested using a two-factor nested analysis of variance (ANOVA) with CO_2 dosing and temperature as fixed factors and tanks as replicates. Specimens were nested within tanks. However, because the tank factor was nonsignificant (data not shown), tanks were pooled in subsequent analyses and specimens were used as replicates (28), hence increasing the power of the analysis. Data from the latter analyses are presented here. When significant interactions between CO_2 and temperature occurred, *t*-tests or independent one-way ANOVAs were used to examine effects. All ANOVAs were followed by a multiple comparisons' test to identify significant groups. Data were tested for variance heterogeneity using Levene's test and normality using the Kolmogorov–Smirnov one-sample test.

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